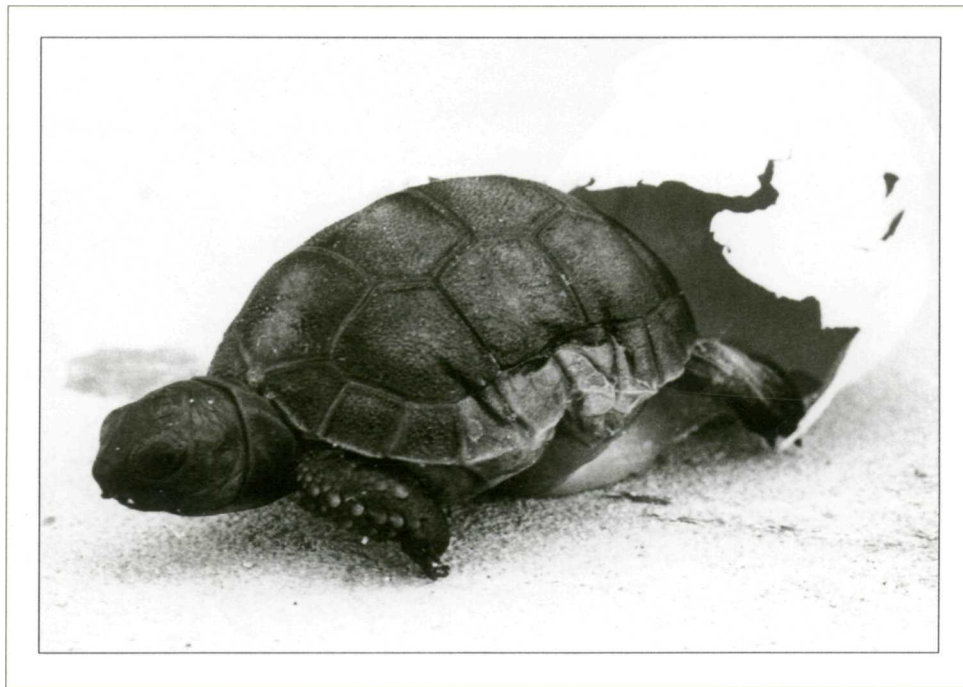


The Conservation Biology of Tortoises

Edited by
Ian R. Swingland and Michael W. Klemens
IUCN/SSC Tortoise and Freshwater Turtle Specialist Group
and
The Durrell Institute of Conservation and Ecology



Occasional Papers of the IUCN Species Survival Commission (SSC)
No. 5



IUCN—The World Conservation Union

IUCN Species Survival Commission

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The Species Survival Commission (SSC) is IUCN's primary source of the scientific and technical information required for the maintenance of biological diversity through the conservation of endangered and vulnerable species of fauna and flora, whilst recommending and promoting measures for their conservation, and for the management of other species of conservation concern. Its objective is to mobilize action to prevent the extinction of species, subspecies, and discrete populations of fauna and flora, thereby not only maintaining biological diversity but improving the status of endangered and vulnerable species.

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2. To maintain an international network of independent volunteer members selected for their expertise in species conservation and to provide a forum for the exchange of views and scientific information on species and populations of conservation concern.
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 - development and review of conservation action plans and priorities for species and their populations.
 - promotion of implementation of species-oriented conservation action plans and response to related issues.
 - periodic evaluation of the status of species and biological diversity conservation initiatives.

The publication is produced by IUCN—The World Conservation Union, in collaboration with The Durrell Institute of Conservation and Ecology at the University of Kent, The World Wide Fund for Nature—International, The American Association of Zoological Parks and Aquariums, and Wildlife Conservation International.

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Cover photo: Hatching Aldabran tortoise (*Geochelone gigantea*). (Photo by I.R. Swingland.)

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The results of "Operation Tortoise,"
a worldwide project conducted by
the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group

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IUCN—The World Conservation Union

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Preface

This contribution to the Occasional Papers of the IUCN Species Survival Commission (SSC) on the status and distribution of the Testudinidae, or terrestrial tortoises, is the result of five years of work by members of the IUCN/SSC Tortoise Specialist Group (which has since become the Tortoise and Freshwater Turtle Specialist Group) and is published on the occasion of the First World Congress of Herpetology at the University of Kent, September 1989. This work was stimulated by our lack of knowledge regarding the forty species of tortoises which became apparent at our inaugural meeting at Oxford in October 1981 and our inability to answer many of the basic questions relating to their conservation. It was executed under the title "Operation Tortoise."

We have provided the latest information on each species, including the Latin name, common names, description, taxonomy, geographic variation, status and distribution, habitat and ecology (particularly behaviour, reproduction, and feeding), threats to survival, conservation reserves and recommendations, and current research. We have also provided the most complete bibliography on the Testudinidae ever published.

In drawing up this report we have been concerned that the information is as up-to-date as possible, but we expect, indeed hope, that it will be redundant in a few years as more and more people work on these fascinating animals. We have also been conscious of the needs of the local people and their interests, a vital part of any successful conservation programme as so clearly demonstrated by the Group's successful Project Angonoka/Kapidolo in Madagascar, and the SOPTOM project in southern France. The SSC Tortoise and Freshwater Turtle Group Action Plan, also published at the Kent Congress, goes even further in an attempt to integrate scientific and practical conservation.

The flaw in all reports investigating the status and distribution of species is that they are always incomplete, inaccurate, and inadequate for real planning. Recently we have pioneered practical methods for analyzing status and distributional data on herpetofauna, and their ecological correlates in an attempt to predict potential conservation problems (The herpetofauna of southwestern New England, Klemens, University of Kent, Ph.D. thesis in prep.). This Occasional Paper is only the beginning of such a process for tortoises.

Since a clear understanding of taxonomy and classification is a prerequisite for scientific conservation, we have adopted the classification of Testudinidae used in *The Evolutionary Ecology of Tortoises* to be published by Oxford University Press (see Appendix 2).

Tortoises have remained unchanged longer than most groups of animals, the Anapsid line becoming apparent over 200 million years ago and modern tortoises from 55 million years ago. They have constantly recurred in old cave paintings and carvings through Cro-Magnon and Neanderthal periods up to 85,000 years ago. Tortoises and other chelonians appear in religious and social contexts throughout the world. In animist Buddhist areas, the owl of wisdom is always placed atop a tortoise or turtle, and in Greek mythology the tortoise was used as symbol of sureness, steadiness, harmlessness, innocence,

and wisdom. In economic terms, the tortoise is an important part of rural dynamics, being used for food in most parts of the world, as a musical instrument (maracas and banjo), as a scoop or water bail in boats, and canned as meat in parts of the Mediterranean. The adults are often kept in village pens for food and as a source of hatchlings, which are becoming a new economic product of this traditional habit. These hatchlings often fetch very high prices and are easily smuggled. Since tortoises are capable of eating almost anything, they are the equivalent of long-lived pigs that do not require feeding or watering daily, and like pigs, every part of their body can be used.

The downside of the economics of tortoises is their rapidly escalating value to private and public collectors (which the European ban on bulk trade in 1984 and their general scarcity has exacerbated) and the ways in which they are used as key species to defend areas programmed for development. In certain areas, the presence of tortoises has stopped the continued destruction of habitats by off-road vehicles and bikes by the enforcement of conservation legislation. In parts of the Mediterranean, local villagers have been impeded from developing seaside areas for profit. The use of CITES regulations to defend these very vulnerable animals is of minimal value as long as those charged with monitoring and policing the areas or countries where tortoises occur remain ignorant of the problem. There are many instances where governments react negatively to CITES decisions, creating an atmosphere counter-productive for species management. In general, ethnic or traditional uses must be integrated into local plans based on sound scientific knowledge. Our experience shows that local rural villagers can be vital partners in a successful conservation project, provided that it is self-sustaining, requiring one initial injection of capital, and family or communally-owned with a fair and equitable administration benefiting all who involve themselves constructively. It may be that a privately or state-owned project will be supported because it provides local employment and attracts tourists from which families can earn an ancillary living. Local interest groups (including urban dwellers) who have taken up the cudgels for tortoise conservation, whether in southern France or in California, have a significant impact on countryside planning, and in so doing make not only an effective contribution to habitat conservation but also fuel the very research necessary to improve the measures taken.

This publication is one of the first dealing with conservation aspects of tortoises. It cannot encompass the anatomical, biological, and ecological adaptations of these long-lived and remarkable animals—this must be left for a larger and more scientific treatise. There is no major work embracing the ecology and biology of tortoises.

Tortoises, while not amongst the most charismatic species that drive the conservation effort, attract attention out of all proportion to their lowly and unassuming station in life (see *The Tortoise: Poems by D.H. Lawrence*, Yorick Books, Canterbury). Some countries use the tortoise as their national symbol or emblem (e.g., Seychelles), or in marketing their tourist industry (e.g., Galapagos), and many companies use the tortoise

to promote the toughness or reliability (an Aesop allusion) of their products. To date we have logged over 1,500 companies, 600 advertisements and 23 countries which use the image of a tortoise. Without question, the Testudinidae are important not only to a nation's national heritage and to international companies, but as a resource to local people. The tortoise can act as the catalyst in conserving areas by attracting attention and help, thereby ensuring the future of all the species within its habitats.

We would like to thank the following groups and corporations for supporting us in the preparation of this report: British Petroleum, Herpetological Conservation Trust, The staff of the IUCN Species Survival Commission Executive Office, People's Trust for Endangered Species, Care for the Wild, Tortoise Firebox Company, British Chelonia Group, WWF—World Wide Fund for Nature—International, WWF—World Wildlife Fund—U.S., and The S.A. Nature Foundation.

In addition to the authors of the species accounts, we would also like to thank the following individuals for assisting us in preparing this report:

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Ian R. Swingland

Michael W. Klemens

September 1989

The Durrell Institute of Conservation and Ecology

University of Kent

The Methodology of Conservation

Michael W. Klemens

The information contained in *The Conservation Biology of Tortoises* is the result of a five-year project to obtain as much information as possible on the current status of the Testudinidae in the wild. This information was compiled from a myriad of primary and secondary sources, including published field studies and unpublished reports, as well as personal communications and observations. When editing these reports we have endeavored to include as much information as possible. Hopefully, this report will stimulate additional studies on tortoises to help fill some of the many gaps in our knowledge.

Although we have aimed for general consistency between the species accounts, there is some variation in the type of information and its presentation. This is due in part to the dearth of knowledge concerning certain species and/or geographic regions, but also to the varying research specializations of our contributors, as well as the different ways that scientists approach the conservation issue. The previous words were carefully chosen, as for most zoologists, conservation problems are just one of many projects a researcher will embark upon in the course of a career.

Not surprisingly, the conservation movement suffers from a lack of unified approach and methodology. This is unfortunate, as conservationists are grappling with complex issues, which often transcend the boundaries of ecology and enter the spheres of education, politics, and economics. All too frequently, important decisions regarding the future of species are made by crudely attempting to balance ecosystems, economics, and politics, often using minimal data. In some instances, conservation initiatives conducted without a sound understanding of a species' biology are potentially disastrous (Mrosovsky, in Swingland 1988:113).

Three basic areas need to be addressed when devising conservation strategies (Swingland 1988:114). These include a management plan integrating life history tables, questions of habitat integrity, behavioural constraints, the role of environmental sex determination, activity patterns, home range, and other ecological parameters. The second area includes the feasibility of implementing a conservation programme including an awareness of local vested interests, education, knowledge of the political and cultural infrastructure, and an assessment of the anticipated returns of the conservation efforts invested. The third area to be considered deals with resource exploitation, including trade, agricultural activity, and tourism.

Although the accounts vary both in amount of information, its presentation, and sources, there are similarities in the types of conservation problems and threats faced by the Testudinidae. In other work (Klemens 1990, Ph.D. dissertation in prep.), a large data set of over twenty ecological parameters has been accumulated over 14 years in the northeastern United States. Included in this database is information on changing land use patterns, exploitation, and historical occurrences. I have compared some of this data against specific trends discussed in some of the tortoise accounts, especially the problems of habitat fragmentation and low recruitment. Due to lack of information, most of the tortoise accounts only allude to these "potential" problems anecdotally. The New England data are more complete, unfortunately confirming the concerns of many of the contributors to this volume.

Many of the trends and potential conservation problems of the Testudinidae noted by the contributors have correlates in the terrestrial and semi-terrestrial turtle fauna of the northeastern United States (*Clemmys* and *Terrapene*). Some of the data collected in New England are sufficient to link declines in species to lowering environmental quality. Frequently these declines have hinged upon a few key aspects of a species' life history (e.g., home range, reproductive output, and recruitment) which are impeded by these environmental changes.

There is a tendency to consider the conservation issues of tropical and subtropical regions as almost mutually exclusive to those of temperate regions. Although each region presents a unique set of species with divergent habitat requirements, as well as varying educational, political, and economic issues, shared ecological and life history strategies of many Chelonia override the zoogeographical differences.

An acute lack of information concerning the distribution, variations, and abundance of the Testudinidae is apparent when reading many of the species accounts. It is difficult to assess the present status of many species due to the paucity of up-to-date information. Even when current distributions are known, the lack of baseline data makes drawing conclusions about declines and range contractions problematic. The drastic declines and range contractions noted in *Gopherus agassizi* and *Gopherus flavomarginatus*, as well as the nominate race of *Testudo hermanni* in the western Mediterranean basin, have been elucidated only because of a comparatively good source of baseline information contained in the literature and museum collections.

Apart from these species and the giant tortoises, we have only scant knowledge of the distribution of the world's tortoises during the last centuries.

Despite three hundred years of increasingly heavy human settlement, prior to my inventories of southern New England's herpetofauna (1975-1988), there was little baseline information. General survey and inventory work is one of the first steps in establishing a sound scientific basis for any conservation work. Unfortunately, there is a general reluctance on the part of many agencies to fund this type of work at the level and duration necessary to produce useful results. Quick inventories are often unsatisfactory, especially for species which have a very narrow window of activity or occur at low densities characteristic of many Testudinidae.

Education is an important component of any conservation programme. Without the support of the local residents, conservation projects are often compromised and operate with reduced efficiency. The success of the SOPTOM tortoise village in the Massif de Maures of southern France is a good example of integrating the local people into a conservation programme. Likewise, project Angonoka/Kapidolo in Madagascar involves the local populace in all aspects of conservation work, including education and hands-on scientific training. The project also stimulates the local economy through purchasing food and providing construction and maintenance jobs. Eventually, an educational facility is planned, which will provide additional economic growth. In many areas it is important for the residents to realize real economic benefits from conservation. In his introduction to the Oriental Region's tortoises, Moll draws a novel analogy between tortoise reserves and savings accounts. In New England, a sanctuary for the regionally endangered bog turtle (*Clemmys muhlenbergii*) was recently created. Had it not been for the education and subsequent support of local landowners, this reserve could not have been established. Local residents are also playing an important role in monitoring the newly created sanctuary against poachers.

A lack of detailed ecological research on most of the Testudinidae is readily apparent. Much of the information concerning life history parameters is either anecdotal or gleaned from very small samples, though some studies on *Gopherus* and *Testudo* are notable exceptions. Generally, information on habitat utilization, activity patterns, and home range is lacking. With so little life history information available, there is the temptation to extrapolate data from one population to another. Recent work by Els (1989) has demonstrated significant differences in body size and physiological ecology between east and west Cape (South Africa) populations of *Chersina angulata*. Preliminary data on New England *Clemmys muhlenbergii* show considerable variance in key ecological and life history parameters when compared to studies conducted several hundred miles southward in Pennsylvania. On a finer level, bog turtles at three different study sites separated by no more than ten miles appear to have different growth rates, and more importantly, attain different maximum sizes.

These data from a relatively small geographic area within the northeastern United States raise several important points rela-

tive to the conservation of the Testudinidae. The danger of extrapolating life history data from one population to another is apparent. Species with large geographic ranges (including *Geochelone pardalis babcocki* and *Geochelone carbonaria*) utilize a variety of habitat types, differ morphologically, and undoubtedly vary in their life history parameters from region to region. These data also raise legitimate concerns about the introduction or release of captive bred specimens, or specimens of unknown origins into existing populations.

Zoos and captive rearing programmes have an important role to play in the conservation of tortoises. The Charles Darwin Research Station (CDRS) on the Galapagos has returned several thousand *Geochelone elephantopus* to the wild. Project Angonoka/Kapidolo, jointly administered by WWF—International, The Jersey Wildlife Preservation Trust, and the IUCN/SCC Tortoise and Freshwater Turtle Group, discussed by Durrell (this volume), is noteworthy in that the bulk of the Jersey Zoo's efforts are in the tortoise's habitat in Madagascar, actively involving local workers. Many of the techniques of incubation and nutrition developed in zoos around the world could be directly applied to on site head-starting and captive breeding programmes such as those conducted at the Mapimi Biosphere Reserve (*Gopherus flavomarginatus*), SOPTOM (*Testudo hermanni hermanni*), and the CDRS (*Geochelone elephantopus*). However, we need to go much further and forge active working partnerships between field ecologists and zoos, to gather data on wild populations, habitats, and ultimately to invest in wild populations through field studies, habitat protection, and the successful, scientifically monitored release of captive-bred tortoises into their habitats.

Habitat protection remains the only viable long-term means to ensure the survival of the world's tortoises. Although tortoises are protected in many of the large parks and game reserves in Africa and South America, unless these areas are adequately patrolled against poaching, serious losses can occur. Walker (this volume) discusses the collecting pressure that populations of *Geochelone carbonaria* are under during Holy Week in parts of South America. Frequently, reserves are drawn up to accommodate geopolitical constraints with little regard for the biology of the animals contained within their boundaries. Detailed studies on habitat utilization, migration, and home range are needed to construct preserve boundaries to encompass sufficient amounts of appropriate habitats to ensure the long-term population survival of the inhabitants.

Almost all species face localized threats as certain accessible populations are exploited for food and the pet trade. Globally, the problem pales when compared to habitat loss and alteration. Likewise, in southern New England, over-collection is a problem in certain areas, but habitat fragmentation and loss are the prime factors in the declines of *Clemmys* and *Terrapene*.

Direct habitat loss is relatively easy to ascertain. Habitat alteration and the ability of tortoises and turtles to adapt to these changes is one of the more insidious problems facing chelonian conservationists. In these matters, those concerned with tortoise conservation might benefit by examining the situation in southern New England, where the effects of habitat alteration,

fragmentation, and low recruitment are more readily observable than in many tortoise habitats where they are "suspected" of playing a major ecological role.

Like tortoises, the terrestrial and semi-terrestrial turtles of southern New England are characterized by delayed maturity (10-15 years), long adult lifespans (some *Terrapene* survive over a century), relatively small clutch sizes (usually less than ten eggs per year), and low juvenile survivorship. Adult terrestrial and semi-terrestrial chelonians (including the Testudinidae) are individually quite important to the population. Morafka et al. (this volume) estimate it takes as long as half a century to replace an adult *Gopherus flavomarginatus*. The effects of removing adult animals from a site may not be apparent during the lifetime of an individual researcher. However, by studying population trends over shorter time spans, with the benefit of some baseline data, the prediction of a recruitment crisis in certain populations subjected to opportunistic hunting (one or two adults collected or killed every few years) appears reasonable.

In southern New England, this is already apparent in one species, *Clemmys insculpta*, which has declined precipitously in southwestern Connecticut and central Massachusetts due to a combination of low recruitment and habitat fragmentation. These two factors are repeatedly alluded to as potentially affecting tortoises in various parts of the globe. Fortunately, there were some collections of *Clemmys insculpta* made in the 1930s (Yale University Peabody Museum) indicating its presence in areas of southwestern Connecticut where it is now extirpated. Fifty years later I was able to compare my data against this baseline. This species has all but disappeared in southwestern Connecticut and adjacent sections of Westchester County, New York. All individuals observed were aged adults: no hatchlings, juveniles, or young adults were found in the course of my survey. This contrasts sharply to sparsely populated, largely rural eastern Connecticut, where all age classes are frequently encountered.

Of the two primarily terrestrial species of turtles in Connecticut, *Clemmys insculpta* has a large home range, often moving several kilometres in a season. The other terrestrial species, *Terrapene c. Carolina* has a much smaller home range, and marked individuals often are found in the same patch of woodland year after year. *Clemmys insculpta* are killed on roads with a much greater frequency than *Terrapene*. In the last fifty years, southwestern Connecticut and Westchester County, New York have developed into a rural suburb of New York City, resulting in a dense road network crisscrossing the countryside, fragmenting the wooded habitat. Although *Terrapene* still survive in healthy populations (all age classes) in these patchwork habitats (even occurring within the city limits of New Haven), *Clemmys insculpta* is functionally extinct in this region. In the last ten years, five individuals have been found, four dead and one alive on roads. All of these were old adults, worn smooth and devoid of growth annuli. Based on these data, concerns voiced by various contributing authors to this volume (e.g., Berry, Branch, Morafka, and Stubbs) about the long-term problems of low recruitment coupled with habitat fragmentation are valid, especially for species with large home ranges.

Apart from setting aside habitat of sufficient size to ensure a population's survival, there is a need to address many of the secondary or ancillary effects of changing land use and habitat alteration. Stubbs (this volume) touches on this several times in his various *Testudo* accounts, questioning whether clearing of the native Mediterranean forests, resulting in scrubby maquis and garrigue, has actually increased available tortoise habitat.

Branch (this volume) reports that extremely hot bush fires generated by burning large stands of invasive Australian *Acacia* result in increased tortoise mortality due to the heat, compared to fires in natural fynbos vegetation. The introduced *Acacia* forms dense thickets, closing the canopy and reducing habitat suitability for *Chersina angulata*. Branch found dense *Chersina* populations in ecotonal habitats created by human activity such as agriculture and ranching.

In the following pages, Swingland describes the havoc created on the Galapagos by feral mammals, Branch suggests the yellow mongoose may be increasing in inhabited areas, and Berry (as well as Stubbs) discusses increases in raven populations due to garbage (food), tree plantations, and electricity poles (roosting and nesting sites) associated with human activities. These species all prey on tortoise eggs and young tortoises, or in the case of feral goats and donkeys, compete for food.

Finally, Baard (this volume) illustrates the unexpected results encountered by fencing a *Psammodromus* reserve to "protect" it against grazing ungulates, only to have the vegetation grow so thickly that the tortoises were forced out of the reserve into the adjacent pasture.

Again, there are parallel situations in southern New England. *Terrapene* favour edge habitats, and are especially common on powerline cuts, logged areas, and edges of fields. Similar to *Chersina angulata*, they reach greater densities in these human altered habitats than in the surrounding deciduous forests which historically covered much of southern New England. Racoons, *Procyon lotor*, are effective predators on small to medium-sized turtles. They favour disturbed areas and farmland, becoming increasingly abundant in suburban areas, even flourishing within New York City. The incidence of successful racoon predation on *Clemmys muhlenbergii* is minimal in areas of low human density, but becomes an increasing problem at sites near habitation.

Invasive alien plants threaten *Clemmys muhlenbergii* habitats by rapidly closing the canopy and forcing turtles to emigrate. Historically, turtles moved from one open wetland patch to another in large dynamic wetland systems. These habitats are becoming fragmented, and overland movement between wetland areas is becoming increasingly difficult and dangerous. Canopy closure usually results in the extinction of small, localized populations. Factors involved in canopy closure are varied, with several often working simultaneously, and can include invasive alien plants (notably *Phragmites* and purple loosestrife), as well as disruption of the water table by boring new wells associated with increased rural development. Accelerated vegetational growth resulting from increased amounts of nutrients entering wetlands from septic tank leaching (sewage) and fertilizer run-off is becoming a major problem. Management techniques include nutrient mitigation and a combination

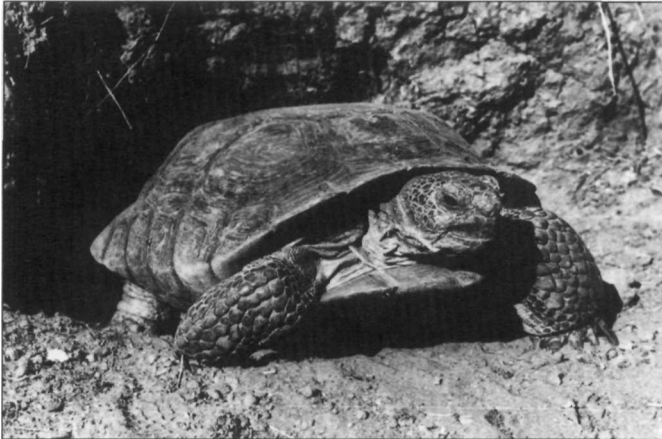
of light grazing and/or pruning emergent shrubbery to maintain bog turtle habitats at their optimum seral stage. Study plots, to monitor yearly vegetational growth, have been set up in these habitats to provide data used to implement pruning and other management techniques.

In summary, many of the conservation scenarios alluded to by the contributors to *The Conservation Biology of Tortoises* have occurred in southern New England. Some of these problems may be solved, but require a thorough understanding of the species' distribution and ecology, as well as implementation of conservation plans that are economically feasible and acceptable to the local population. Habitat fragmentation is the major problem in southern New England. Ideally, large reserves are the answer, but some small reserves have been quite effective in protecting species with small home ranges, pro-

vided these reserve boundaries correspond with a species' biological needs and contain an adequate buffer zone. In some portions of New England, a mixture of reserves and semi-protected land used for light agricultural and forestry activities have adequately protected large populations of *Clemmys insculpta*. Local landowners have been offered property tax relief in exchange for participation in these programmes. In many instances, secondary ecological (ancillary) effects have been mitigated, and the main obstacle is awareness of their often subtle influences. Autecological studies on *Clemmys muhlenbergii* and their habitats have revealed previously unreported ancillary ecological problems which were discussed earlier. Discovering these secondary ecological problems is a valuable byproduct of long-term autecological studies which are lacking for most species of the Testudinidae.

Gopherus agassizi Desert Tortoise

Kristin H. Berry



Female desert tortoise (*Gopherus agassizi*). West Mojave Desert, California, U.S.A. (Photo by B.F. Steveson.)

Introduction

The desert tortoise is one of four allopatric North American tortoises. It occurs in the Mojave and Sonoran deserts of the southwestern United States and Mexico.

Auffenberg (1976) divided the genus *Gopherus* (consisting of four species, *G. agassizi*, *G. berlandieri*, *G. flavomarginatus*, and *G. polyphemus*) in two osteological groups. Bramble (1982), using morphological and palaeontological data, divided the genus *Gopherus* into two separate complexes, each with two species. He established a new genus, *Scaptochelys*, for *agassizi* and *berlandieri*, retaining *Gopherus* for *polyphemus* and *flavomarginatus*. Bour and Dubois (1984) noted that *Xerobates* Agassiz had priority over *Scaptochelys* Bramble. Using mitochondrial DNA (mtDNA), Lamb et al. (1989) evaluated the evolutionary relationships of the North American tortoises, particularly the desert tortoise. They concluded that the mtDNA analysis provides strong support for generic recognition of the two distinct species groups described by Bramble (1982).

Until a few decades ago, the desert tortoise was widespread at lower elevations throughout the Mojave and Sonoran deserts of the U.S.A. In the northern and western parts of the geographic range, large and relatively homogeneous populations with densities exceeding 1,000/sq km extended throughout parts of California, and probably into Nevada and Utah. In

terms of biomass, the tortoise played an important role in the ecosystems. In most areas, numbers have declined dramatically and the extent of populations has been reduced. Most populations are now isolated and low in numbers. Conservation of the desert tortoise is a highly visible and political issue in the U.S.A., but not in Mexico.

Description and Taxonomy

The desert tortoise can be distinguished from other North American tortoises by the relatively narrow head with alveolar ridges of the upper jaw meeting at a sharp angle and by the large hind foot. Adults are sexually dimorphic and range in carapace length from about 190 to 380 mm, with females smaller than males.

Substantial variation exists within the species. Using mtDNA, Lamb et al. (1989) reported three major phylogenetic assemblages, each of which is separated by a major geographic barrier (riverine or riverine/canyon complex). Two assemblages occur in the U.S.A. with the third in the extreme southern part of the geographic range in Mexico. Each genetic assemblage is as different from each other as they are from *G. berlandieri*. The northwestern-most genetic assemblage also contains three clones or genotypes.

Weinstein and Berry (1987) used discriminant analysis to evaluate shell shapes in the U.S.A. They found three distinct types, each associated with geographic distribution, habitat and behavioral preferences. The major phylogenetic assemblages and clones described by Lamb et al. (1989) and the distribution of shell shapes reported by Weinstein and Berry (1987) are parallel in most respects. Much still remains to be done on taxonomic relationships, particularly in Mexico.

Status and Distribution

Status and distribution are treated geographically by phylogenetic assemblage and clone (Lamb et al. 1989). Data on population status are from Berry (1984), Bury (1982), annual Desert Tortoise Council Symposia (1976-1988), and reports from federal and state government agency personnel in the U.S.A. The first phylogenetic assemblage contains most of the tortoises and occurs to the north and west of the Colorado River/Grand Canyon complex in the states of California, Nevada,

Utah, and extreme northern Arizona (U.S.A.). These desert tortoises occurred in widespread and frequently homogeneous populations occupying thousands of square kilometres in the Mojave and Colorado deserts until the 1930s to 1950s. Since then numbers and habitat have declined markedly. In the 1970s and early 1980s, government agencies established more than 40 plots (size = >2.6 sq km) to monitor status. Between 1979 and 1989, most remaining populations declined 30-70% over time spans of 6 to 10 years. Few (if any) viable populations are likely to exist in another 10 years unless major changes occur in land use patterns.

The second phylogenetic assemblage lies to the south and east of the Colorado River/Grand Canyon complex and encompasses most of Arizona (U.S.A.) and extends south into Mexico to the Yaqui River. In the U.S.A., tortoise populations are confined primarily to small islands on mountain slopes in the Sonoran Desert, and are low in numbers. Populations and habitat are declining from human-related causes. Status and distribution are not known for Mexico. The third phylogenetic assemblage is in southern Mexico, and the status and distribution of populations are also unknown.

Habitat and Ecology

Habitat and behaviour vary substantially from one part of the geographic range to another. To the north and west of the Colorado River/Grand Canyon, tortoises occur in valleys and on alluvial fans in creosote bush and tree yucca plant communities where soils are suitable for digging and where annual plants and perennial grasses offer adequate forage. Burrows are constructed on open ground, under shrubs, and in wash banks. Tortoises are primarily active in spring, although summer activity is prevalent when rains provide moisture and forage.

To the south and east of the Colorado River/Grand Canyon in the U.S.A., tortoises occur in small, island-like populations on the steep, rocky slopes of mountain ranges in palo verde-cactus communities. Burrows are often under rocks and may be very shallow. Surface activity occurs in spring and is probably more common in summer. Little is known about habitat and ecological preferences of tortoises in Mexico. They occur in thornscrub and oak woodland communities.

Threats to Survival

Threats to survival vary by site and region. Population losses occur through poaching for pets and food, vandalism, disease, vehicle kills above and below ground, trampling by livestock, and excessive predation on juvenile tortoises by expanding common raven populations. Habitat has deteriorated or has been lost through urban and agricultural development, highway and road construction, military and industrial development, livestock grazing, energy development, mineral exploration and development, harvest of vegetation, and disposal of toxic and radioactive wastes. The mixture of public and privately

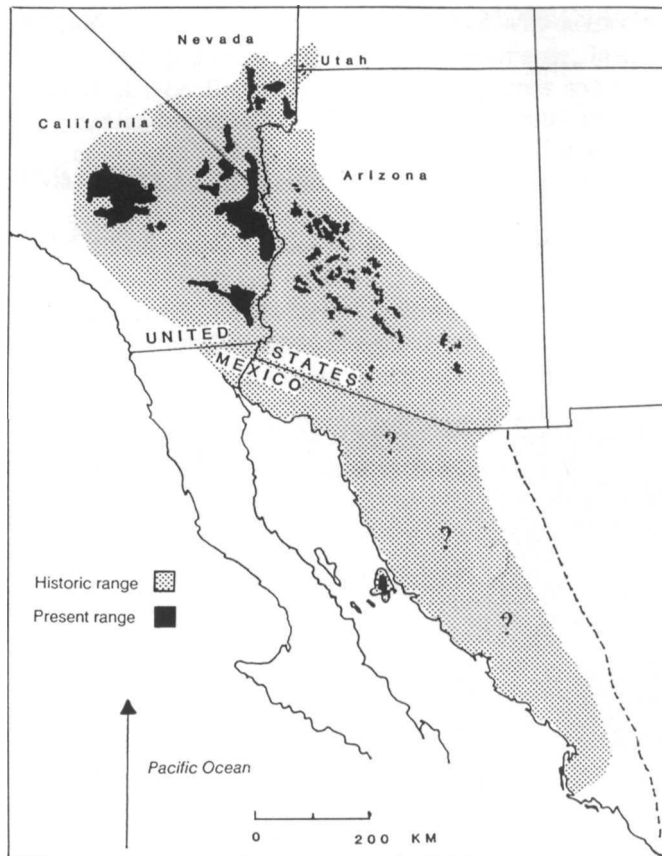


Figure 1. Distribution of *Gopherus agassizi*.

owned land throughout the geographic range in the U.S.A. contributes to the threat. All of the above problems continue to occur in the U.S.A., and at least some are operative in Mexico. Most sites experience more than one type of impact, contributing to serious population and habitat fragmentation.

Conservation

In the U.S.A., the tortoise is a protected species. A small population occupying 100 sq km is federally listed as threatened under the Endangered Species Act of 1973 (as amended). Remaining populations also warrant federal listing. Habitat, especially on private land, receives far less protection. The U.S. Bureau of Land Management (BLM) prepared two recent plans with recommendations for maintaining viable populations on public lands (U.S. BLM 1988). Reserves have been established only in one phylogenetic assemblage, in the northwestern part of the geographic range. Two reserves are in California, the 98 sq km Desert Tortoise Research Natural Area and the 368 sq km Chuckwalla Bench Area of Critical Environmental Concern (U.S. BLM 1988). A multi-million dollar land acquisition programme is underway to acquire private holdings at both reserves. A 6 sq km reserve containing a few tortoises exists in Utah.

Current Research

Most research and monitoring of populations and habitat are conducted by federal and state governments, including state fish and game agencies in California, Nevada, Arizona, and Utah. The U.S. BLM has the largest monitoring programme and is collecting long-term data from more than two dozen sites. Government agencies also fund research on disease, excessive predation by ravens, effects of livestock grazing, efficacy of relocation, etc. Several corporations developing land in tortoise habitat also fund projects, usually under the direction of government agencies.

The following individuals and/or agencies can provide information on various aspects of the biology and conservation of *Gopherus agassizi*.

Population biology and status

Dr. Kristin Berry (U.S. BLM, 1695 Spruce Street, Riverside, California 92507 U.S.A.).

Physiology (water balance, energy requirements)

Dr. Ken Nagy and graduate students Brian Henen and Charles Peterson (Laboratory of Biomedical and Environmental Sciences, University of California, 900 Veteran Avenue, Los Angeles, California 90024 U.S.A.).

Diseases

Walter Roskopf, D.V.M. (Avian and Exotic Animal Hospital of Los Angeles County, 4871 W. Rosecrans Ave., Hawthorne,

California 90250 U.S.A.). James Jarchow, D.V.M. (2729 West San Juan Terrace, Tucson, Arizona 85713 U.S.A.).

General research, management, meetings and symposia

Desert Tortoise Council (5319 Cerritos Ave., Long Beach, California 90805 U.S.A.).

Conservation

Desert Tortoise Council, Desert Tortoise Preserve Committee (P.O. Box 453, Ridgecrest, California 93555 U.S.A.).

Conclusions

In the U.S.A. future survival of the desert tortoise is dependent on government agencies at federal, state, county, and local levels taking rapid and coordinated action to set aside and preserve representative populations of sufficient size for long-term viability. Existing plans for maintaining the species must be implemented quickly and updated frequently to deal with new threats. Current threats are so numerous and decline rates so precipitous that prospects are poor for preserving representative populations within known major genetic assemblages and clones. Rapidly growing human populations in the southwestern U.S.A. further complicate the situation. In Mexico, the prospects are not well-known, but are likely to be somewhat similar.

Gopherus berlandieri

Berlandier's Tortoise, Texas Tortoise

Francis L. Rose and Frank W. Judd

Description and Taxonomy

Gopherus berlandieri is the smallest and most sexually dimorphic of the *Gopherus*. The head is small and narrow, and the snout more pointed than in the other three extant species. The angle between the alveolar ridges is usually more than 65°, but less than 70° (Bogert and Oliver 1945). Carapace width (relative to length) as well as depth is greater than in other *Gopherus*. Adults average between 12-24 cm carapace length. The carapace is unkeeled, with the highest point usually on the third vertebral. The marginals are flared above the limbs. At hatching, the scutes are black with yellow centres. As tortoises age, the black fades to light brown. In old individuals, the yellow centre is absent. The gular projection is well developed in males, as are integumental glands, one located beneath the angle of each lower jaw ramus (Smith and Brown 1946; Rose et al. 1969; Rose 1970). The forefeet are spatulate, but narrower than those of *G. polyphemus* and *G. flavomarginatus*; the hind feet are elephantine but narrower in diameter than *G. polyphemus* and *G. flavomarginatus*, and wider than *G. agassizii* (Carr 1952).

Status and Distribution

The range of *G. berlandieri* is well delineated in Texas, extending from Val Verde County eastward across the state through Kinney, Uvalde, Bandera (Robert W. Mitchell pers. comm.), Bexar, Guadalupe, La Vaca, Jackson, and Matagorda counties. There are reports from Sutton (Dixon 1987), Fort Bend, and Galveston counties, but these may represent released animals. A Brewster County report is probably incorrect. In Mexico, this tortoise occurs from sea level to an elevation of 884 m. It is found throughout most of Tamaulipas (and just enters northeastern San Luis Potosi), the north and eastern portions of Nuevo Leon, and in Coahuila from Monclova north through Nuevo Rosita to Ciudad Acuna. This range corresponds closely with the Tamaulipan Biotic Province (Blair 1950; Dice 1943).

The status of this species in Mexico is unknown. Its densities do not appear high and populations are disjunct. In Texas, population density estimates range from 10 to 23 tortoises per ha (Judd and Rose 1983), but in areas of extensive agriculture, numbers are declining. This is especially marked in the Rio

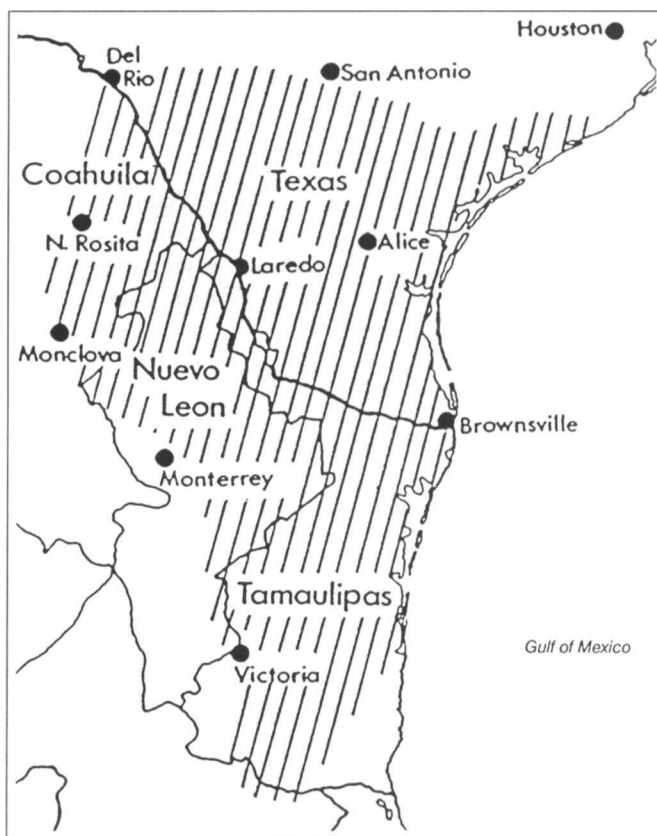


Figure 2. Distribution of *Gopherus berlandieri*.

Grande Valley, where Rameriz (1986) reports that 90% of the natural brushlands have been eliminated since the 1930s. He estimated that 80% of the remaining brushlands are unprotected and threatened by development. In much of Texas, the tortoise is protected in large blocks of land where agriculture is limited. In fact, under certain managed grazing techniques for cattle, the tortoise is favoured. However, the act of clearing this land of shrubs and trees devastates local populations. Few tortoises are taken for food by humans in Texas, but many are killed by vehicular traffic and by ranch personnel who believe that tortoises eat quail eggs. However, the highest numbers are killed when habitats are destroyed. In the past, many animals

were sold in the pet trade. Individuals are killed in Mexico, dried, shellacked, and sold in curio shops. Tortoises are also eaten in Mexico. In 1967, the Texas legislature legally protected *G. berlandieri*.

Habitat and Ecology

The habitat of *G. berlandieri* is best described as semidesert scrub, although the tortoise probably inhabits several barrier islands. Substrates range from sand to clay to caliche. Unlike the other three *Gopherus*, this tortoise rarely makes tunnels exceeding 40 cm in length. Mammal burrows are occasionally used, but usually the tortoise constructs a shallow concavity called a pallet (Auffenberg and Weaver 1969). There are morning and afternoon activity periods. Tortoises are more frequently active in the afternoon (Rose and Judd 1982). Tortoises maintain high selected body temperatures ranging between 30-35°C (Judd and Rose 1977; Voigt and Johnson 1976; Rose et al. 1988), as do other *Gopherus*. They have high critical thermal maxima of 42.5-43.2°C (Hutchison et al. 1966; Judd and Rose 1977). High body temperatures probably aid in digestion of coarse vegetative matter (Rose 1983; Rose et al. 1988), however, this species is known to feed occasionally on carrion and snails. The red tuna (fruits of the large cactus *Opuntia lindheimeri*) are extensively eaten. The primary diet is low grasses and herbs.

Gopherus berlandieri is generally inactive from December through March (Rose and Judd 1982). Copulation usually occurs in late summer, although in captivity males may initiate courtship in early May. Combat between males is well documented and vigorous. Weaver (1970) recognized Type I and Type II combat, depending on whether both males were combative. Tortoises do not defend territories (Judd and Rose 1983). Egg laying begins in early April, but the primary months are May and June. The eggs are laid in a constructed concavity that is often softened with bladder fluid (Auffenberg and Weaver 1969). When laid, the shell is pliable, but hardens quickly to an almost porcelain-like appearance. Eggs are usually oval in form. Because of pelvic girdle constraints (Long and Rose, in press), this tortoise increases egg size through elongation of the egg (Judd and Rose, in press). Females probably deposit a single clutch annually of 1-5 eggs, which are distributed in multiple nests over a period of time (Judd and Rose, in press). Not all females develop an egg clutch each year. Four tortoises (including one female) are known to be in excess of 70 years old (Judd and McQueen 1982; Judd and Rose, in press). This female is still laying fertile eggs.

Incubation periods range from 88-118 days and hatching success is about 60% (Judd and McQueen 1980). Hatchlings are about 40 mm (carapace length as well as width) and weigh about 21 gm. Increase in carapace length and width is 56% and 46% respectively during the first year (Judd and McQueen 1982). Weight increases 229% the first year (ibid). Age at attainment of sexual maturity has not been determined but

unpublished data (Judd) suggest that females do not lay until ten years old.

We established a free access study grid of 3.3 ha in Cameron Co., Texas in 1972 (Rose and Judd 1982; Judd and Rose 1983). A second study grid (2.0 ha) 6.4 km southwest of the first was established in 1977. Between 1972 and 1987, 336 tortoises were marked and released. Only 4 of the 42 tortoises resident on the original study area in 1972 were found in 1986-87. Thus, there has been almost a complete turnover in this population in 15 years. Little of the change in numbers is attributable to mortality. Some tortoises appeared to be nomadic, others used a limited area of a grid (home range) for many years (Rose and Judd 1982; Judd and Rose 1983). Sex ratios vary among local populations but overall it appears to be 1:1 (Judd and Rose 1983). Juveniles comprise 9% to 27% of a population. The local populations of *G. berlandieri* are quite plastic regarding demographic parameters and it would be an error to conclude that data generated from one population are applicable to other populations, even though they might be in close proximity.

There is geographic variation in the average size of males but not in females. Coastal males are larger than those from more inland areas (Rose and Judd 1982).

Conservation

There are no reserves set aside specifically for *G. berlandieri*. However, there are reserves such as the Laguna Atascosa National Wildlife Refuge and the Welder Wildlife Refuge where the tortoises are protected. Bury and Smith (1986) recommended restriction of tillage and cattle grazing to areas away from lomas, and prescribed means to enhance (make more open) tortoise habitat at Laguna Atascosa. Although large cattle ranches do provide some protection for this tortoise, much habitat is being modified to increase cattle foraging potential and for agriculture. To the best of our knowledge, no protective measures are employed in Mexico. Efforts should be made to determine the status of *G. berlandieri* in Mexico. The Texas legislature has made it illegal to "own" or sell this tortoise, though few state enforcement officials are aware of the law. Increased awareness of this law with greater responsibility exerted by local and State environmental agencies and organizations would be helpful. Several relatively large tracts of land should be set aside for this tortoise in the lower Rio Grande Valley.

Current Research

We are continuing our research on the biology of *G. berlandieri*. Our goal is to develop a life table that will serve as a base for long-term management. Current research focuses on age-specific fecundity, mortality, growth, and site fidelity. To the best of our knowledge, no one else is studying the general biology of this tortoise.

Gopherus flavomarginatus

Bolson Tortoise

D.J. Morafka, G. Aguirre, and G.A. Adest

Taxonomy

The Bolson tortoise is the largest terrestrial reptile in North America. First made known to science by Duges (1888) as *Xerobates polyphemus* (= *Gopherus polyphemus flavomarginatus*), the validity of *Gopherus flavomarginatus* as a full species has been clearly demonstrated (Legler 1959; Legler and Webb 1961).

Summary

Largest of the entirely terrestrial genus of North American gopher tortoises, this species is endemic to Mexico, confined to the Bolson de Mapimi in the Chihuahuan Desert's north-central plateau. Populations are localized and discontinuous. Disjunct northern populations tend toward darker carapaces and may be morphologically distinct. Many colonies are already extirpated, many are depleted. Total numbers are estimated between 7,000 and 10,000 adults. Maximum known density is seven per ha; typical densities are less than one per ha. It primarily inhabits Tobosa (*Hilaria mutica*) grasslands on gentle slopes fringing basin floodplains with a diet consisting of tobosa, grama grasses, and local forbs. The species digs deep long burrows for shelter from predators and temperature extremes. It becomes dormant during the cold, dry winters, but surfaces episodically during mild weather. Sexual dimorphism is poorly developed. Mating typically occurs in May, followed by oviposition of one to three clutches between May and October, averaging five eggs each and hatching in 100-130 days. Sexual maturity requires approximately 15-20 years. The species is severely threatened by use as human food, habitat degradation by livestock and agriculture, and illegal trade. Range contraction, depressed fecundity, nest destruction, and low juvenile survivorship delay successful recruitment and replacement to an estimated 50 years.

The species is protected by Mexican federal law. Some populations are actively conserved within the Mapimi Biosphere Reserve, Durango, and tentatively, at the Cerros Emilio, Chihuahua. The Mapimi Reserve programme includes both a hatchery and nursery. Most populations are unprotected, and existing regulations are not adequately enforced. This species is listed on CITES Appendix 1.

Distribution

The species is at present restricted to north central Mexico, where populations exist in a series of disjunct closed basins collectively known as the Bolson de Mapimi (centred approximately near the convergence of the Mexican states of Chihuahua, Coahuila, and Durango), within the Mapimian subprovince of the Chihuahuan Desert. The species total range has a maximum diameter of 150 km, and covers an area of about 7,000 sq km. Populations are generally divided into three major and three minor fragments. Only the Diablo fragment (Chihuahua), the Americanos fragment (Coahuila), and the Mapimi fragment (primarily in Durango) sustain large reproducing populations.

Pleistocene epoch fossils indicate the Bolson tortoise ranged as far west as southwestern Arizona, east to Trans-Pecos Texas, north to Oklahoma, and south to the Mexican state of Aguascalientes. If the species occurred at and between these points simultaneously, its current distribution has contracted into a relict pattern constituting less than 10% of its former distribution. Among the factors thought to constrain or reduce Bolson tortoise distribution has been overkill scenarios involving palaeoindian predation at the end of the Pleistocene Epoch, the advent of cold winter storms, and seismic activity in geological fault zones collapsing burrows (Bramble, pers. comm.).

Population Structure

Populations of *G. flavomarginatus* are discontinuous and often concentrated into narrow zones above the uniform tobosa grass or alkaline evaporative pans that dominate the floors of closed drainage basins (bolsons). The upland limits of these belts are usually determined by the replacement of silty, sandy soils by coarse gravel alluvium or rock exposures. Only six high density belts have been located, all within the three larger fragments previously identified. Based upon partial sampling of these high density belts, it is estimated that adult populations do not exceed 6,000 individuals. Combined with smaller fragments and isolated low-density clusters of individuals, total adult numbers are estimated at a maximum of 7,000-10,000 individuals.

The species is, and continues to be, subject to heavy exploitation and habitat loss. Many colonies have been extirpated

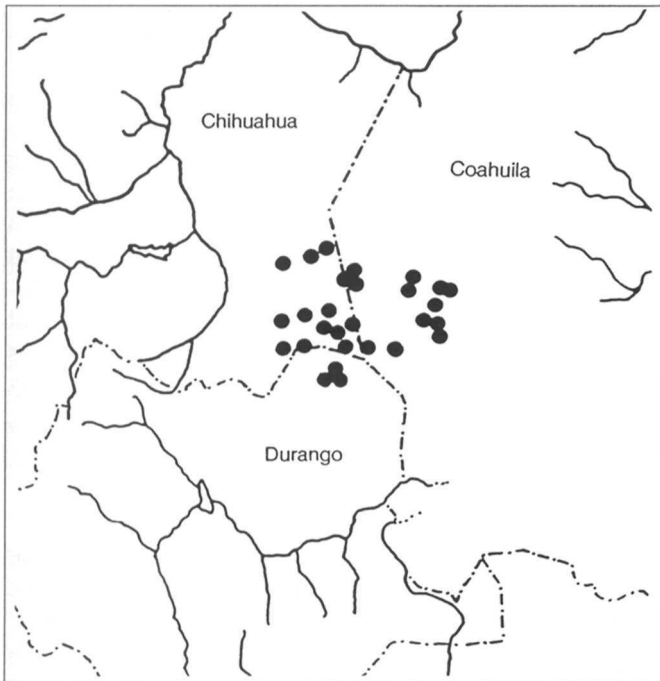


Figure 3. Distribution of *Gopherus flavomarginatus*.

while others are severely depleted. For example, of the three localities that provided specimens for the first scientific description of the species (Legler 1959), the species is rare and still subject to human consumption at the Americanos (Coahuila) site, and extirpated at the two others (Carrillo (Chihuahua) and north of Lerdo (Durango)). Interviews with local residents indicate recent extirpation from several areas including the northern edge of Laguna Mayran agricultural district (Durango), most of the Bolson de Mapimi west of Mexican Federal Highway 49 (from Jimenez, Chihuahua south to Bermejillo, Durango), and from a 10 km strip on either side of National Railroad line from Escalon (Chihuahua) running west to Cuatro Ciénegas (Coahuila). This strip bisects the core of the entire distribution of this species. Similar corridors of extirpation characterize all major roads and rail lines intruding into historical Bolson tortoise range. Most surviving populations continue to be subject to some predation by humans. The maximum known population density is seven tortoises per ha at Cerro Emilio (Chihuahua). The maximum density of active burrows in the Mapimi Biosphere Reserve (Durango) is two per ha in well preserved colonies, but densities vary from five to 26 per sq km in other areas within this reserve. Contradicting the assumption that each tortoise utilizes a single burrow, radiotelemetric studies reveal that 64% of the tortoises at the primary Mapimi study colony use one or two burrows, and the remaining 36% occupy four to eight burrows. Thus, burrow concentrations and tortoise density cannot be equated. Age structure of this same Mapimi population in 1986 was 67.7% adults, 4.0% subadults, 22.2% juveniles, and 6.1% hatchlings to one

year old. The percentage of young tortoises is as high as 14% in less disturbed areas. 1981-86 comparison of Mapimi demographics revealed a striking increase in adults (41-67.7%) coupled with drastic decreases in all other categories except hatchlings.

The Bolson tortoise may be extinct as a wild species within two or three decades unless effective conservation action is widely implemented on a sustained basis (Smith and Smith 1979). Factors contributing to this situation include limited, shrinking and fragmented habitat; specialized habitat requirements; agricultural alterations to habitat, particularly when irrigation and plowing is involved; overgrazing by cattle and goats; direct human predation; and lack of active protection of any populations outside of the Mapimi and newly created Cerro Emilio Reserves.

Habitat and Ecology

This is a large terrestrial tortoise approaching 40 cm in shell length (fossils may have reached one metre). It prefers low grade slopes (0.5% to 2% grade), fine textured soil (averaging 48% sand and 32% silt with both gravel and clay each comprising 10% of the total) and mixed sclerophyll shrub and desert bunch grass vegetation. Perennial scrub is dominated by the creosote bush (*Larrea divaricata*) and mesquite (*Prosopis juliflora*), followed by guayule (*Parthenium incanum*) and tarbrush (*Flourensia cernua*). Tobosa grass (*Hilaria mutica*) is virtually always present, but may or may not be dominant, often coexisting with grasses of genera *Bouteloua*, *Sporobolus*, *Scleropogon*, *Aristida*, and *Tridens* (Appleton 1978; Auffenberg and Franz 1978; Barbault and Halffter 1981). Burrows may occur as much as 12 m upland from primary grassland belts. This species occurs between 1,000 and 1,400 m elevation. The warm desert climate is borderline between temperate and tropical in seasonal fluctuations. The average monthly temperatures vary from a January low of 11 °C to a high of 28°C in June. Extreme temperatures include episodic winter lows of -16°C and summer highs of approximately 45°C. At the Mapimi Reserve, November through March solar radiation ranges from 250-475 cal/cm sq/day, while from April through October solar radiation ranges from 375 to 500 cal/cm sq/day. Seventy-two percent of Mapimi rainfall is concentrated in June through September, while December through February accounts for only 8%. In only eight of the past 28 years has the average Mapimi rainfall exceeded the annual average of 271 mm. The seasonal cycle is characterized by peaks of activity in the spring and winter months, reduced activity in autumn, and November through March dormancy, punctuated by opportunistic activity during episodes of mild weather (especially if coupled with precipitation).

Mating has been frequently observed during the warm, dry period from April through June, typically continuing throughout the summer rainy season. Oviposition peaks in June, but can occur from April through September. Hatchlings appear from July through October.

In dry spring weather, Bolson tortoises exhibit a markedly bimodal daily activity pattern, with peaks at 10:00 and 17:00 hours. After the onset of summer rains, tortoise activity is concentrated around midday, but retains a weak bimodal pattern. Activity is most frequent during the afternoon (Nathan 1979). The most prolonged activity occurs during or immediately following summer rains, which may even elicit nocturnal emergence. Length of surface activity is limited by an estimated critical thermal maxima of 44°C as well as individual heating rates. On a yearly basis, Bolson tortoises average 45 minutes per active day on the ground surface. Combined with activity averaging one day out of every three, tortoises are on the surface less than one percent of their entire lives.

Bolson tortoises dig burrows up to 8 m long and 2 m in depth, depending on these structures for defense from predation and shelter from exposure to climatic extremes. A mound of soil, 10-15 cm high, typically rims the burrow entrance, possibly deflecting flood waters from entering the burrow and also serving as a perch for early morning and late afternoon basking. Burrows appeared to be concentrated in clusters of five to 50 in the upslope circumstances previously described, often above the primary concentrations of tobosa grass. Less frequently, these clusters also occur in the better drained flats, where vegetation is patchy, even if they are subject to occasional localized flooding. Isolated, scattered burrows also occur, but whether these are relics of depleted colonies, or constructed by naturally wandering tortoises is not known. Hatchling and juvenile tortoises frequently dig their own burrows, but may retreat into rodent burrows, packrat (*Neotoma*) middens, or burrow directly into the leaf litter beneath small bushes. This species shows a degree of social organization. A dominance hierarchy exists among males. Mean home range is 4.1 ha for adult males, 3.1 ha for adult females, and 1.2 ha for juveniles.

The species is herbivorous. Twenty-one plant species have been identified in faecal samples. Grasses comprise 64% of the diet, shrubs 14%, and annual herbs 5%. The most important species in the diet (dry weight percentage) are: *Bouteloua barbata* (22.7%), *Hilaria mutica* (15.2%), *Tridens pulchellus* (14.9%), *Sidaleprosa* (13.5%), *Sphaeralcea angustifolia* (9.8%) and *Chloris virgata* (5.0%). *B. barbata* is the most important food item during the last part of the summer, and *H. mutica* and *S. leprosa* are the main food items during the rest of the year.

In addition to the seasonality of sexual reproduction, considerable information on sex ratios is now available. Male to female sex ratios are skewed in both the Mapimi study colony and the Biosphere Reserve as a whole. Ratios range from 0.43 to 0.83. While captive females at the Laboratorio del Desierto may produce three clutches per annum, wild females average only 1.3 clutches per year (two maximum). At Mapimi, seven out of every eight clutches were destroyed by predators. Infertility among eggs averaged 35%. Mean clutch size is 5.2 eggs. Thus, an average female may produce only 3.4 offspring over an eight year period. With probable survivorship to adulthood (20 years) of less than 5%, replacement of an adult may require half a century.

Sexual maturity probably requires 15-20 years. Individuals longer than 250 mm are presumed to be reproductive adults. Hatchlings typically range 45-70 mm in length. Early growth in captives ranges from 50% in the first year to 30% in the second (absolute shell length increments were typically about 20 mm in both cohorts). While captive growth has stalled in later years, wild juvenile shell growth rings indicate a peak in absolute growth during years four through seven. Sexual dimorphism is inconspicuous, though evident in the proportionally longer gular projections, the slightly increased plastral concavity, marginal carapace flare, and lower maximum lengths all of which tend to distinguish males. Females typically achieve maximal carapace lengths in excess of 370 mm.

Threats to Survival

Several factors are negatively affecting this species. Habitat destruction through overgrazing, ploughing, and irrigation have apparently contributed to the extirpation of large tortoise colonies. Over-utilization as a food source is probably the main factor in the species' decline. Illegal trade has also depleted large populations. Tortoises and their eggs have probably been an accessible and constant food source to inhabitants of the desert since pre-Columbian times. Human predation has increased since railroad construction in the 1940s. Tortoises were eaten by construction workers and freight cars were loaded with tortoises to be shipped as a delicacy to coastal Pacific cities.

Removal of ground cover due to overgrazing may contribute to the nest predation, skewed sex ratios (temperature-dependent sex determination is suspected), dehydration, and malnutrition of hatchlings. These consequences are exacerbated in dry years.

Conservation Measures Taken

The species is protected by Mexican law and is effectively protected within the boundaries of the Mapimi Biosphere Reserve through the collaboration of the residents of ranches and "ejidos" (cooperative farms of the Mexican Government Resettlement Programme) participating in this reserve. Enforcement of legal protection is inadequate over most of the range due to lack of active resident personnel. Protection is also afforded by some private property owners. Mexican and U.S. border officials have been alerted to the identity and legal status of the tortoise.

Cooperative studies between Mexico and the U.S.A. on the autoecology of the species have been operating since 1978 and are the basis of a management programme. The Bolson tortoise is listed as "Endangered" under the U.S. Endangered Species Act 1973 and on Appendix 1 of the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES). Appendix 1 listing requires that domestic and international trade in the taxon and its products is strictly regulated by the ratifying states.

Conservation Measures

Declaration of more actively protected areas is a priority. One such area now being established is at Cerros Emilio, near Ranch Sombreritillo, in Chihuahua. Hatchery operations started in 1987. These are being developed through cooperation between private land owners, residents, the Mexican Wildlife Agency, and the World Wildlife Fund. Existing protection under Mexican federal law needs better local enforcement and increased education throughout the tortoises' range, although existing efforts have had a very positive effect. The present comprehensive joint Mexican-American project, involving autecological studies, hormonal assays, microbiology, and nutrition, and diagnostic blood cell counts and chemistry should be continued.

There are captive breeding colonies in Mexico and the United States. At the Mapimi Reserve headquarters, eggs have been collected by oxytocin-induced oviposition from gravid wild females, and incubated in captivity. Hatchling success has been increased to 65% in 1986 and the survival rate for third-year juveniles raised in the Mapimi open-air nursery averages

60%. In 1986, the first crop of nursery-reared tortoises was released into the wild. Several breeding adults are also housed at the headquarters. A passive solar incubator is used for oxytocin-induced egg clutches and a nursery with twenty pens, capable of housing 200 juveniles, is now in operation. The Aragon Zoo in Mexico City has a pair of Bolson tortoises which have not yet bred. A few individuals in Camargo and Jimenez (in Chihuahua) and Torreon (in Coahuila) have succeeded in rearing young. The Mexican Wildlife Agency (SEDUE) and the Institute of Ecology have implemented a recovery programme for relocating former captive tortoises from Torreon to Mapimi, where they potentially contribute to breeding stock being maintained in a seminatural, protected setting.

Editorial Note

This report draws heavily upon nine papers authored or coauthored by the contributors. In the interests of clarity, these numerous, repeated literature citations have been deleted from the text. These papers can be found in the bibliography under Adest, Aguirre, Lieberman, and Morafka.

Gopherus polyphemus

Gopher Tortoise

Joan E. Diemer

Summary

Formerly common in the southeastern United States, this species has been extirpated from parts of its range. Many remaining populations are declining. The principal threat is loss of habitat to intensive land use. Exclusion of burning from natural and planted woodlands has led to habitat deterioration. This species has a low reproductive potential, hence is vulnerable to over exploitation. Collection is prohibited in Alabama, Florida, Georgia, Mississippi, and South Carolina. It is listed as a federally threatened species in Louisiana, Mississippi and western Alabama. This species is listed on Appendix II of CITES. Habitat protection and suitable forest management are needed to protect *Gopherus polyphemus*.

Distribution

Gopher tortoises range from southwestern South Carolina through southern Georgia and most of Florida (except the Everglades), westwards through southern Alabama and Mississippi, just entering eastern Louisiana (Auffenberg 1978; Auffenberg and Franz 1982). They also occur on islands off the Gulf coast of Florida (Logan 1981) and as far south as Cape Sable, at the tip of the Florida peninsula (Auffenberg and Franz 1982; Kushlan and Mazzotti 1984; Logan 1981).

Population Status

Formerly common, this species has now been extirpated from parts of its range and many remaining populations are declining. Habitat destruction, habitat degradation (fire exclusion), and human predation have reduced the original number of gopher tortoises by an estimated 80% over the last 100 years (Auffenberg and Franz 1982). In South Carolina, four disjunct populations remain in Jasper County and isolated tortoises also occur in southern Hampton County (Wright 1982). In southern Georgia, *G. polyphemus* still occurs on sand ridges in at least 81 counties. Some of the largest and most continuous populations are found in the western Fall Line Sand Hills and the central Tifton Uplands (Landers and Garner 1981). Elsewhere in Georgia, populations are small and discontinuous. Throughout the Georgia Coastal Plain, populations have been fragmented by urban and agricultural development and depleted by over-



Figure 4. Distribution of *Gopherus polyphemus*.

harvesting and habitat deterioration (Auffenberg and Franz 1982; Landers and Garner 1981).

In Florida, the gopher tortoise remains widely distributed, occurring in all 67 counties. However, its range in extreme southern Florida is restricted by unsuitable habitat and increased urbanization (Auffenberg and Franz 1982). Gopher tortoises are still common in northern and central parts of peninsular Florida, but peripheral populations in the west and south have disappeared or are declining rapidly. Urban growth, phosphate mining, and citrus production have had an impact on populations in central Florida. Human predation has depleted populations in the Florida Panhandle, and west Florida tortoise hunters now travel to Georgia or the Florida peninsula to obtain tortoises (Auffenberg 1978; Auffenberg and Franz 1982; Diemer 1986).

Tortoises occur in at least 21 counties in southern Alabama. Populations in the state appear to be recovering from past exploitation, however, exclusion of fire from upland habitats remains a problem (Lohofener and Lohmeier 1984; Spillers and Speake 1986). Agricultural and forestry practices have had a severe impact on tortoise populations in their 14 county range in southern Mississippi. The largest remaining population

occurs in the DeSoto National Forest (Lohofener and Lohmeier 1984). Extensive, thickly-planted stands of loblolly pine (*Pinus taeda*) have contributed to the tortoises' near extinction in Louisiana. Scattered tortoises remain only in Washington and possibly Tangipahoa parishes (Jennings and Fritts 1983; Lohofener and Lohmeier 1984).

Habitat and Ecology

The gopher tortoise generally occurs on well-drained to dry soils, with adequate sand depths (in excess of one metre) for burrowing. Such areas and their associated vegetation are usually referred to as sandhills. Low-growing herbaceous vegetation, open nest sites and shade are required. Natural stands of longleaf pine (*P. palustris*) and scrub oaks (*Quercus* spp.) are favoured habitat, but planted stands are also occupied when the canopy is sufficiently open to allow growth of abundant herbs and provide nest sites with almost full sunlight. Roadsides, fence-rows, old fields, berms, and the edges of denser plantations are also common burrowing sites. In Florida, tortoises also occur in sand pine (*P. clausa*) scrub, xeric hammocks, pine flatwoods, dry prairies, and mixed hardwood-pine communities (Auffenberg and Franz 1982; Diemer 1986; Garner and Landers 1981; Landers 1980; Landers and Buckner 1981; Landers and Speake 1980).

Adult burrows average about 4.5 m in length with a chamber approximately 2 m from the surface. Burrow lengths in excess of 14 m have been reported. Placement and depth of gopher tortoise burrows vary with soil type, geographic location, and ground water levels. In northern Florida, gopher tortoises use more than one burrow during an activity season. Burrows often occur in high densities, forming colonies (Diemer 1986; Hansen 1963; McRae et al. 1981).

Gopher tortoise density and movements are affected by the availability of forbs and grasses. Home range is inversely related to the amount of herbaceous ground cover. As the principal sandhill grazer, *G. polyphemus* feeds primarily on grasses (*Poaceae*), grasslike plants, (certain species of *Cyperaceae* and *Asteraceae*), and legumes (*Fabaceae*). Legumes appear to be particularly important in the diet of juveniles (Auffenberg and Iverson 1979; Garner and Landers 1981; Landers 1980; McRae et al. 1981).

The gopher tortoise exhibits deferred sexual maturity, low fecundity, and a long life span. Mating generally occurs from April to early June, but males may attempt to breed at other times during the activity season. Nests are generally constructed in the burrow mound from mid-May to mid-June. A single clutch of white, nearly spherical eggs with thick, calcareous shells is laid annually. In southwestern Georgia, clutch size was found to average seven eggs; mean clutch size in the northern Florida peninsula was five. The incubation period varies latitudinally from about 80-110 days. Nests are very liable to predation. Nest loss of 87% has been recorded in southern Georgia. Egg predators include armadillos (*Dasypos novemcinctus*), raccoons (*Procyon lotor*), grey foxes (*Urocyon cinereoargenteus*), and striped skunks (*Mephitis mephitis*). Juvenile tortoises are also vulnerable to a variety of mammalian, avian, and ophidian predators. Based on burrow counts in

northern Florida, it has been estimated that from the time of egg laying through the first year, the recruitment potential can be reduced by about 94%. While some hatchlings immediately construct burrows, others may utilize adult burrows or merely seek shelter opportunistically under sand or litter (Alford 1980; Diemer 1986; Douglass 1978; Iverson 1980; Jennings and Fritts 1983; Landers 1980; Landers and Garner 1981; Landers et al. 1980; Wright 1982).

Sexual maturity is reached at 16-21 years in southwestern Georgia and 10-15 years in northern Florida. Individuals may live more than 40-60 years. Given such low reproductive potential, heavy or sustained harvest can lead to rapid depletion, and recovery of depleted populations is slow (Diemer 1986; Iverson 1980; Landers 1980; Landers and Garner 1981; Landers et al. 1980, 1982; Taylor 1982).

G. polyphemus is a particularly important component of xeric communities. The gopher tortoise serves as a seed dispersal agent for native grasses and returns leached nutrients to the surface during burrow construction. More than 30 commensals are found in burrows, including state or federally listed species such as the gopher frog, *Rana areolata*, and the eastern indigo snake, *Drymarchon corais couperi* (Auffenberg 1969, 1978; Diemer 1986; Hutt 1967; Landers 1980; Landers and Speake 1980).

Threats to Survival

The most significant threat is loss of habitat to intensive land use, particularly housing projects, industrial centres, broad-scale agriculture, intensive forest management, phosphate strip-mining, and sand extraction. Another factor of importance is the exclusion of fire from natural longleaf pine-scrub oak habitats. An open canopy and relatively litter-free ground are necessary for food production and nesting, and such conditions are favoured by regular burning. Tortoise numbers may be reduced by as much as 60-80% when burning is excluded for eight or more years. The use of heavy machinery to reduce logging debris in preparation for planting trees may be detrimental to gopher tortoises. However, studies in southern Georgia and northern Florida demonstrated that gopher tortoises are able to dig out following chopping treatment on deep sandy soils (Auffenberg 1978; Auffenberg and Franz 1982; Diemer 1986; Diemer and Moler 1982; Landers 1980; Landers and Buckner 1981; Landers and Garner 1981; Landers and Speake 1980; Lohofener and Lohmeier 1984; Wright 1982).

Tortoise response to more intensive site preparation techniques may vary markedly (Diemer and Moler 1982). Increasing urbanization in Florida has focused attention on displacement of gopher tortoises. Tortoise relocation is being advocated by environmental consultants and regional planning councils with little thought to such biological impacts as population disruption, gene pool mixing, and parasite or disease transmission (Diemer 1984, 1986).

Given its low reproductive potential, this species is very susceptible to over-harvesting. Exploited in Florida for over 4,000 years, the gopher tortoise was a major food source for many families during the Depression. Due to prohibition or regulation of harvest, diminished tortoise populations, and the in-

crease in "posted" private lands, the practice of collecting gopher tortoises for consumptive purposes has declined. However, illegal commercialization still occurs in some areas. Although a one-time harvest is not necessarily the "death knell" for a colony, intensive predation pressure sustained over a long period could have a serious impact on local populations. Gopher tortoises are often considered pests on livestock production areas, and local hunters are sometimes enlisted to remove tortoises in pastures. Other threats include mortality on highways and the collection of tortoises for pets or racing purposes. Large-scale rattlesnake roundups and the use of agricultural chemicals may also have deleterious effects on tortoise populations (Auffenberg and Franz 1982; Diemer 1984, 1986; Hutt 1967; Landers and Garner 1981; Lohoefer and Lohmeier 1984; Taylor 1982).

Conservation Measures Taken

Georgia and Alabama list the gopher tortoise respectively as a protected "nongame species" and a "game species" with no open season. Mississippi and South Carolina consider it "endangered," and Louisiana affords it no protection. In Florida, the gopher tortoise is a "species of special concern": tortoise harvest is prohibited. Florida also prohibits the introduction of gasoline or other toxic substances into tortoise burrows. The U.S. Fish and Wildlife Service lists the gopher tortoise as a threatened species in Louisiana, Mississippi and western Alabama.

G. polyphemus is listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Appendix II listing implies that commercial trade is allowed providing a permit from the country of export is obtained. This can provide a method of monitoring trade levels.

Conservation Measures Proposed

Forest management that promotes grassy, open canopy habitat is necessary. Recommended management in natural longleaf pine-scrub oak stands includes thinning of dense oaks, reestablishment of the pine component (to aid in carrying fire), and prescribed burning at least every 5-10 years where summer burns are feasible or every 2-4 years if winter burns are used. In commercial pine plantations, using low intensity site preparation, planting fire-tolerant species at wide spacings, maximizing edge, and burning annually or biennially will benefit tortoise populations. Other suggested conservation measures include establishment of preserves, protection from over-harvesting, restocking, and public information (Auffenberg and Franz 1982; Diemer 1986; Landers 1980; Landers and Buckner 1981; Landers and Garner 1981; Landers and Speake 1980; Lohoefer and Lohmeier 1984; Spillers and Speake 1986; Wright 1982).

Captive Breeding

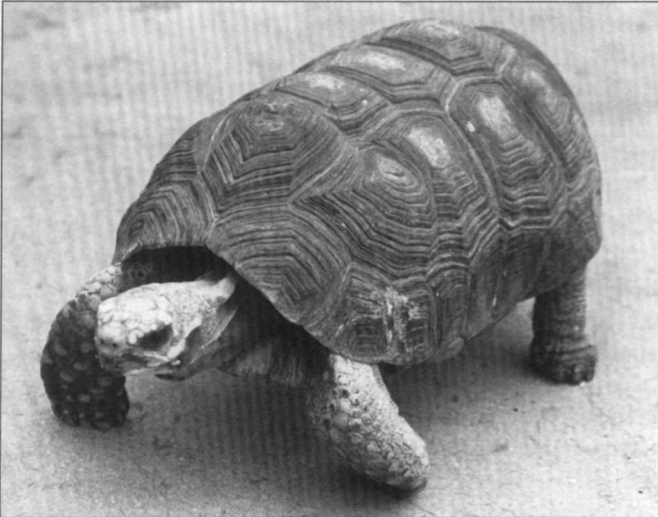
Four gopher tortoises were hatched at Palm Desert Zoo in 1979 (Olney 1981). Captive propagation has been undertaken by private individuals within the species range (Spillan 1982). In some cases, juveniles have been returned to the wild. Organized breeding programmes are not required at this time.

Editorial Note

Due to the large volume of *Gopherus polyphemus* literature, including comprehensive descriptive studies, many references were repeatedly cited. Throughout most of this account, references have been grouped at the end of paragraphs to which they pertain, eliminating many duplicate citations.

Geochelone carbonaria Red-footed Tortoise

Paul Walker



Red-footed tortoise (*Geochelone carbonaria*). (Photo courtesy of Zoological Society of London.)

Summary

This Neotropical species is found in the lowlands of southern Panama to northern Argentina, in the drier forests and grassland savannas. These regions are typically hot and relatively dry for much of the year. Although *Geochelone carbonaria* was described in 1824, it has a long history of human utilization. Used for food by many South American tribes, it was then eaten by European colonists, even being introduced onto some Caribbean islands as a convenient food source. Human predation is now considered to be the major threat to the species. Although not listed by IUCN as a threatened species, it is under considerable pressure over much of its range, and is thought to be declining in some areas. Although protected by national legislation throughout much of its range, this protection is often nominal. The seasonality of hunting pressure gives potential for a concentration of patrol effort in reserves.

Description and Taxonomy

This is a relatively large species, with a mean adult carapace length of about 300 mm. The carapace is typically black, with a small yellow area around the areola of each scute. The plastron is yellow-brown. A mid-carapace "waist" constriction is normally apparent in adult specimens, and is generally more pronounced in males. Several of the head scales are yellow. The species gets its common name from the bright red coloration of some of the leg scales. With its extensive range and habitat fragmentation (Pritchard and Trebbau 1984), *G. carbonaria* exhibits considerable geographic variation in terms of shell size, colour, and morphology. The northernmost Panamanian populations have dark brown carapaces, rather than the typical black. The extent of the light areolae is very varied. The plastron ranges from predominantly yellow (Venezuela) to overall black (Argentina). In contrast to the bi-lobed, spatulate, or denticulate gular region typical of most populations, Pritchard and Trebbau (1984) report that the Venezuelan populations have a smooth anterior plastron margin.

Auffenberg (1971) concluded that the South American *Geochelone* diverged into two species groups during the Oligocene. The modern species *G. carbonaria* and *G. denticulata* diverged into one group while *G. chilensis* and *G. elephantopus* formed the other. Some authors (e.g., Bour 1980) have elevated the subgenus *Chelonoidis* to generic status, but this has not been widely accepted by authors, including Pritchard and Trebbau (1984) and Iverson (1986).

Status and Distribution

Groombridge (1982) reported the status of *Geochelone carbonaria* as "Insufficiently Known," based on the reports of Pritchard (1979). Further investigation resulted in the omission of this species from the 1988 IUCN Red List of Threatened Animals. The species is nominally protected, throughout much of its range, by national legislation. It is listed on Appendix II of CITES, indicating that international trade is permitted if export permits from the country of origin are provided.

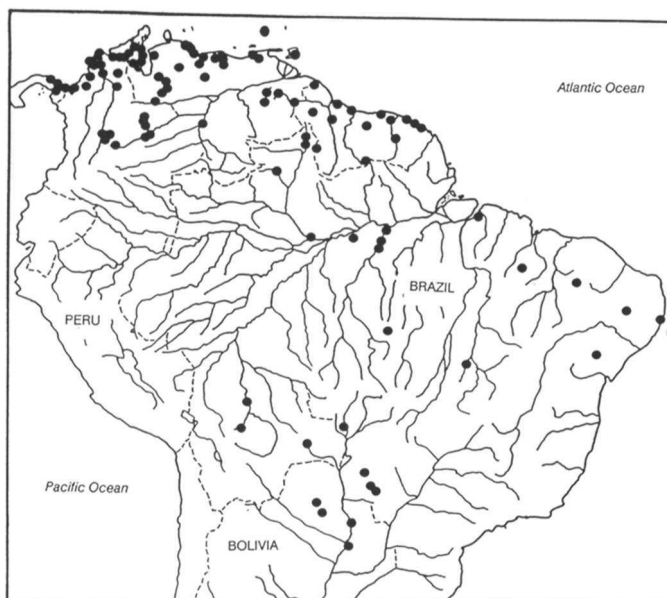


Figure 5. Distribution of *Geochelone carbonaria*.

Williams (1960), Pritchard (1975), and Pritchard and Trebbau (1984) summarize the distribution of *G. carbonaria* as widespread throughout the drier lowlands of northern and central South America, ranging from southern Panama, Colombia, Venezuela, Guyana, Surinam, French Guiana, Brazil, Bolivia, and Paraguay into northern Argentina. It is found on several Caribbean islands, where it was probably introduced as a food source in the seventeenth century (Pritchard and Trebbau 1984). Carrillo de Espinosa and Lamas (1985) describe specimens taken from the Tarapoto region of San Martin Province in Peru. It is not yet possible to determine whether this is an isolated population, an extension of the Bolivian or Brazilian populations, or an introduction resulting from the Manaus-Iquitos trade route. Walker (1987) suggested that a locality record from Nova Olinda in the Brazilian Amazonas, suspected by Pritchard and Trebbau (1984) as incorrect, may actually represent a bridge between the Brazilian and Peruvian populations. For a detailed distributional analysis, with map and locality records, see Pritchard and Trebbau (1984), with additions mapped by Walker (1987).

Habitat and Ecology

G. carbonaria inhabits dry lowlands, preferring grasslands and adjacent dry forest areas. In some localities it is found in rain-forest belts adjoining more open habitats. These rain-forest areas are probably marginal habitats.

The red-footed tortoise is a fully terrestrial, primarily herbivorous species. Moskovits (1985) reports it as eating small

plants, fallen fruits, leaves, flowers, and carrion. Throughout its range, mating appears to be synchronized with the onset of the rainy season. Courtship behaviour consists of sideways jerky head movements by males, described in detail by Auffenberg (1965). Males challenge other tortoises during the breeding season, and rival males will engage in combat, attempting to overturn each other. Up to 15 eggs may be laid in a season (Medem 1962), generally in clutches numbering between 1-5 eggs. They are deposited in a hole dug by the female. Medem et al. (1979) report incubation periods varying from 105-202 days, with a mean of 150 days.

Threats to Survival

The species has a long history of human predation, both for consumption by local Indian populations, and transported live to many South American cities to be sold as delicacy (Pritchard 1975). Such consumption, particularly during Holy Week (tortoise is classed as "fish" by the Catholic Church) is thought to be the greatest threat to this species. While it remains plentiful with densities of over 75 individuals per square kilometre over much of its range (Moskovits 1985; Pritchard and Trebbau 1984) and unlikely to be seriously threatened at the national level, some populations must be significantly depleted. Although *G. carbonaria* can withstand some forms of habitat alteration, even living on agricultural lands (Legler 1963), such infringements into its habitat almost invariably facilitate hunting. There is an international demand for the pet trade which may amount to hundreds of specimens a year. This export pressure cannot be compared with that of human predation and habitat disturbance.

Conservation

At the national level, *G. carbonaria* is likely to fare moderately well in existing national parks and wildlife reserves, as long as adequate patrolling can be provided. However, as tortoise hunting is often seasonal (they are more easily located during the rainy season), or is aimed at the provision of tortoise meat during Holy Week, increased patrolling may be required at these times. Stubbs (1987) reports such a system of wildlife protection, operated in Venezuela by the National Guard, is a relatively economical approach which could be mirrored by reserves in other countries.

Current Research

Few studies have concentrated on this species, most data having been collected as part of broader herpetological projects. Moskovits (1985) is the major exception, providing considerable information on its ecology and behaviour. The Venezuelan

National Guard is attempting to estimate the scale of illegal hunting for tortoise meat and to formulate more effective protection plans. The Fundacion Para La Defensa de la Naturaleza (FUDENA) of Venezuela proposes to conduct a survey of *G. carbonaria*, and to monitor the scale of its trade. Staff at the Museum of Natural History in Lima, as part of their herpetological surveys of the Peruvian Amazonas region, are examining the distribution of the recently discovered population there.

Conclusions

Geochelone carbonaria is thought to be declining throughout much of its range, though is not yet considered "threatened". There is a demand for this species by the international pet trade, but this occurs on an insignificant scale compared with other

forms of exploitation. The major pressure is human predation, which is largely seasonal. Tortoise meat is a delicacy and is classed as "fish" by the Catholic Church, creating a huge demand during Holy Week. In Venezuela, the National Guard has for some time patrolled areas against the illegal collecting of live tortoises for meat, but improved access to some areas has caused a setback to their efforts. They now propose to examine the scale of this trade and to provide additional transport for patrolling activities. Seasonal patrolling against illegal exploitation of this species is more realistic, economical and effective than with many other animals. Unless this exploitation can be at least minimized, even populations within wildlife reserves and national parks remain threatened. With its slow growth to maturity, coupled with a modest reproductive rate, this species will not withstand regular hunting pressure. It is quite probable that it will become "vulnerable" before the turn of the century.

Geochelone chilensis

Chaco Tortoise

Paul Walker

Summary

Geochelone chilensis inhabits the arid Chaco regions of Argentina and Paraguay, where seasonal temperature and rainfall fluctuations are considerable. Typically this habitat consists of desert scrub and dry deciduous woodland. There has been much debate about the partitioning of *G. chilensis* into three species. Most authors now recognize only one species comprised of two subspecies (*G. c. chilensis* and *G. c. donosobarrosi*).

The species is under considerable pressure from the domestic and international pet trade, habitat destruction by agriculture, and to a lesser extent for human food. It is estimated that 75,000 animals are collected for sale each year in Argentina with exports (3,000) amounting to only 5% of this figure. Large areas of its habitat are reported as destroyed each year.

Description and Taxonomy

This is the smallest of the three mainland Neotropical tortoises, reaching a mean adult carapace length of about 200 mm. Its head is proportionately larger than either *G. carbonaria* or *G. denticulata*. The carapacial margins are frequently serrated. The carapace coloration varies from ochre-yellow to clay brown, with darker scute edges. The head and limbs are usually light ochre-yellow. Specimens from dry, sandy areas are lighter in colour than those from wetter clay regions (Auffenberg 1969).

Authors including Bour (1980) have elevated the subgenus *Chelonoidis* to the generic level. Most authors (e.g., Pritchard and Trebbau 1984; Iverson 1986) retain *Geochelone* as the genus, relegating *Chelonoidis* to subgeneric status. Freiberg (1973) described two new species, *G. donosobarrosi* and *G. petersi*, but this subdivision of *G. chilensis* into three species is not widely accepted. Rather, *G. petersi* are considered to be juvenile *G. chilensis*, whereas *G. donosobarrosi* is considered valid only at the subspecific level. However, current work by Richard (in prep.) supports the elevation of *donosobarrosi* to the specific level.

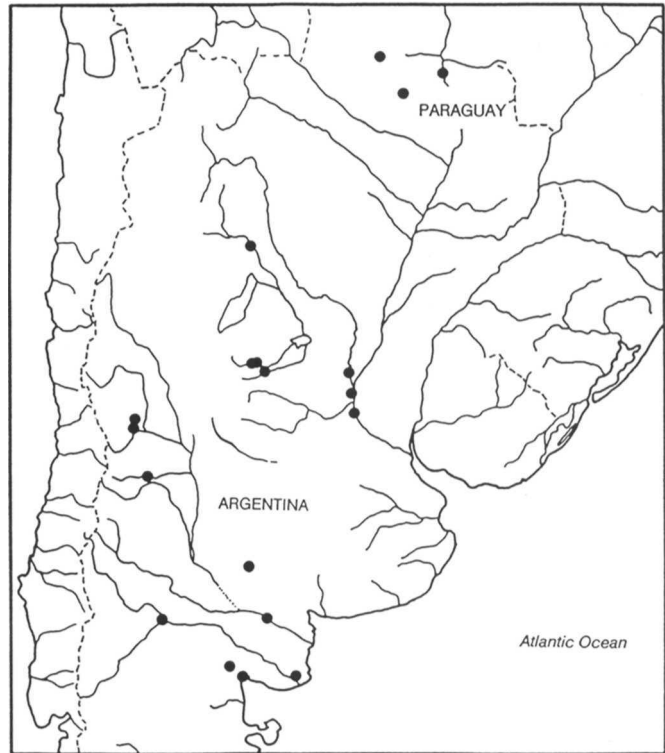


Figure 6. Distribution of *Geochelone chilensis*.

Status and Distribution

G. chilensis is listed in the 1982 IUCN Amphibia-Reptilia Red Data Book (Groombridge 1982) as "Insufficiently Known." Subsequently it has been elevated to "Vulnerable" in the 1988 IUCN Red List of Threatened Animals. This categorization seems more appropriate in light of the most recent studies (Waller 1986, 1987). These Argentinean studies indicate the populations are under significant pressure and may be in dramatic decline. No quantitative data are available for Paraguayan populations, but there appears to be no evidence for a similar decline (Groombridge 1982).

G. chilensis is widespread in the dry lowlands from the Gran Chaco region of Paraguay (and possibly adjacent Bolivia) southward through the Chaco region of north and central Argentina. *G. c. donosbarrosi* is reported from the southern portion of the range, from Mendoza to Rio Negro in Argentina (Freiberg 1973). For detailed analysis of this species range, see Waller (1986).

Habitat and Ecology

The species habitat is typical of the Chaco region consisting of desert scrub and deciduous dry forest (Waller 1986). Seasonal fluctuations in temperature and rainfall are considerable. Tortoises dig shallow pallets in which to spend much of the day and all night (Auffenberg 1969). A deeper pallet is used during cold months, during which tortoises emerge only on the warmest days. Their diet includes fruits of various trees, shrubs, and cacti, as well as cacti pads and grasses. In captivity they take meat, and therefore may take carrion in the wild.

Mating takes place in November and December, the eggs (up to two; typically three egg clutches) are laid in January to March. Incubation may last more than a year (Auffenberg 1969). The eggs of captive specimens in Cordoba Province, Argentina hatched 14-15 months after they were laid (Waller, pers. com.).

Threats to Survival

In Argentina, *G. chilensis* is under heavy threat from habitat destruction and the pet trade (Waller 1986, 1987), and as a human food source in some areas (Richard 1987). Although nominally protected in Argentina, and listed on Appendix II of CITES (trade is permitted if an export permit from the country of origin is provided), the greatest demand is for the Argentinean domestic pet trade. The Chaco tortoise is a popular pet in Argentina, and it is estimated that 75,000 specimens are sold within the country each year, of which 32% die within one year (Waller 1987). Up to an additional 3,000 tortoises are exported annually, the main consumers being Chile, Denmark, Germany, Japan, The Netherlands, U.S.A., and Uruguay. Considerable discrepancies occur between actual sizes of certain exported shipments, compared to the numbers reported to obtain legal documentation (Waller 1987).

Burning of chaco vegetation for conversion to cattle pasture and cropland is destroying the tortoises' habitat by destroying the deciduous trees and shrubs needed for shade. The burning also removes the ground vegetation, enabling tortoises to be

more easily detected. Direct competition for food is reported between tortoises and goats. The tortoises are an easily found food resource for pioneering farmers who are "opening up" the region. Tortoises are most easily captured after rains, and gravid females are preferred (Richard 1987).

Conservation

The Argentinean studies are being conducted as a prelude to developing a conservation management plan. While it is desirable for certain populations (e.g., *G. c. donosbarrosi* in the volcanic region of El Nevado, Mendoza) to receive priority treatment, the rapid agricultural expansion into this species' Argentinean range must be regulated. If not, tortoise numbers will be seriously diminished. This will require establishment and patrolling of reserves to safeguard portions of the Chaco ecosystem. The enforcement of protective legislation is not likely to be effective in areas close to human activities.

It is very desirable for the illegal international pet trade in this species to be reduced, but the internal pet trade and its resulting mortalities are of far greater concern. Surveys of the magnitude and morbidity of tortoise pet trade within Argentina (conducted by the Fundacion Vida Silvestre Argentina) can be seen as a first step in its regulation. International support for an enforced regulatory programme and production of associated educational materials is desirable.

Current Research

The work of Waller (1986, 1987), Grass (1986) and Richard (1987), under the umbrella of the Fundacion Vida Silvestre Argentina, is the most current research, providing considerable data to develop a management plan.

Conclusions

Geochelone chilensis is declining throughout much of its Argentinean range. Habitat destruction and domestic pet trade are the primary pressures. Up to 3,000 individuals may be exported each year, however, this number is small compared to the domestic pet market of 75,000 specimens per year. Undoubtedly, many individuals reach the pet market as a result of increasing agricultural development in the Chaco which diminishes species habitat and facilitates collecting. Conservation efforts should be divided between reducing the domestic pet trade and establishing patrolled reserves.

Geochelone denticulata

Yellow-footed Tortoise, Forest Tortoise

Paul Walker

Summary

Geochelone denticulata is found in the tropical and subtropical wet forests of the Neotropics, from Venezuela to Bolivia. Although rainfall in these forests is often seasonal, the humidity is usually high, and temperatures rarely fluctuate on a month-to-month basis. Described in 1766, the species has always been an important food item for local forest Indians. Hunting pressure is relatively minimal as human densities are low in its habitat, and this species is not easy to hunt on a systematic basis. Habitat destruction is the major threat to this species. However, even with the enormous destruction of Amazonian rain forests fragmenting tortoise populations, the species as a whole is not yet threatened.

Description and Taxonomy

This terrestrial species is larger than the closely related *G. carbonaria*, having a mean adult carapace length of about 400 mm, with records of over 700 mm. Its carapace is dark brown, the scutes gradually lightening towards the centre but without sharp contrast (e.g., areolae) as in *G. carbonaria*. It also differs from *G. carbonaria* in not having mid-body constriction. The larger scales on its limbs are yellow-orange rather than red.

The elevation of the subgenus *Chelonoidis* to generic status (Bour 1980) has not been widely accepted, most authors retaining *Geochelone*. Auffenberg (1971) concludes that *G. carbonaria* and *denticulata* share a common ancestry, diverging from the other South American tortoise lineage (represented by the extant *G. chilensis* and *elephantopus*) in the Oligocene.

Geographic variation is less marked than in *G. carbonaria* with variations in colour ranging from light to dark brown shell coloration not correlated with habitat or geography (Pritchard and Trebbau 1984).

Status and Distribution

The species is not listed in either the 1992 *IUCN Amphibia—Reptilia Red Data Book* or the 1988 *IUCN Red List of Threatened Animals*. Its omission from these lists indicate it is not

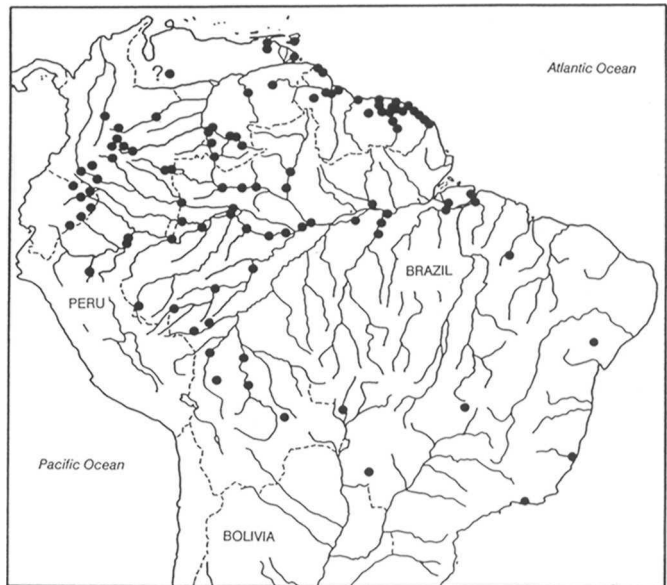


Figure 7. Distribution of *Geochelone denticulata*.

considered a threatened species. However it is listed on Appendix II of CITES, permitting international trade only if export permits from the country of origin are obtained. The species is nominally protected by national legislation throughout much of its range.

G. denticulata ranges over a large part of northern South America including north and western Brazil, northeastern Bolivia, Amazonian Ecuador and Peru, Guyana, Surinam, and French Guiana, as well as southern Colombia and Venezuela. Historically it occurred in the Atlantic forest belt of eastern Brazil, but it is now considered extirpated by hunting in the remaining fragmented forest (Pritchard and Trebbau 1984). *G. denticulata* also occurs on Trinidad where the population is considered indigenous, in contrast to Guadeloupe, where it is thought to have been introduced from French Guiana. For a detailed analysis of distribution including with maps and locality records, see Pritchard and Trebbau (1984).

Habitat and Ecology

The habitat range of *G. denticulata* is typically Amazonian tropical and subtropical wet forest. It is restricted to humid forests, sympatric (syntopic) with *G. carbonaria* only in moist forests adjoining grassland savannas. *G. denticulata* is mainly herbivorous, and its diet includes leaves, flowers, fruit, and fungi, although carrion is taken when available (Moskovits 1985; Moralez 1985 pers. comm.). Heavy tick infestations have been reported in some populations (Moskovits 1985), but in a Peruvian population, tick parasitism, though endemic, was not heavy.

In the subtropical wet forests of eastern Peru, the species is markedly seasonal in its activity patterns. There, it is more readily encountered in the wet season (Moralez 1985 pers. comm.). Peruvian Indians report that tortoises lay eggs in late January and February, towards the end of the wet season. The eggs hatch in August before the onset of the following rainy season. This seasonality of reproductive activity may be less pronounced in forests lacking a seasonal climate (Pritchard and Trebbau 1984).

Auffenberg (1965) studied the courtship behaviour of both *Geochelone carbonaria* and *G. denticulata*, and found the "challenge" head movements of males to differ. *G. denticulata* moves its head in single sideways sweeps as opposed to *G. carbonaria*, which moves in a series of lateral jerks. Although large clutch sizes have been reported, the usual number ranges from 1-8 eggs with 4-5 eggs being the most frequent. Occasionally eggs are laid directly upon the forest floor, but usually are at least partially buried in a shallow scrape. Incubation is reported to take from 125 to 150 days.

Threats to Survival

G. denticulata is considered a delicacy and is hunted by forest Indians. However, its inaccessible habitat limits its availability to urban markets, in marked contrast to *G. carbonaria* which is consumed in large numbers. In the small village of Infierno located in southeastern Peru, tortoises are collected when encountered in the forest. During the rainy season, they are collected at an average rate of 6-7 per month, and kept alive until eaten. Until recently (within the last decade), aquatic turtles were eaten in large numbers. As turtles have been depleted through overhunting in nearby rivers and lakes, tortoises now make up more of the villagers' diet. Tortoises are believed to have medicinal properties, the burnt shell being used against a variety of ailments (Walker 1987).

G. denticulata are kept as pets throughout much of their range, primarily in rural areas. On a larger scale, the carapace is used as a musical instrument, being incorporated into a soundbox for small "banjos". These instruments are sold throughout this species' range, especially in Peru and Ecuador. However, these combined pressures are still far less than those upon *G. carbonaria*, largely because *G. denticulata* habitat provides more cover and human densities are low. Human

encroachment into its habitat is undoubtedly the greatest threat to this species. Unlike *G. carbonaria*, it cannot tolerate significant habitat degradation. The combined assaults of logging, agriculture and oil exploration throughout much of Amazonian South America are fragmenting the species into smaller populations.

Conservation

Although *G. denticulata* is encountering considerable habitat fragmentation and reduction, the species is not yet threatened. The large sections of rain forest protected as national parks, reserves, and wildlife sanctuaries are ensuring the species' survival. Large-scale poaching is difficult, as the tortoises are well concealed in their forested habitat. This contrasts with *G. carbonaria*, which is more vulnerable in its open grassland habitat.

The enforcement of international trade legislation (the species is listed on Appendix II of CITES), with particular emphasis on the sale of carapace souvenirs to tourists, should be increased both in the countries of origin, and in main international airports with flights to South America.

Current Research

The Venezuelan National Guard is attempting to survey the extent of illegal hunting of both *G. denticulata* and *G. carbonaria*, as a prelude to the formulation of more extensive protection plans within national parks. The Venezuelan organization, FUDENA, proposes to conduct a similar species survey to monitor trade in tortoises. A detailed study on the effect of timber extraction from tortoise habitat would be valuable. To date no such study has been initiated. A market study of the sales of tortoise shell banjos in Peru and Ecuador is needed, determining numbers sold to tourists, who unknowingly breach CITES regulations by taking them home.

Conclusions

Although *G. denticulata* is a locally important food item for forest Indians throughout much of its range, the inaccessibility of its habitat prevents large-scale shipment to cities for consumption. This is in contrast to *G. carbonaria*, which is consumed in large numbers during Holy Week. Additionally, the dense cover of its habitat offers considerable protection against over-collection by local peoples. Habitat destruction is the major threat to this species. The combined effects of agriculture, logging, and oil exploration fragment and restrict tortoise habitat. Despite these impacts, as a whole, the species is not threatened. It is probably the most abundant of the three mainland South American tortoises. Conservation efforts to protect this species are best served by expanding wildlife reserves and national parks. Where significant tracts of forest remain, the species is likely to fare moderately well.

Geochelone elephantopus Galapagos Giant Tortoise

Ian R. Swingland

Summary

Eleven of the thirteen accepted races still survive in Ecuador's Galapagos Archipelago, but the island populations are much reduced from 17th century historical reports. Large populations since have been decimated by whalers and naval ships for provisions. Introduction of domestic pests and livestock, which excavate nests, destroy nesting grounds, eat hatchlings, and successfully compete for food, was especially prevalent in the 19th century. Moreover, the numbers of feral mammals have dramatically influenced the vegetational structure and effectively interfered with the tortoises' ecology and behaviour.

Reproduction and recruitment in the wild has either stopped or continues at a very reduced level. A moderately successful captive breeding, rearing, and restocking programme was started nearly 20 years ago at the Charles Darwin Research Station (CDRS). The entire populations of *hoodensis* and *abingdoni* have been removed to CDRS to secure a future for the races, but *abingdoni* has only one male left alive ("Lonesome George") which is unlikely to breed, so the race will ultimately go extinct. Feral mammal control programmes continue with mixed success. The tortoises are strictly protected in Ecuador, which declared the Galapagos Archipelago a National Park in 1959. They are listed on Appendix 1 of CITES.

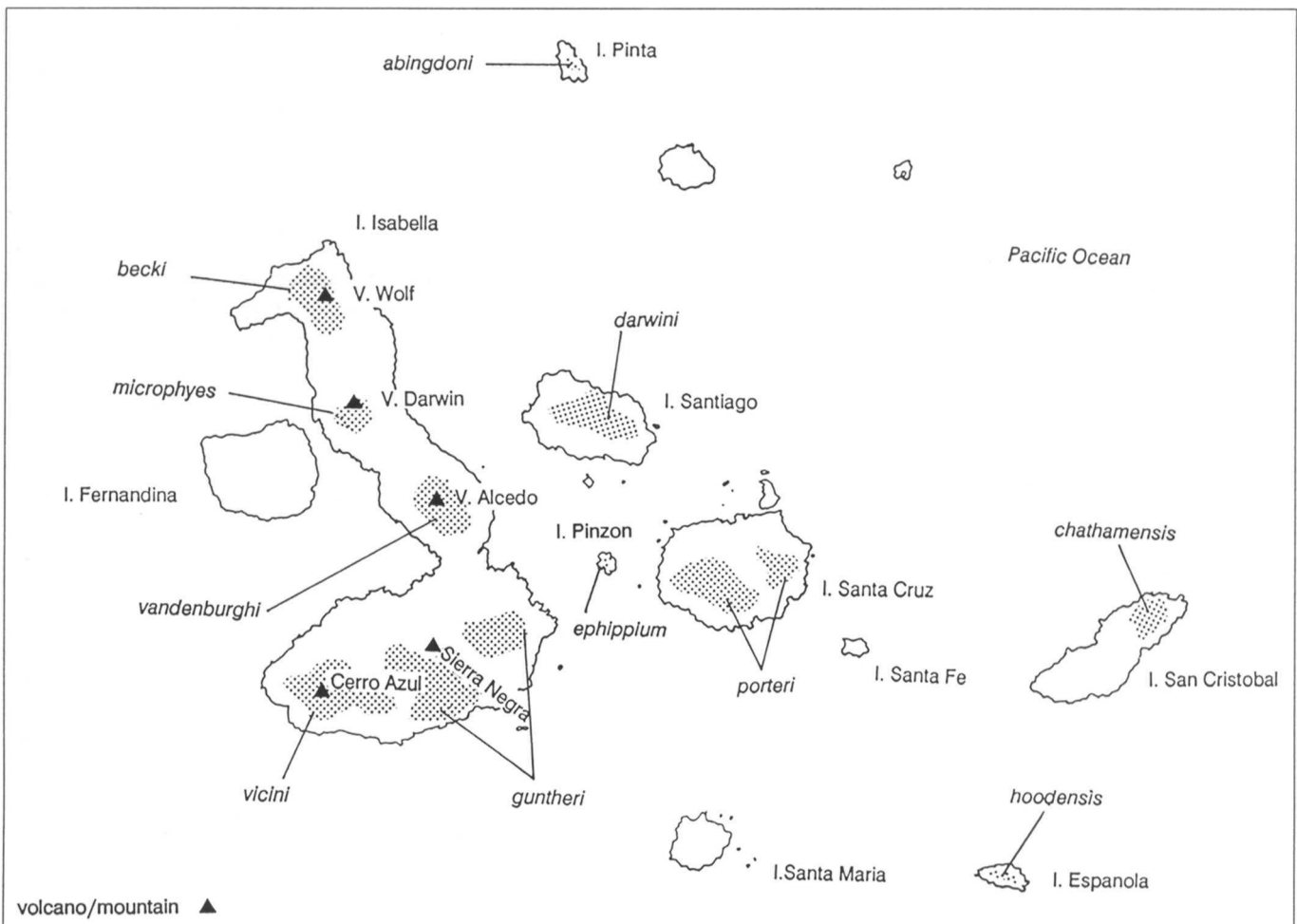


Figure 8. Distribution of *Geochelone elephantopus*.

Distribution

The entire species is restricted to the Galapagos Archipelago, Ecuador (See Fig. 8).

Population

The overall situation is reviewed in Table 1. Much of the data derives from MacFarland et al. (1974) and Groombridge (1982).

Table 1. Galapagos tortoise subspecies distribution, population sizes, and threats.

Subspecies	Location	Threats	Status
Living			
<i>abingdoni</i>	Pinta	G	1 male
<i>becki</i>	Volcan Wolf	r,c	2000
<i>chathamensis</i>	NE S.Cristobal	D,b	5-700
<i>darwini</i>	Santiago	p,g	5-700
<i>ephippium</i>	Pinzon	R	150-200
<i>guntheri</i>	E Sierra Negra	g	2-300
	S Sierra Negra	P,d,c	100
	W Sierra Negra	c	100
<i>hoodensis</i>	Espanola	G	20-30
<i>microphyes</i>	Volcan Darwin	r,c	500-1000
<i>porteri</i>	SW Santa Cruz	P,c,g	2-3000
	E Santa Cruz	P,c,g	50-100
<i>vandenburghi</i>	Volcan Alcedo	b,r	5000
<i>vicina</i>	Cerro Azul	P,D,C	4-600
Extinct			
<i>galapagoensis</i>	Floreana	-	0
<i>chathamensis</i>	SW S. Cristobal	-	0
Doubtful if Ever Existed			
<i>phantastica</i>	Fernandina	volcanic	-
unnamed	Santa Fe	-	-
<i>wallacei</i>	Rabida	-	-

Threats past or present: p=pigs, c=cats, d=dogs, g=goats, b=burro or donkey, r=rodents and black rats; upper case indicates a major threat. Some islands have had the larger feral mammals eradicated.

From I. Pinta, a single male *abingdoni* called Lonesome George is left alive (discovered November 1971) and has been kept at the Charles Darwin Research Station since 1972. Others of the subspecies probably exist in zoological parks or even on the island (two dead animals and signs of more living individuals were found in 1971); a tortoise dropping was found on Pinta ten years after the male was removed.

The known living specimens of *hoodensis* (3 males and 12 females) from I. Espanola are all at CDRS, as the population had been almost extirpated by over-collecting and competition with feral goats, and during the 1950s and 1960s, little if any copulation or reproduction was observed (Hendrickson and Weber 1964). By 1982, 113 young had been returned to Espanola (Reynolds 1982) and the goats eradicated.

The populations on I. Pinzon, I. San Cristobal, I. Santiago, and I. Isabella (Cerro Azul and Sierra Negra) have all been affected by predators and herbivores, and consist of adults with very few young, although reproduction still occurs. Rats and other mammals are decimating recruitment

Though *ephippium* was extinct on I. Pinzon by the 1920s (Beebe 1924) because of black rats (which are almost 100% efficient in killing hatchlings), a small population of 120 old individuals survives. A head-starting programme has been carried out since 1965, which had returned 226 young by 1985 (Tierney 1985), although some were released too young and killed by rats (Moore 1979). Van Denburgh (1914) described a now-extinct population of *chathamensis* on I. San Cristobal but another population exists in the dry northeast. Feral dogs threatened this population, but a dog control programme using canicides may have successfully eliminated them. A head-starting programme has released over 139 young tortoises back into the population.

The density of goats and pigs on I. Santiago (*darwini*) is startling, and although reproduction occurs, the number of young found is insufficient to maintain recruitment. Large, old males occupy the highlands, which are now cut off from the lowlands by goat-induced vegetation modifications. Subadults and adults are mainly found on lower slopes in the south and southeast, quite separate from the main goat concentrations in the northwest.

Five races live around the volcanic peaks on I. Isabella. The slopes of south and west Volcan Sierra Negra (*guntheri*) support about 100-200 tortoises that survive after the depredations of culling, habitat alteration, and feral mammals, particularly dogs. The area is agriculturally fertile, and the existing population is divided into two groups by the settlement, with only the eastern one near Cerro Ballena (200-300 animals) reproducing freely. The Cerro Azul population (*vicini*) has as many as 700 individuals covering the volcano's eastern lowlands to the summit (1,700 m) but they are menaced by feral mammals, especially dogs and pigs. A conservation head-starting programme has been removing eggs from this population to CDRS, and by 1979, 114 four-year-olds had been returned. The once-large Iguana Cove population had been expunged by cattle company employees during the 1950s and 1960s (Pritchard, pers. comm.). The small population (probably <300) in the lowlands of southern Isabella near Cabo Rosa has not been surveyed. The Volcan Wolf population (*becki*) is 1,000-2,000 but is probably nearer 1,000. Cats are the only feral species found here, and young tortoises are found fairly frequently. Volcan Darwin (*microphyes*) has a population of 500-1,000 with a high proportion of young, cats being the only feral species. Volcan Alcedo (*vandenburghi*) has the largest population of tortoises 3,000-5,000 which appears to be reproducing. Feral donkeys tend to roll on the nest sites and destroy eggs, but the drought of 1984-85 decimated the donkey population, which if not followed by an eradication programme will result in their resurgence. The status of these populations is less certain but the prognosis appears good, since few feral animals, settlers, or fishermen are present.

A single specimen of *phantastica* was collected from Fernandina by Beck in the early part of the century, and Hendrickson, using a helicopter, found a large dropping and tortoise bitemarks in an *Opuntia* cactus (Hendrickson 1966). Although both of these clues could remain intact for many years, a few individuals may remain alive. Since the subspecies is distinct and not a transplant from elsewhere, and since there are no human activities on this island, the reason for its apparent demise is unknown. No feral animals exist. Fernandina is volcanically active (e.g., a major drop in the volcano floor of 0.6 cubic mile was observed by Skylab), and such activity may have destroyed the limited nesting areas or cut them off from feeding areas. The land iguanas (*Conolophus subcristatus*) mainly nest in the volcano floor, which is inaccessible to tortoises.

In southwest I. Santa Cruz, *porteri* (2,000-3,000) suffers from poaching and predation on their nests and young. The population has large numbers of young, although they are probably insufficient to sustain a stable population (MacFarland et al. 1974). Feral dogs and pigs prey on the eggs and young, but reproduction in the wild still occurs. The relict eastern population (50-100) is so small as to be virtually doomed from occasional poachers.

Extinct by about 1840, *galapagoensis* was already hard to find by the time of Darwin's visit to I. Floreana in 1835. Darwin did not see any live specimens. Steadman (1986) reports a tortoise scute on I. Floreana 310±B.P., and it was considered extinct on this island by 1850 (Broom 1929).

The extreme arborescent form of the *Opuntia* cactus suggests that a substantial tortoise population once existed on I. Santa Fe, but Beck (Van Denburgh 1914) only found fragments of 14 individuals, some old eggs, and old dung. Tortoises had been temporarily placed here by man, and hunting is unlikely to have removed all the living specimens. Feral goats used to be here in large numbers but feral predators have never been found.

Habitat and Ecology

This is a large species weighing up to 263 kg and attaining 134 cm length. Darwin alluded to the different shell shapes on the various islands of the archipelago when formulating his theory of natural selection.

Clutch size reported by Beck (1902) was 8-17. By dissecting several *guntheri* he estimated the interclutch interval was one to two weeks. Dissection revealed 10-20 shelled eggs ready for laying, with an additional 20-30 more of 50-75% of final size (presumably pre-ovulatory follicles). Females found in a nesting area contained 10-14 hard eggs (Porter 1815). Average egg mass varies from 157 gm for the larger races like *darwini* to 82 gm for the smallest races such as *hoodensis*.

Clutch sizes vary between females and populations, and also vary from year to year. The average clutch sizes of *porteri* (9.6) and *ephippium* (4.6) differ greatly within and between years, as do clutch sizes of *G. gigantea* on Malabar and Grande Terre (Aldabra). Over a six year period the mean clutch sizes of these two Galapagos subspecies were not significantly different from

each other. Over 95% of clutch size variance was due to variation within, not between, years (MacFarland, pers. comm.). He tested the hypothesis that mean clutch size and total rainfall were correlated during the five month hot season prior to nesting. He theorized that the rainfall would affect available forage and thus clutch size, but found no significant correlations ($r=0.02$ and $r=0.03$ for *ephippium* and *porteri* respectively). Significant variance in clutch sizes were found between *gigantea* populations of differing densities, as well as between years of differing rainfall in the high density population on Grande Terre, but not in the low density populations. More rain results in more food and greater reproductive output (Swingland and Coe 1979). This species had environmental sex determination and lacks heteromorphic chromosomes.

Large Galapagos subspecies live on large or elevated islands (>800 m) with lush highland vegetation and xerophytic lowlands; small subspecies live on small, generally dry, low islands (<500 m) with little vegetational variation. During the regular garua (misty, cold rain characteristic of the Galapagos) season (June to December), fine rain falls mainly in the highlands of elevated islands, while little rain falls on the lower islands or on the low coastal plains of the elevated islands. During the hot season (January to May) rainfall is highly irregular, ranging from none in 1977, drying out the vegetation (Grant 1986), to torrents in 1982-83 producing lush vegetation everywhere. On average, in a five year cycle, one year has a dry season (<80 mm rainfall) for five months, one year is wet (>450 mm rainfall), and the remaining three years are intermediate (MacFarland, pers. comm.). In most years the rainfall is concentrated in a few weeks or into two widely spaced periods. On the larger islands these extremes are buffered by altitude, rainshadows, cloud cover, soil type, and depth, but on the lower islands food becomes severely limited for tortoises in dry hot seasons. Older tortoises spend most of the year at higher altitudes where food and water is most plentiful. During the nesting season, females migrate down the slopes from the high, lush feeding areas to the nesting grounds.

Generally, the larger races are dome-shaped, living in lush habitats where there are ample grazing opportunities, while the smaller races are saddle-backed, inhabit dry areas, and are predominantly browsers. On some larger, elevated islands where rainshadow leaves one side dry and the other wet, tortoises of differing shapes can be found.

Insular gigantism and dwarfism have been hotly debated for a long time. Without doubt, the occurrence of gigantism in tortoises is the result of ecological factors. Case (in litt.) gave several possible reasons for large body size in insular endemics, including food availability, predation, and socio-sexual factors. For island species, the absence of competing mammalian herbivores, intraspecific competition for food during the frequent droughts that occurred over evolutionary time, and the increased tendency to store energy in response to food supply fluctuations might select for an increase in size. Certainly Arnold (1979) felt this was the case for Indian Ocean species, and it concurs with Case's own view (in litt.). The preservation of gigantism once evolved was possible on uninhabited islands,

but mainland giant species were quickly extinguished by man (e.g., during the Pleistocene in North and South America).

Selection for large dominant males possessing large territories and mating with more females than smaller tortoises was proposed as another possible explanation for island gigantism. There is no evidence for this. Additionally, there would be selection for females to be large also, as large females have a greater annual reproductive output than smaller ones. There is evidence that larger males do not mate with more females than small males, nor that large males mate with larger, more fecund females (Swingland and Stubbs 1985), and there is still the question of why this phenomenon should occur exclusively on islands. Male *elephantopus* compete by rearing their heads up and whichever reaches the highest "wins" (Fritts 1983; Schafer and Krekorian 1983) but it is the males with the greatest reach, not the largest males, that succeed. The saddleback types often have a greater reach than the domed subspecies, yet a much smaller body. Indeed, the early explorers often remarked on the "snake-like" and scrawny neck of the smaller saddlebacks. Perhaps this long neck evolved to compensate for the smaller body size where both types are sympatric.

While some authors thought tortoises were deaf (Darwin 1845; Heller 1903), it was demonstrated both physiologically and behaviorally that they could hear (Van Denburgh 1914).

Tortoises give every appearance of "sleeping" during inactive periods of the day. During the midday heat on Volcan Alcedo, Galapagos tortoises sleep in the open, with head and limbs extended. During the cool evening they can be found asleep in forms with their head and limbs retracted (Hayes, pers. comm.). Similarly, the Aldabran species will sleep at night in the open with limbs and neck sprawled on the ground, and while shading during the midday heat, they will sleep in a similar fashion. This behaviour has been examined electrophysiologically in turtles (review by Granda and Maxwell 1978), but in laboratory confined *G. denticulata* there was no evidence of this behaviour. Close observation of tortoises convinces me that testudinids do sleep and that further field work would confirm this.

Ancient accounts of mating in giant tortoises are redolent with humour. In the Galapagos during the breeding season, males utter a hoarse roar or bellow while copulating; males "bellow like bulls" (Porter 1815) but more correctly they emit a "low prolonged note" (Heller 1903), which can be heard from some distance, e.g., "300 yards" (Beck 1902).

Apart from male tortoises, which vocalize during mating, and vocalizations made by both sexes during agonistic encounters, no other sounds are produced by the Testudinidae except the usual exhalations of air (in the form of hisses or groans) associated with withdrawal into the carapace. The "groan-thrusting" described by Frazier (1973) for male Aldabran tortoises can be heard from up to 2 km away (depending on circumstances), probably the loudest noise any reptile makes. A similar yet quieter noise is made by the Galapagos tortoise. In all species of tortoise, rhythmical groans or squeaks are made by the copulating male, the frequency and intensity being determined by body size with large species giving vent to lower, louder noises.

The mating calls of Aldabran tortoises are less prolonged than those of the Galapagos species. This may result from the much greater size of the latter species. In my view, it is merely the physical exertions of copulation which cause this exhalation. The rhythmical withdrawal of the limbs partly or completely into the body cavity (which has a finite volume within the shell's rigid constraint) produces the vocalizations we associate with copulation in Testudinidae. Frazier and Peters (1981) defends the proposition that the groaning is not merely an accident of the male's physical efforts but a means of intimidating a female by "bellowing in her face from a few centimeters away," thereby dissuading her from moving. He also suggested that it could be a means of communication, and that a female might be persuaded to cooperate actively using this call by raising her rear end, making intromission easier. Not only is there no evidence for this, but elevating her posterior would actually make intromission more difficult to achieve since the male's rear legs would have to stretch even further for the necessary thrusting. Jackson and Awbrey (1978) reported that the mating calls of male *elephantopus* are low frequency (<0.8kHz) but high intensity, while Campbell and Evans (1972) demonstrated the calls of smaller species (e.g., *carbonaria* and *travancorica*) are higher frequency (>5kHz) and lower intensity. The copulatory calls of *gigantea* begin before intromission and are accompanied by periodic thrusting motions. These consist of lifting the hindlimbs off the ground (or bending them) causing his body to slide down the females back, and with the tension in the forelimbs holding him to her, a rocking motion results. Frazier and Peters (1981) analyzed the calls of male *gigantea* in the wild and confirmed that pitch is related to body size, and that call rate may be temperature dependent as it is in other reptiles and amphibians.

In the Galapagos, well-defined trails to the waterholes or springs are used frequently (Porter 1815) throughout the year, particularly during seasonal migrations between the coast and upland areas. Like the Aldabran species, this species has defined and traditional movement patterns. The water sources are found in the central highlands of the larger islands, and the trails stretch to the coast. Some individuals used rocky basins which collected rainfall and to which numerous trails led (e.g., at Vilamil, Beck 1902).

Galapagos tortoises drink through their mouths and take on large quantities of water, spending several days in the vicinity before leaving. After such a visit their bladders are full, and local inhabitants, overcome with thirst when in the coastal regions, would drink this fluid, which has a slightly bitter taste. Apparently, however, the water at the "root of the neck," presumably from the pericardium, was preferable (Porter 1815). As much as two gallons could be obtained in this manner without killing the animal simply by nicking the "bulge". I can personally confirm that the same holds true for the Aldabran species.

In the Galapagos, where sources of fresh water are frequently absent and rainfall scant on the lower islands, nasal drinking has not evolved as on Aldabra. The substrate is not the highly permeable Aldabran limestone, but impervious granite.

Rainfall and early morning dew collect in rock depressions, remaining for sometime. These depressions can easily be licked out by tortoises, and on the more xerophytic, desert-like islands, certain boulders have been licked clean of their normal lichen coverings. These boulders have half-sphere depressions on their surfaces caused by centuries of use by tortoises drinking the collected morning dew.

Most *elephantopus* frequented the damp upper slopes, eating a wide selection of leaves, berries, and green filamentous lichen (*Usneaplicata*) that hangs from the trees (Darwin 1845) and *Opuntia* pads provided water. Heller (1903) found their diet during the rainy season consisted of grass and woody perennials; during dry periods, *Opuntia* was an important food source. He found one specimen on Tagus Cove with spines sticking through its palate and pharynx. The *Opuntia* spines penetrate deeply, and unless dislodged, eventually come to lie along the muscle fibres.

Tortoises exhibit a variety of responses to the approach of intruders or potential predators, including fleeing, species-specific defence posture, biting, hissing, flailing of limbs, release of glandular or excretory secretions, vocalization, burrowing into the substrate, hiding, and wedging into burrows or crevices. In predator-free insular environments, fearlessness is common in chelonia. Observations on *elephantopus* following a suggestion by Arnold (1979) suggested that the loss, reduction, or modification of antipredator devices was a key event leading to the development of morphological features, especially gigantism, characteristic of island tortoises. Studies of *G. e. vandenberghi* described withdrawal of limbs and neck on the approach of an observer, and raising of the rear when the anterior part of the carapace was tapped (and lowered when the posterior part was touched). These defence postures have also been seen in *Geochelone gigantea*, *G. pardalis*, and *Gopherus agassizii*. Head bobbing often occurred after this behaviour. The distance at which withdrawal occurs appears independent of the animal's body size and age, although frequency of disturbance by man may increase this distance. While man has preyed on tortoises for centuries, particularly the oceanic giant species, there is no *a priori* reason to believe that the defence behaviour of tortoises arose as a result. Rather, this behaviour was probably inherent in the colonizing stock which arrived on the archipelago 1-2 million years ago (Wyles and Saeich 1983). Baur (1889) reports visitors in 1707 remarking that Galapagos tortoises withdraw their extremities when approached. Such behaviour may have arisen through competition, agonistic interactions, defence against threat (approaching fire causes *Testudo hermanni* and *T. graeca* to burrow head-first, posterior up) or the presence of mammalian predators, which are probably responsible for the extinction of Testudinidae in many areas of their former distribution.

Threats to Survival

Predators have the greatest impact on populations of tortoises. Pigs destroy the majority of nests and kill large numbers of young (>35 cm curved length or >4-6 years old). Dogs are able to kill larger animals than pigs (>55 cm curved length or >10

years old), and they excavate nests as well. Cats and rats are able to eat hatchlings (1-2 years old) by biting straight through the soft shell, but they do not destroy nests. On different islands, exotic species have differing effects; dogs on I. San Cristobal dig up nests but not on Cerro Azul or Sierra Negra; on I. Pinzon (very dry), the black rats kill virtually all hatchlings but nowhere else, since the rats appear concentrated in the humid highlands but not in the dry nesting zones. On Aldabra, the brown rats appear to have only limited effects on hatchlings.

Feral herbivores (goats, and to a lesser extent, donkeys and cattle) in the drier areas of the elevated islands and on the less elevated islands devastate the vegetation even in dry years and leave little for young to eat. Young tortoises only start to migrate to the higher ground from the coastal nesting areas (which are in these drier zones) when they are 10-15 years old; thus on I. Pinta, I. Espanola, northeast I. San Cristobal, and the dry parts of I. Isabella, I. Santa Cruz, and I. Santiago, they must face severe competition for food. Older animals spend most of their time in the moist and productive highlands and can circumvent direct competition with the feral competitors.

Fishermen poach young tortoises for the international pet trade (MacFarland et al. 1974) and have reintroduced or introduced feral animals, particularly goats. Young tortoises were offered for sale by local dealers and a Swiss dealer was selling them for DM 1,800-2,000 each. The latter acquired stock from a local dealer (now operating from Colombia) whose partner's son was stationed in the Galapagos (Kramer 14/2/77). The expanding communities of settlers slaughter tortoises on Santa Cruz and eastern Sierra Negra and clear more virgin land for agriculture.

Conservation Measures Taken

Legislation in 1959, 1969, 1970, and 1971 in Ecuador and the U.S.A. prohibit the taking, export, import, or trade in this species. Nest protection is carried out in the field; eggs were removed to CDRS for hatching and rearing; CDRS also has all the known adults of *hoodensis* as a breeding reservoir for restocking purposes, and *vicini*, *darwini*, and *ephippium* are also bred for restocking. The rearing programme has been recently enhanced by using environmental sex determination techniques. Feral mammal shooting programmes continue, some islands being cleared of goats, and a pilot dog eradication programme using canicides has been implemented. In captive collections, *becki* at Zurich, *guntheri* at Sydney, and *porteri* are bred. All together the breeding programmes, especially from CDRS, have probably restocked the wild populations by some 3,500 animals.

Current Research

Continuing programmes support the conservation effort in the Galapagos and research efforts being continually directed at improving the success of control methods against depredations of the animals in the wild. A re-evaluation of the effectiveness of these long-term projects is urgently needed by surveying the current population structure and distribution.

Regional Introduction

David Stubbs

Formerly the genus *Testudo* was used inclusively for all tortoises, but now it is restricted to five species. A sixth, *Testudo zarudnyi*, was published in March 1989 (*Journal of Chelonian Herpetology*, 1). The genus is separated from *Geochelone* by the presence of supranasal scales, a nuchal scute, a prootic generally concealed dorsally by the parietals, and a hind plastral lobe that is often slightly movable (Pritchard, in Harless and Morlock 1979). The smallest species, *T. kleinmanni*, is allocated to a separate subgenus *Pseudotestudo* because the maxilla is unridged and the quadrate does not enclose the stapes (Loveridge and Williams 1957). *T. horsfieldi* is also somewhat divergent and was recently placed in the revived genus *Argri-onemys* (Mlynarski 1966), but was relegated to subgeneric status (Auffenberg 1974).

No single geographical or ecological area adequately describes the range of the genus *Testudo*. Mediterranean is most appropriate for the majority of species and subspecies, but it does not include populations of *T. graeca* and *T. horsfieldi* found further east in Asia. If some licence is taken with the eastern boundaries of the Western Palaearctic biogeographic realm (i.e., to include southern USSR, Iran, Afghanistan, and northwestern Pakistan), *Testudo* could be considered a Western Palaearctic genus. The IUCN/SSC Tortoises and Freshwater Turtles—An Action Plan for their Conservation (IUCN 1989) takes this approach. Within this realm the only land tortoises are the five species of the genus *Testudo*.

Naturally occurring populations are not found in the Atlantic climatic regions of northwestern Europe, although numerous individuals survive in the wild for some years following escape from captivity. The range of each species appears to be limited chiefly by climatic factors, temperature and amount of sunshine being most important.

Although in global terms the *Testudo* are distributed over a relatively small area, they occupy several contrasting bioclimatic types; Mediterranean (*T. hermanni*, *T. marginata*, and some races of *T. graeca*), desert (*T. kleinmanni*) and semidesert and steppes (*T. horsfieldi*). Within these areas individual species occupy widely differing habitats, including coastal dunes, garigue, riparian vegetation, farmland and dense evergreen oak and pine forests. In general, Mediterranean species

occupy habitats which have been impacted and managed by man for thousands of years, resulting in the degradation of most of the original evergreen forest cover. Tortoises appear to be strongly dependent on the maintenance of traditional land management in this region.

All species and subspecies appear to be declining in numbers because of widespread habitat destruction and fragmentation, and from the long-term effects of large scale collecting for the pet trade. Many local populations are no longer viable. The natural, low density population structure of these species can only be maintained in unfragmented, extensive habitat units. Some habitats support large concentrations of tortoises (>10 per ha) but such sites are becoming increasingly scarce in Europe due to development pressures, particularly at coastal sites. Field densities of eastern races and species are not well-known, but the prevailing harsh, arid conditions over much of the eastern part of the region may preclude high densities. *T. hermanni*, *T. kleinmanni* and *T. graeca* are listed as "Vulnerable" in the IUCN Red Data Book (Groombridge 1982).

Conservation legislation has been introduced at a number of levels to help protect *Testudo* sp., although implementation and enforcement efforts are frequently lacking. On an international level, each species is listed on Appendix II of CITES, and the European species (*T. hermanni*, *T. graeca*, and *T. marginata*) are covered by an EEC-wide trade ban (as of 1/1/84) and are listed on Appendix II of the 1979 Bern Convention on the Conservation of European Wildlife and Natural Habitats. Illegal collecting and trading is still widespread, but on a much reduced scale compared to the mass exploitations prior to these regulations.

The Mediterranean *Testudo* species have received considerable attention from ecologists and herpetologists. The distribution and status of *T. hermanni* is as well known as that of any tortoise species. Conservation efforts have focused on the more western sections of the generic range, principally because of proximity to major human population centres. The more sparsely populated and remote eastern sections, where *T. horsfieldi* and races of *T. graeca* occur, are less well-known, and planning for their conservation is therefore all the more difficult.

Within the Mediterranean area, a number of important research and practical conservation initiatives have taken place during the 1980s, the most notable being the formation of La Station d'Observation et de Protection des Tortues des Maures (SOPTOM) in southern France, and the establishment there of "Le Village des Tortues", a conservation/visitor centre dedicated to the protection of the last remaining Hermann's tortoise population in mainland France. This project has attracted widespread publicity and interest, and is developing techniques which can be applied to other tortoise conservation problems. Significant projects are developing in Italy and Spain and potentially in Corsica and Greece. There is also an ongoing

project involving the repatriation of tortoises from Czechoslovakia to Dalmatia in Yugoslavia, which is attracting much local publicity. However, there appears to be no control over the origin of the released animals, and the effectiveness and ultimate desirability of such an operation must be questioned.

Coordination at a European level to embrace current and proposed tortoise conservation projects is strongly recommended. This could be sponsored through an IUCN/SSC Tortoise and Freshwater Turtle Specialist Group subcommittee, in concert with the Conservation Committee of the Societas Europaea Herpetologica (which now acts as the IUCN/SSC European Reptile and Amphibian Specialist Group).

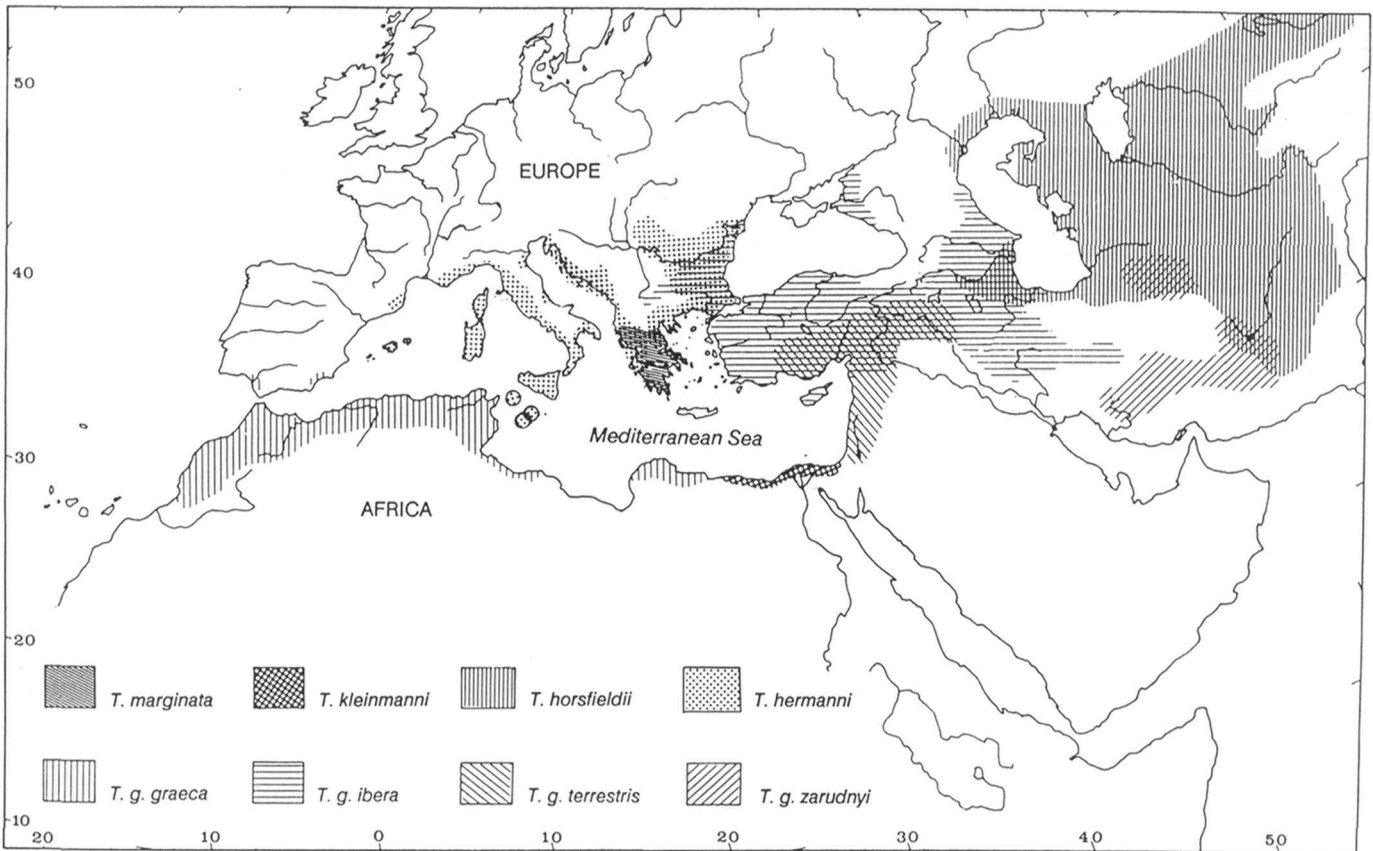


Figure 9. Distribution of genus *Testudo*.

Testudo graeca

Spur-thighed Tortoise

David Stubbs

Description

T. graeca

This species varies in size across its geographical range, with western populations smaller than the larger eastern races. Coloration and patterning vary, even within races and are not reliable for identification. Reliable distinguishing features are an undivided supracaudal, absence of horny terminal tail scale, a flat to subconical horny tubercle or "spur" on the inside hind part each thigh, enlarged scales on the forelimbs forming 4 to 6 longitudinal rows, and five claws. Six subspecies have been described but only four are widely recognized.

T. g. graeca

The basal colour varies from yellowish to pale olive, brownish or reddish brown. Each scute is often bordered with black and brown to reddish brown and usually bears a central black spot (Loveridge and Williams 1957).

It occurs naturally in Europe at two localities in southern Iberia (Donana, Huelva, and the northern part of Almeria Province, extending into southern Murcia). It is widely believed to occur on the Balearic Islands (e.g., Lopez-Jurado et al. 1979), but this is strongly rejected by Cheylan (1981). In north Africa it is found from the Atlantic coast of Morocco to north-east Libya (Loveridge and Williams 1957).

Some introduced colonies are known from Sardinia (Fretey 1975; Tortonese and Lanza 1969) and from continental Italy, Sicily, and Malta (Bruno and Maugari 1976).

T. g. iberica

This race is longer and broader, with a less domed carapace than the nominate form (Mertens 1946). In Europe it occurs in north-eastern Greece, Bulgaria, southeast Romania to the southwestern Black Sea coast, and apparently west into southern Yugoslavia (Macedonian Republic). Details concerning populations of this species in an area of sympatry with *T. hermanni* are scant, and the present day occurrence of *T. graeca* in Yugoslavia may be doubtful. The species' alleged occurrence in Yugoslavian Macedonia may be the result of misinformation from collectors. In Greece the natural range extends as far west as the Chalkidiki Peninsula and the isolated population at Alyki, west of the Axios Delta, is suggested to have been an anomalous

natural introduction beyond the normal range by sea borne drift (Wright et al. 1988). Sympatric populations with *T. hermanni* occur, but no reliable evidence is known for sympatry with *T. marginata*.

T. g. iberica is also known from northern Aegean islands, Thasos, Samothrace, Limnos, Samos, and Kos near the Turkish mainland (Watson 1962). The suggested occurrence on Euboea (Wettstein 1953 and quoted by Watson 1962) is now thought very unlikely, or the result of introduction at that time.

It is found in European Turkey (Basoglu and Baran 1977), Cyprus (Honneger 1978) where almost certainly introduced, and through into Asia Minor and Anatolian Turkey, except the northeast (Basoglu and Baran 1977), southwestern Caucasus and Azerbaijan in the U.S.S.R. (Bannikov et al. 1977), northern Iraq and western Iran (Schleich 1977; Tuck 1977; Anderson 1979). Possible intergrades with *T. g. terrestris* have been reported in southern Turkey and northern Syria (Basoglu and Baran 1977).

T. g. terrestris

This race has a high and domed carapace, with a yellow spot on the superior and lateral sides of the head (Wermuth and Mertens 1961). It is smaller and paler than *T. g. iberica* (Flower 1933).

It is found in the southern part of Asiatic Turkey, northern and western Syria, Lebanon, and western Jordan, north and central Israel.

T. g. zarudnyi

This race has a narrow, jagged carapace with the posterior part broader than the anterior part (Mertens 1946). It is being proposed as a full species *T. zarudnyi* (Highfield, pers. comm.).

It is found in east and south Iran in Kerman, Fars, Khorassan, Seistan, and Baluchistan Provinces; southwestern Afghanistan and western Pakistan (Baluchistan) (Werner 1938; Tuck 1977; Schleich 1977).

T. g. nikolskii

This race has long and pointed, clear claws on the forelimb, and vertebral scutes with well-developed pineal prominences. It has elongated and pointed scales forming four longitudinal rows in the forelimbs. It occurs in northwest Transcaucasia, but is not a widely accepted subspecies.

T. g. flowered

This is a small form with a pale yellow carapace and a black central spot on each scute. It is found in southern Israel extending into the Gaza Strip (Flower 1933; Lambert 1984 after Hoofien in litt.), and is not a widely accepted subspecies.

Status

The western race *T. g. graeca* is listed as "Vulnerable" on the IUCN Red List (Groombridge 1982 and updated 1987 in litt). The designation was applied in view of the well recorded mass exportation of animals from north African countries, especially Morocco and Algeria, continuing to the end of the 1970s. Current information is required on the status of remaining wild populations in these countries as well as Tunisia and Libya. Field studies by Lambert (1969, 1982) reported very low densities over wide areas.

The situation in Spain is well documented by Andreu (1988). A small, restricted, but seemingly viable population of 5,000 to 6,000 individuals, with a density varying from about 2 to 5 per ha, survives entirely within the Coto Donana National Park, although introductions have been made of animals from northern Morocco. The more widespread eastern population in Almeria and Murcia is less studied but is thought to have very low densities with few viable concentrations remaining.

The eastern races are almost entirely unknown, with the exception of *T. g. ibera* in northeastern Greece, where a number of sizeable populations have been reported and studied (Stubbs et al. 1981; Wright et al. 1988; Willemsen and Hailey in press), but most of these are declining, or exist on threatened sites.

The main centre of the species' eastern range is Asia Minor. Anecdotal reports from the western half of Turkey indicate the species is widespread and numerous. They are presumed to be widespread over the rest of the range in Turkey, Iran, Afghanistan and southern U.S.S.R., but most likely at very low densities in arid, semidesert areas. The Palestinian race, *T. g. floweri*, is the most vulnerable of all the subspecies in view of its very limited distribution and threats from habitat destruction in a densely populated region.

Habitat and Ecology

A wide variety of habitats and bioclimatic zones are inhabited over the entire species' range. Typically found in semi-arid hill scrub, open maquis and garigue type vegetation and at coastal sites, on sand dune ecosystems, and open pine and oak forests. Eastern populations inhabit much more arid, semidesert conditions. Occurs at a wide altitudinal range from sea level to a maximum of 2,700 m reported for *T. g. zarudnyi* at Kerman in Iran (Werner 1894 in Cheylan 1981). The typical average altitudinal range for the Asiatic races varies from 1,000-2,000 m. The western nominate race generally occurs at altitudes below 1,000 m, but in the High Atlas it has been recorded at 1,900 m (Cheylan 1981).

Where sympatric with *T. hermanni*, the two species tend towards habitat segregation, with *T. graeca* occupying open coastal sand dune systems at the western extreme of its range in Greece. *T. graeca* moves into farmland, hill scrub, evergreen, and deciduous forest further eastward towards Turkey, as the occurrence of *T. hermanni* decreases (Stubbs et al. 1981; Wright et al. 1988).

Detailed ecological studies have been carried out on three widely separated populations; *T. g. graeca* at Donana, southwestern Spain (Andreu 1988) and *T. g. ibera* at Alyki and Epanomi, northern Greece (Hailey and Lambourdis 1988). Both studies have concentrated on reproductive parameters and growth.

In Spain, the smaller western race occupies open pine scrub along the rear sand dunes and occurs at low densities (less than three per ha). They also inhabit a small flat area bordering marshland occurring in scrub habitat characterized by *Pteridium aquilinum*, *Halimium halimifolium*, *Stauracanthus genistoides*, and ericaceous scrub, attaining slightly higher densities of over five per ha. The active season is from February to June with mating at the beginning and nesting towards the end of this period. Following aestivation, activity picks up in September when hatchlings appear. Mating takes place until the onset of hibernation in late November. Clutches number 3-4 eggs, with each female depositing two or three clutches per year. Reproductive potential is estimated at 5.5 eggs per female per year. Hatching success varied from 24% to 35% to 50% in three years of a study.

In Greece, the larger eastern race was studied on open coastal dune habitats with clumps of marram grass (*Ammophila arenaria*) and cottonweed (*Otanthus maritimus*). A small population of 25 adults at Alyki was found to be viable, with normalized adults and healthy growth rates among younger animals. At Epanomi, average clutch size was 4.5 eggs with a range of 3 to 7 eggs, and annual egg production varying from 6 to 18 (average 10.6) with a clutch frequency of 2.8.

In both races studied, egg predation was found to be insignificant, possibly due to the low density of nests. Hatching success was dependent on fertility and incubation conditions. Adult sex ratio in Donana, Spain was 1.5 males to each female (n=229) and at Alyki in Greece, 13 males to 9 females.

In the Spanish population, males are sexually mature at 128 mm carapace length and females at 155 mm. Females are generally larger than males, but this is less marked in *T. g. ibera*. Both sexes are markedly sedentary during adult life.

Threats to Survival

Testudo graeca is not in immediate danger. The majority of its natural distribution is in remote, inaccessible areas of Asia Minor and North Africa. Former heavy collecting for the pet trade must have taken a serious toll on selected populations, but recovery can be anticipated providing long-term habitat conditions remain suitable.

Presently, the most critically threatened populations are in areas of high human activity, where large-scale habitat destruction and modification, as well as casual collection by tourists, constantly depletes tortoise numbers. Potentially, the small Spanish populations are the least secure, but the protection afforded by the Coto Donana National Park should ensure their survival. The most threatened populations are those on coastal sites in Greece and Turkey, where tourist associated developments are rapidly destroying remaining natural habitats.

Conservation

The only practical conservation measures for this species have been enacted in Spain. The Donana population is closely monitored within a strictly protected reserve area. In Almeria (southeastern Spain), surveys have been undertaken to identify potential reserve sites in the Sierra de Cabrera. A private centre at Elche in Alicante Province aims to recover tortoises from captivity and reintroduce them into the wild in recently depleted areas. This has not yet been done as there is a lack of knowledge concerning suitable sites.

Repatriation of tortoises of foreign origin (principally Morocco) is not yet considered feasible. The Agencia del Medio Ambiente in Andalucia has conducted an experimental release of 200 tortoises in enclosed state property at Cadiz. Feasibility studies for conservation projects in Morocco and Algeria would be highly desirable.

The most urgently required action is to secure long-term protection of coastal sites in northern Greece and along the Mediterranean coast of Turkey. Priority sites should include Alyki, Epanomi, Nestos at Keramoti, and Dalyan, Turkey. As with all *Testudo* species, strict enforcement of national and international protective legislation is essential to curb the effects of illegal trade.

Current Research

Ongoing studies by Andreu at Donana are the only current research known. Populations in northern Greece are being monitored from time to time by the University of Thessaloniki.

Testudo hermanni

Hermann's Tortoise

David Stubbs



Hermann's tortoise (*Testudo hermanni*). (Photo by D. Stubbs.)

Description

This is a small to medium sized tortoise, adults ranging from 120 mm carapace length in the smaller western race to a maximum of about 230 mm in the larger Balkan race. Key distinguishing features are the horny scale at the tip of the tail and a divided supracaudal scute. In some eastern populations the divided supracaudal is absent in a small proportion of individuals. In general, Hermann's tortoise has a slightly domed carapace, usually with distinctly contrasting black patches on an ochre yellow base colour. Colour pattern and degree of contrast vary considerably in the eastern race but is fairly constant in the western race.

Two subspecies are recognized. The smaller nominate western race of *Testudo h. hermanni* (until recently this race was widely known as *T. h. robertmertensi*, see Bour 1986), has a rather more domed shell, a strongly contrasting and brighter shell pattern, a pale yellowish green spot on the side of the head and two continuous parallel black bands along the length of the plastron, not extending onto the gular scutes. The key distinguishing character of this subspecies, in addition to the above, is the shortened pectoral scute, distinctly less (about 1.5 times) than the femoral scute when measured along the plastral midline.

The eastern race, *T. h. boettgeri* (formally considered the nominate race), has a duller coloration and less distinctly defined black markings. The black bands along the plastron are clearly discontinuous and the median lengths of the pectoral

and femoral scutes are more or less equal. While the carapace can be almost as domed as the nominate race, the vertebral peak is located toward the posterior, as distinct from *T. h. hermanni* whose peak is more central. In contrast to *T. graeca*, the females' rear plastral portion is unhinged with only slight kinesis.

Status and Distribution

Over most of its entire European range, Hermann's tortoise is still very numerous, and as a species is under no immediate threat. However, in many areas it has drastically declined in recent decades, and at many locales it is distinctly threatened. The western subspecies is most vulnerable, especially in Spain, mainland France, and Italy.

The stronghold of *T. h. hermanni* is the island of Corsica, and to a lesser extent the Massif des Maures, Var, in southern France (where it is declining but receiving active conservation attention), and the Balearic Islands. Of the latter, the only apparently viable populations remain on Majorca, centered in the southeast near Arta. Only small, fragmented populations remain on Minorca, principally in the ravines along the south coast and on some wooded hills in the northwest. It formerly occurred on Ibiza, and its current presence on Formentera has not been confirmed. It is considered native on these latter two islands.

Elsewhere, a very small relict population exists in the Mont Alberes in the eastern Pyrenees of Spain near the French border. In Italy, a few isolated populations remain along the western coast, and in the south, in the provinces of Liguria, Tuscany, Latium, Campania, Calabria and Pouilles (Tortonese and Lanza 1969; Bruno 1971; Bruno and Maugeri 1976, in Cheylan 1981). Populations formerly reported from the eastern (Adriatic) side of Italy are considered extirpated.

Populations occur on Sicily and Sardinia, where rather localized populations are found mostly in the northeastern part of the island. Natural populations probably occur on the islands of the Tuscan Archipelago, specifically Elba, Pianosa and Monte Argentario. Other insular populations in the Sicilian Channel, on Pantelleria, Lampedusa and Linosa, are of doubtful origin. There are no valid records for Malta.

The eastern race occupies much of the Balkan peninsula and is generally considered to be plentiful over much of this range, although considerably less common than a few decades ago. In Yugoslavia it occurs along the entire Adriatic coast from Istria

in the North to Albania, but does not extend very far inland in Dalmatia and Herzegovina (5-15 km on average), while in Montenegro, Serbia, and Macedonia it is much more widespread, especially around Titograd and Skopje. It occurs on Lopud in the Elaphite Archipelago as well as on the island of Hvar near Split (Klemens, pers. comm.).

In Bulgaria, it occurs throughout the country below 1,300 m (Cheylan 1981), and likewise in Albania. In Romania, the species is limited to the southeastern part of the country, north of the Danube.

Hermann's tortoise is also found throughout much of Greece, although it is rare or absent from large areas of arid mountains in the central and Athenian regions. Many populations in the central and southern parts of Greece are sympatric with *T. marginata*, while in the northeast, between Thessaloniki and the Turkish border, populations sympatric with *T. graeca* occur. *T. hermanni* extends into European Turkey, although there are no precise details on its distribution there.

Few of the Greek islands are inhabited by tortoises, other than occasional escapees from captivity, but natural populations are widespread on Corfu, and also on Santa Mara and Euboea (Wettstein 1953, in Cheylan 1981).

Habitat and Ecology

Hermann's tortoise appears to favour evergreen Mediterranean oak forest, the climax vegetation of the region. However, much of the original forest cover in the Mediterranean has long since been cleared and has degraded to a scrubby maquis or garigue. Thus, the typical habitat cited for the species is usually arid, scrubby hillsides and farmland, but this does not reflect its true preference. Large populations are also known from several coastal sites where tortoises inhabit dune scrub and maritime grassland communities. This is particularly noteworthy in Greece and a few sites in Italy, and presumably Albania and Yugoslavia. However, tourist developments have greatly reduced this type of habitat.

Evidence from detailed studies in France (Stubbs and Swingland 1985; Stubbs 1986; Devaux, Pouvreau, and Stubbs 1986) suggest that originally Hermann's tortoise favoured low-lying plains with a mosaic of forest, dense maquis, and natural clearings. Natural populations over much of its formerly extensive range are thought to have occurred at low densities (less than 5 per ha), but recent development has caused considerable habitat fragmentation. This has led to a general range contraction, resulting in a number of small populations at particularly favorable sites.

Maximum population densities in the Massif des Maures (France) are 11 per ha, although slightly larger figures for the western race are anticipated at a number of sites in Corsica, (Cheylan, pers. comm.). Some eastern populations attain very high densities. At Alyki in northeastern Greece, a thorough mark and recapture study from 1980 to present (Stubbs et al. 1985; Hailey 1988) found average densities of about 50 per ha for a population of over 3,000 animals. Within this site, local densities exceeded 60 per ha. However, due to a major disturbance resulting in the loss of 40% of this population in

1980, densities are presently much lower. Other anecdotal reports confirm the presence of large concentrations at sites in Greece and southern Yugoslavia. Typically, the species is found at low to moderate densities of between 1-5 per ha.

Most population studies reveal age structures skewed in favour of adults, and corroborative evidence of high nest and juvenile mortality suggest a general widespread decline in numbers. Few strong, viable populations have been identified. Although populations recover well from isolated catastrophes such as fires (Stubbs et al. 1985; Wright et al. 1988), the long-term effect of the pet trade and casual collecting, increased frequency of fires, habitat destruction, fragmentation, and changing land-use patterns are resulting in slow but perceptible population declines.

Recent studies by Hailey on the Alyki population have demonstrated that recruitment of adult males is higher than females due to shorter time to maturity (9 compared with 11 years). Mean annual survival is slightly greater in males (0.914) and females (0.877), equivalent to mean adult longevity of 11.6 and 8.1 years respectively. Thus average adult tortoises at Alyki are adult for about 56% and 42% of their lives respectively. Generation time is roughly twice the time to maturity and three times the time to development of secondary sexual characteristics.

The higher female mortality is thought to be due to infections resulting from physical damage during courtship. The well-developed horny tip on the tail is unique to *T. hermanni*, and is repeatedly used to stimulate the female's cloacal region prior to mating, whereas in other *Testudo*, shell-butting alone is used to ready females for mating. In high-density populations with regular male/female encounters, continual courtship can cause damage to the sensitive skin above the tail, setting up serious infections which may ultimately lead to death. At lower population densities this effect is not likely to be significant.

Detailed studies on different populations have revealed some regional variations in activity patterns and reproductive parameters, but the following comments generally apply. Hermann's tortoise hibernates from November to early March or April, occasionally emerging for brief periods in midwinter. The spring season produces high levels of adult activity, essentially feeding and also some mating. Egg laying takes place from mid-May to early July in France and somewhat earlier in Greece. Incubation lasts three months and hatching takes place after the first autumn rains in early September. Midsummer activity is considerably reduced, but from the end of July males become increasingly active in their search of females. The greatest amount of mating behaviour occurs in late summer. Early mating is thought to offer a competitive advantage since females can store sperm for many months.

Average clutch size is three eggs in France, and four to five eggs in Greece. Most females lay more than one clutch per season, at intervals of up to 20 days. This is believed to be a reflection of the morphological constraints of packaging shelled eggs within the body (Hailey and Lambourdis 1988). Size at maturity in males is about 120 mm in France and 130 mm in Greece, and for females about 150 mm in both countries. Growth rates are slightly higher in young females, and age at sexual maturity is about 12 years for both sexes.

Sex ratios in wild populations show considerable variation. Long-term mark-recapture studies, eliminating the errors of short-term sampling bias, show equal numbers of males and females in forest habitat in France. This is in contrast to a strong male bias (increasing with age) on open coastal grass and scrubland in Greece. In each case, the sex ratio at maturity is approximately in parity. Secondary sexual characteristics are not clearly distinguishable until tortoises have reached 100 mm in length.

In all populations studied, most animals are sedentary for most of the year. The most striking exception occurs in dense forest habitat where nest sites are located at specific, isolated clearings, and females migrate to them from their normal home range in spring. Between nestings, females return to the forest, and at the end of the nesting season may take up a different, but similar sized home range of about 1 ha. Home range utilization is uneven throughout the year, with activity concentrating around the best food sources. Juveniles spend their first 4-5 years within a few metres of where they hatched. During their subadult years, they explore a greater area in an apparently haphazard fashion before establishing an adult home range.

Threats to Survival

The most serious threat is habitat loss. This arises from a variety of human activities, most notably agricultural intensification and urbanization. Both of these activities often result in increased frequencies of forest and scrub fires. However, the biggest problem is the increase in tourists visiting the Mediterranean region each summer. While holiday complexes account for a relatively small percentage of overall habitat loss, many key habitats and sites are lost by their construction, especially along the coast. Fragmentation of habitat has affected populations which formerly survived at low densities over considerable undivided areas. The viability of many extant populations is in question.

Habitat modification by changing agricultural methods has been a significant factor in population declines in France. Tortoises relying on forest clearings maintained by man are now forced to nest in a few isolated sites which remain open. This concentration of nests attracts many mammalian predators. Over 90% of the nests are destroyed yearly, virtually halting recruitment.

Collecting for the pet trade has taken a heavy toll on many populations of both subspecies. Though this has been reduced to a relatively small scale black market operation, many animals are still taken for pets each year by tourists and local people. In France, it is believed there are more native tortoises in captivity than remain in the wild. Even low levels of collecting may be serious in low-density populations. Collecting, added to the habitat changes previously discussed, has a cumulative effect resulting in local population declines.

Conservation Measures

Hermann's tortoise is officially protected throughout Europe by both national and international legislation (see regional introduction). Enforcement is unfortunately minimal in all countries within its range.

In Greece, the well-studied site of Alyki was saved from development in 1980 after local people set fire to the vegetation. To date, the site with its large tortoise population still survives. However, it is not fully protected, and no specific conservation measures have been enacted.

Small-scale, private tortoise reserves have been established in Majorca and northern Spain, but work on these projects appears to be sporadic. A number of other populations, notably on Corsica and in Italy, have been studied and recommended for conservation action but without results.

The most significant tortoise conservation programme for any species of *Testudo* involves the French population of Hermann's tortoise in the Massif des Maures. In May 1988, the "Village des Tortues" (Tortoise Village) was established in SOPTOM (Station d'Observation et de Protection des Tortues des Maures), a locally based voluntary body dedicated to conserving French tortoises. The project is founded on the scientific studies carried out in the Massif in the early 1980s (Cheylan 1981; Stubbs and Swingland 1985), and is formulated in a detailed conservation proposal "Programme de Sauvegarde" (Devaux, Pouvreau, and Stubbs 1986).

The Tortoise Village provides a combined visitor centre and conservation facility for captive breeding and head starting. It serves as a base for carrying out population surveys. Eventually, a large scale restocking programme with appropriate habitat management is planned in the Massif des Maures. The visitor centre facilities assure the financing of conservation work, while serving to educate and develop public awareness.

A new tortoise conservation centre, similar to the Tortoise Village, but from an independent initiative, is to be established near Grosseto in west central Italy in 1989. This will be managed by the RANA group and is partly funded by the EEC and WWF—Italy.

Current Research

Intensive studies of *T. hermanni* at Alyki in northeastern Greece have been completed, and only occasional monitoring work continues. The principal focus of research on this species is centred at Le Village des Tortues in France. Current work concerns a regional population census and monitoring of released animals. The village holds great potential for accommodating further research projects, provided that they contribute to the conservation of the species. Other current surveys are being conducted in Corsica by Marc Cheylan. In collaboration with SOPTOM, the establishment of a conservation programme on Corsica is envisioned in the near future.

Testudo horsfieldi

Horsfield's Tortoise

David Stubbs

Description

This is a relatively flat species, with an oval carapace becoming almost round and globular in older specimens. Larger animals may have serrated carapace margins. There is a long, narrow nuchal shield and an undivided supracaudal. The plastron is solid and dark. The general colour is yellow to olive with dark blotches, and the head and limbs are yellowish. The front feet have four claws and small tubercles or spurs on the thighs. No subspecies have been described.

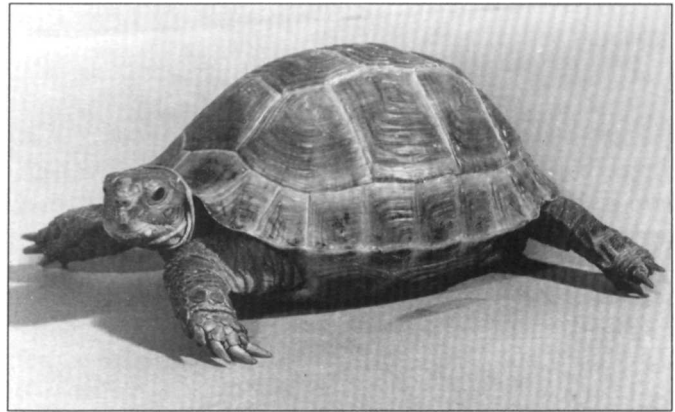
Status and Distribution

This species occurs east of the Caspian Sea, in southern U.S.S.R., Afghanistan, eastern Iran and northwest Pakistan, and possibly in extreme western China.

Very few published studies exist to date. In Pakistan, *T. horsfieldi* occurs in Baluchistan Province and Northwest Frontier Province (Khan and Mizra 1976). There is no evidence for it occurring in Punjab or Sind. Nawaz and Nawaz (1987) reported on the status and distribution of the species in Pakistan, recording it as an "endangered species" as a result of survey data collected in 1984-85. They found it had virtually disappeared from the North West Frontier Province except in tribal areas adjoining Baluchistan.

In Baluchistan, *T. horsfieldi* is found sparsely distributed at the Hazargangi Chilton National Park near Quetta. It has also been reported from the Kuchlak, Saryab, Mastung, Nushki, Pishin, Chaman, Zhob, Muslin Bagh, Lorali, Ziarat, Hernai, Sanjavi, and Dukki areas. It does not occur in coastal areas.

In Southern Turkmen SSR, Makeev, Bozhanski, and Frolov (1986) estimate the total population over the whole Maryji region (86,800 sq km) at 26.8 million tortoises. This is an average of 308 animals per square kilometre, or just over 3 per ha, which is characteristic of a low-density, widely distributed tortoise. Concentrations of individuals occur at favorable sites (up to 12.7 per ha at Namah-Saar Stow in the centre of Badkhyz). Populations are thought to be declining in all areas of the range, although there are no "hard data" to back this up.



Horsfield's tortoise (*Testudo horsfieldi*). (Photo courtesy of the Zoological Society of London.)

Habitat and Ecology

Information on habitat is given by Makeev et al. (1986) for the Maryji region of southern Turkmen SSR. Six habitat subdivisions were identified containing tortoises: ephemeral communities on foothills and lowlying sandy bush desert (4.47 tortoises per ha); ephemeral communities on loess foothills, deserts, and semideserts (4.47 tortoises per ha); valley habitats, marshes, and floodplains (0.44 tortoises per ha); white saxual, *Haloxylon* sp. sandy deserts (0.48 per ha); white saxual argillaceous deserts (2.46 tortoises per ha); saline argillaceous deserts (1.54 tortoises per ha).

The species occurs in all the regional landscape subdivisions except salt pans (see also Shamakov 1981). In river valleys and cultivated areas, density counts were particularly low (0.05 to 1.26 per ha), while the most favoured habitats were the loess foothills and sandy deserts of the Badkhyz and Karabil plateaus vegetated with gramineous forbs. The peak activity period in southern Turkmen is April and May, and coincides with maximum sexual activity. Tortoises were active between 09:00-19:00h.

Threats to Survival

In the U.S.S.R., the combined effects of heavy collection for the pet trade and habitat loss through cultivation of desert and semidesert areas have been the principal causes of a marked decline in numbers. Collecting supposedly has been restricted since 1984, but contemporary reports indicate that large numbers still arrive in Western Europe and elsewhere.

The situation in Pakistan results from different causes, particularly recent habitat destruction in war refugee zones (presumably also in many parts of Afghanistan). Other serious threats arise from increased livestock grazing and killing of tortoises by farmers, who claim they eat significant amounts of vegetables and fruit tree seedlings. Stray dogs and small mammals destroy nests.

Conservation Measures

Full enforcement of national and international protective legislation is essential to curb the effects of illegal trade. However, habitat protection must be a priority. This is a difficult if not

impossible goal, as large parts of its range are vulnerable to continued agricultural development, and there is little in the way of an established, active conservation movement to counteract these pressures. However, much of the species' range is in remote and dangerous areas, where no organized collecting or intensive development is likely at present.

For the foreseeable future the species is secure, but large-scale range fragmentation and reductions in population densities are anticipated in many areas. Therefore, representative areas and habitat should be designated as protected reserves in the U.S.S.R., and Pakistan. Local information and education campaigns should be coupled with these reserves, making inhabitants aware of the importance of such conservation initiatives. As with all other conservation programmes, success will be achieved only if local people perceive benefits to their economies and livelihoods from the conservation measures.

Current Research

None known.

Testudo kleinmanni

Egyptian Tortoise

David Stubbs

Description

This is one of the world's smallest tortoises. Average adult length is 100 mm and weight 200 g. The carapace is generally oval in shape, moderately domed, and has a deep nuchal notch. The supracaudal scute is undivided and the plates on the hind end of the carapace are slightly raised. The coloration is pale yellow to greenish yellow, with some scutes possessing a small black patch in the centre. The plastron sometimes has a dark brown patch. The scales on the forelimbs are exceptionally large and there is no enlarged scale on the tip of the tail. No regional variations or subspecies are recognized.

Status and Distribution

The Egyptian tortoise is found principally in Egypt, but its range extends into parts of Israel and Libya, in the region of Cyrenaica. In Egypt it is confined to the northern part of the country, in the low-lying areas of Alexandria, Port Said, Damiette, and along the Mediterranean coast of the Sinai. Its distribution is interrupted by the alluvial plain of the Nile delta.

In Israel, its distribution is limited to sandy areas and dunes in the western Negev and to isolated sand areas of Mishor Yamin and Mishor Rotem. The inland range limit from the Mediterranean coast is about 60 km. The climate further inland is too arid for tortoises.

The Egyptian tortoise is not common anywhere within its restricted range. In Israel, although well protected by law, there have been severe population declines due to habitat destruction. In contrast, in its larger Egyptian range, the habitats are less impacted, although development is increasing. In Egypt, collecting pressure is great and tortoises are killed by locals. There is no information on its status in eastern Libya or the Egyptian frontier, but as this species occurs at low densities, these outlying populations may not be large. Overall this species can be considered "Vulnerable," and it is listed as such on the IUCN Red List.

Habitat and Ecology

This species is restricted to desert environments. These areas have an average air temperature of 20°C and a mean maximum of 30°C and a mean minimum of 12°C. Rain falls in winter only with an annual range of 50-200 mm. This corresponds to the Sahara-Arabic bioclimatic region. The principal vegetation in these areas is a sparse scrubby association dominated by *Artemisia monosperma*. Vast areas of the species' range have been overgrazed by Bedouin goats. For example, there is virtually no shrubby plant cover remaining in the Sinai. This may account for the extremely low population densities of 4-5 per sq km (Groombridge 1982). However, Geffen (1985) carried out detailed studies on a population in the Negev reporting densities of 21-41 tortoises per sq km (0.2-0.4 tortoises per ha). This comparatively dense population is much sparser than populations reported for all other species of *Testudo*. Sex ratio in Geffen's population was 2:1 in favour of males. Fifteen percent of the tortoises were juveniles, which constitutes a relatively high proportion compared with other field studies on *Testudo*.

Home range is well defined, but varies considerably between individuals and sexes. The average home range for males is 0.19 sq km, for females 0.07 sq km, but no significant difference was detected between these two figures, and many home ranges overlapped. Similar to other *Testudo* species, home range utilization is patchy, with all parts being visited during the year, but small areas being used more frequently. Movement is limited during summer, while winter and spring are the most active periods. Unimodal daily activity occurs between December and February, changing to bimodal activity in March and April. In summer, activity is limited to short periods usually early in the morning. Nocturnal activity has not been recorded. Typical body temperatures of active tortoises ranged from 28-32°C, while air temperatures ranged from 21-24°C (but with a much greater variation in substrate temperatures). Many inactive animals hide in rodent burrows, which during summer have mean temperatures of 29.5°C, and are relatively humid.

Mating occurs in March. Eggs appear in the oviducts as early as March-April and disappear in all females by late June. Two to three clutches are laid during this period, each clutch ranging between 1-3 eggs (usually 2). There is an interval of 20-30 days between clutches. There is no significant correlation between body length or weight and the number or size of eggs. Eggs are relatively large, being up to 28% of the female's body length. Nests are located under small bushes, offering shade, and usually face south or east. Nest temperatures during incubation ranged from 24.3-38.2°C. Observed hatching time is 70-90 days, but these data are from a very small sample.

Threats to Survival

Throughout the species' entire range habitat destruction is the primary threat. This results from agricultural expansion as well as traditional pastoral practices (such as overgrazing by goats). Off-road vehicles also threaten habitat. Grazing results in changes to the desert's vegetational composition which are less favorable to rodents. This results in fewer rodent burrows, vital for the summer survival of tortoises.

Encroaching agricultural development into desert areas also brings human settlement, introducing trees to the formerly treeless environment. These provide nesting habitat for brown necked ravens, *Corvus ruficollis*, which prey on tortoises. Army camps in the desert also serve to increase the raven population. Other predators encouraged by human settlements are domestic and feral dogs. Potential natural predators such as the desert monitor (*Varanus griseus*), wolf, hyaena, and desert red fox are either nocturnal, very rare, or prey only on juveniles. Since 1980, when border fencing prevented Bedouin goats

from grazing in the Negev, there has been considerable regeneration of vegetation with a substantial increase in tortoise densities. However, this localized recovery is offset by increased pressure on populations in the Sinai. Some tortoises are deliberately clubbed to death, presumably by shepherds. In Egypt, a major additional threat comes from collecting, both for the pet trade and for "research." Despite official protection since 1982, no enforcement activity has been noted (Buskirk, in litt.).

Conservation Measures

The priority in Israel must be the establishment of protected areas to protect this species effectively. A sizeable area (at least 40-50 sq km) between the Agur and Halutza sands is proposed as a major reserve area. As it is a border area, it has the advantages of restricted access and little military activity. The vegetation is recovering and there is already a healthy population of *T. kleinmanni* on site. A nature reserve of this size could sustain a viable population of 500-1,000 individuals. Other reserve areas are needed and should become an integral part of development planning for the Negev region. In Egypt, habitat protection is similarly required but in conjunction with strict enforcement of legal restrictions governing the collection of tortoises. An educational programme is necessary to inform local people of the need for tortoise conservation.

Current Research

None known.

Testudo marginata

Margined Tortoise

David Stubbs

Description

T. marginata is the largest of the *Testudo* species inhabiting the Mediterranean basin. Adults possess an elongated carapace with strongly flared rear marginal scutes, which are sometimes serrated. The supracaudal is undivided and there is a small nuchal shield. The plastron is solid (i.e., not hinged along the femoral line as in *T. graeca*) and there is no horny tip at the end of the tail, nor spurs on the thighs. All feet have five claws.

Coloration is mainly black, except for the characteristic light orange or yellow areolae on the costal and vertebral scutes. Some old specimens may be entirely black, whereas juveniles are much lighter in colour and unless the elongation of the carapace is apparent, they can be confused with juveniles of *T. hermanni* and *T. graeca*. On the underside, the colour is mainly yellow-olive, with dark triangles on the larger scutes (the base of these triangles lies along the anterior end of the scutes).

There is considerable variation in size range between populations. The maximum recorded length in the wild is about 350 mm straight carapace length. In some southern Peloponnese populations, adult males do not exceed 230 mm and adult females 215 mm in straight line carapace length (Keymar and Weissinger, 1987). No subspecific variations are recognized, and there is no firm evidence to indicate whether morphological distinctions between populations result from genetic or environmental factors.

Status

This is the least studied of the Mediterranean *Testudo* species. This may result from its apparently uniform distribution over large parts of mainland Greece, but with few identifiable concentrations suitable for detailed studies. Many locality references of individual sightings or small groups of animals are contained in the literature. From these it may be inferred that *T. marginata* is widespread, but thinly scattered over much of Greece. *T. marginata* is endemic to Greece as well as introduced onto Sardinia. However, a summary of locality records through the early 1980s Bour (1986), includes a questionable citation from southern Albania.

Contemporary records have been provided by Keymar and Weissinger (1987), Willemsen and Hailey (in press), and Bover

(pers. comm.). With the exception of a single high-density population (>200 animals marked) in the southern Peloponnese, records were of up to a dozen individuals located at scattered sites. Most records are from the southern and eastern Peloponnese, with a number of localities along the eastern coast as far as Katerini near Mount Olympus. On the western coast it is found up to Igoumenitsa, near the Albanian border. Inland in central Greece records are sparse, due to the mountainous terrain and heavily cultivated plains. The northern range limit is in the Vermion Mountains, roughly 40°30' N. *T. marginata* does not occur naturally in Yugoslavia. Locality records from Yugoslavia appear to emanate from pet trade collectors, escaped/translocated animals, or misidentifications. The species is also absent from northeastern Greece (Thessalonika region and eastward to Turkey). Therefore, it is not sympatric with *T. graeca*.

On the Aegean islands *T. marginata* occurs on Skyros, a number of the northern Sporades, Euboea, and in the Argosaronic Gulf, south of Athens on the east side of the Peloponnese. An introduced population occurs on Sardinia, but there is no contemporary information on its status.

Habitat and Ecology

No detailed autecological studies have been undertaken. There are a few casual accounts and short-term studies on small populations.

The typical habitat is phrygana (garigue), usually on hillsides close to cultivated areas. The thorn scrub vegetation and open rocky hillsides of the phrygana is typical of vast areas of rural Greece, but it must be remembered that this is a degraded habitat, following centuries of forest clearance, burning, and browsing by goats. It is not clear whether the margined tortoise inhabits scrub areas by preference, having expanded its range due to human-induced landscape modifications, or whether it naturally occurred in the prehistoric Mediterranean evergreen oak forests, having adapted to sparser conditions.

In springtime, individuals are often seen at lower altitudes in the tall, grassy vegetation bordering cultivated areas, where there is a more abundant food supply and possibly better nesting habitat.

Threats to Survival

The potential habitat in Greece is immense, and generally there is little threat to the species' survival. It is certainly less vulnerable than the high-density coastal populations of *T. hermanni* which are threatened by tourist development.

The principal drain on populations is in agricultural areas, where animals are killed by machinery or herbicide sprays. *T. marginata* is especially vulnerable to these losses since it is the slowest maturing *Testudo* species (adult females weigh about 2500 gm). Only 6% of the specimens obtained by Willemsen and Hailey were juveniles, compared with 15% and 22% for *T. hermanni* and *T. graeca*, respectively.

Keymar and Weissinger consider illegal collecting for the pet trade still to be significant, and were noted by Van Mook in 1986 (*Societas Europaea Herpetologica* unpublished report), when a collector was arrested on the island of Milos with 48 *T. marginata* collected on the mainland in his car. It is unlikely that such collecting is more than a local threat to certain populations. Coupled with habitat loss and fragmentation, as well as the effects of agricultural improvement and intensification, a marked decline in the overall population can be anticipated.

Conservation

All European *Testudo* are protected under EEC and national regulations, forbidding the collecting, killing, or trading of individuals. Under the terms of the 1979 Bern Convention, the species' habitat must be protected. No reserves or special conservation projects have been undertaken to date. Law enforcement is lacking and is unlikely to be implemented without some concerted conservation education aimed at both officials and the general public in Greece. The large, relatively dense population at Gytheion in the Peloponnese is the only known concentration of this species. Therefore, this site deserves special protection and further study.

Current Research

None known. Some basic ecological parameters may be deduced from detailed work on *T. hermanni* and *T. graeca*, but this is far from satisfactory. Apart from detailed surveys and ecological studies, identification of potential reserve areas is a priority. Increased public awareness of the need for conservation within Greece is also vital.

Geochelone pardalis
Leopard Tortoise (English)
Bergskilpad (Afrikaans)

Donald G. Broadley

For a list of vernacular names see Loveridge and Williams (1957: 238).

Description

Beak scarcely to strongly hooked, edge of jaws dentate; prefontal large, frequently single but usually divided longitudinally; frontal broken up; remaining upper head scales small, irregular; forelimb anteriorly with large, unequal, usually scattered or rarely juxtaposed, generally imbricate scales forming 3-4 longitudinal and 7-9 transverse series from elbow to outer of five claws; posterior side of thigh with two or more very large (rarely small) conical tubercles; heel with large, conical, spur-like tubercles, claws four; tail without terminal claw-like tubercle.

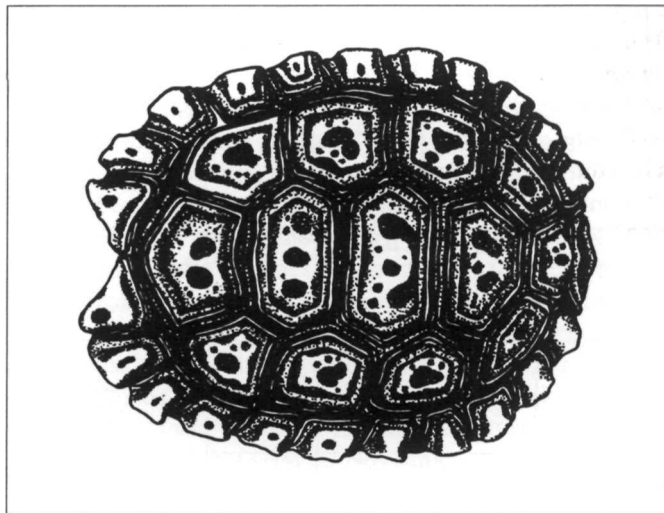
Carapace convex, sides descending abruptly, deeply notched in nuchal region except in the very young, anterior margins not, and posterior margins only sometimes, expanded, reverted, and more or less strongly serrated; dorsal shields concentrically striated, sometimes swollen, subconical or convex, nuchal absent; vertebrals five, rarely six, more or less convex, first as broad as, or broader than, long, the rest broader than long, broader than the costals; costals four, rarely five, not forming an angle with the marginals 10, 11, or 12; supracaudal undivided, somewhat incurved.

Plastron with front lobe not or but slightly produced and not or but weakly notched; gulars paired, pectorals very narrow, their anterior border usually straight, widening abruptly towards the axillary notch; axillaries 2, one large, the other minute; inguinal small to moderate, normally in contact with the femoral, rarely separated; hind lobe deeply or slightly notched posteriorly, usually angular, occasionally crescentic, an interanal scute sometimes present.

The plastron is strongly concave in males of the typical form, but in *G. p. babcocki* only the posterior third is slightly concave. The tail is also longer in males.

Coloration

Juveniles of the typical form are dull yellow, with a red-brown border to the areola of each carapace scute, each vertebral and costal usually with two or more irregular blackish spots or blotches; the plastral scutes have red-brown margins and may



Juvenile leopard tortoise (*Geochelone pardalis pardalis*). Victoria West, Cape Province, South Africa. (Illustration by J. Duff.)

have central red-brown blotches, especially on the abdominals and femorals; the growth zones along all sulci are black. The head and limbs may be uniform yellow or peppered with black.

Juveniles of subspecies *babcocki* differ in having at most a single central dark spot (often absent) on each vertebral and costal, this is often confluent with the posterior dark areolar margin; the plastral scutes may be uniform yellow or with a dark margin, but without central spots. The head and limbs are uniform yellow.

Adults are yellow with variable black markings which may be zonary in smaller specimens (e.g., Duerden 1907, pl. vii, fig.7), but are usually semi-radial or speckled in larger specimens. In some large adults the black pigment predominates, but in others black pigment is entirely absent.

Size

In the typical form, the largest male recorded is "Domkrag," a well known inhabitant of the Addo Elephant National Park in the eastern Cape Province. He died in 1976 after getting trapped in an antbear hole. At that time, he measured 656 x 408 mm and

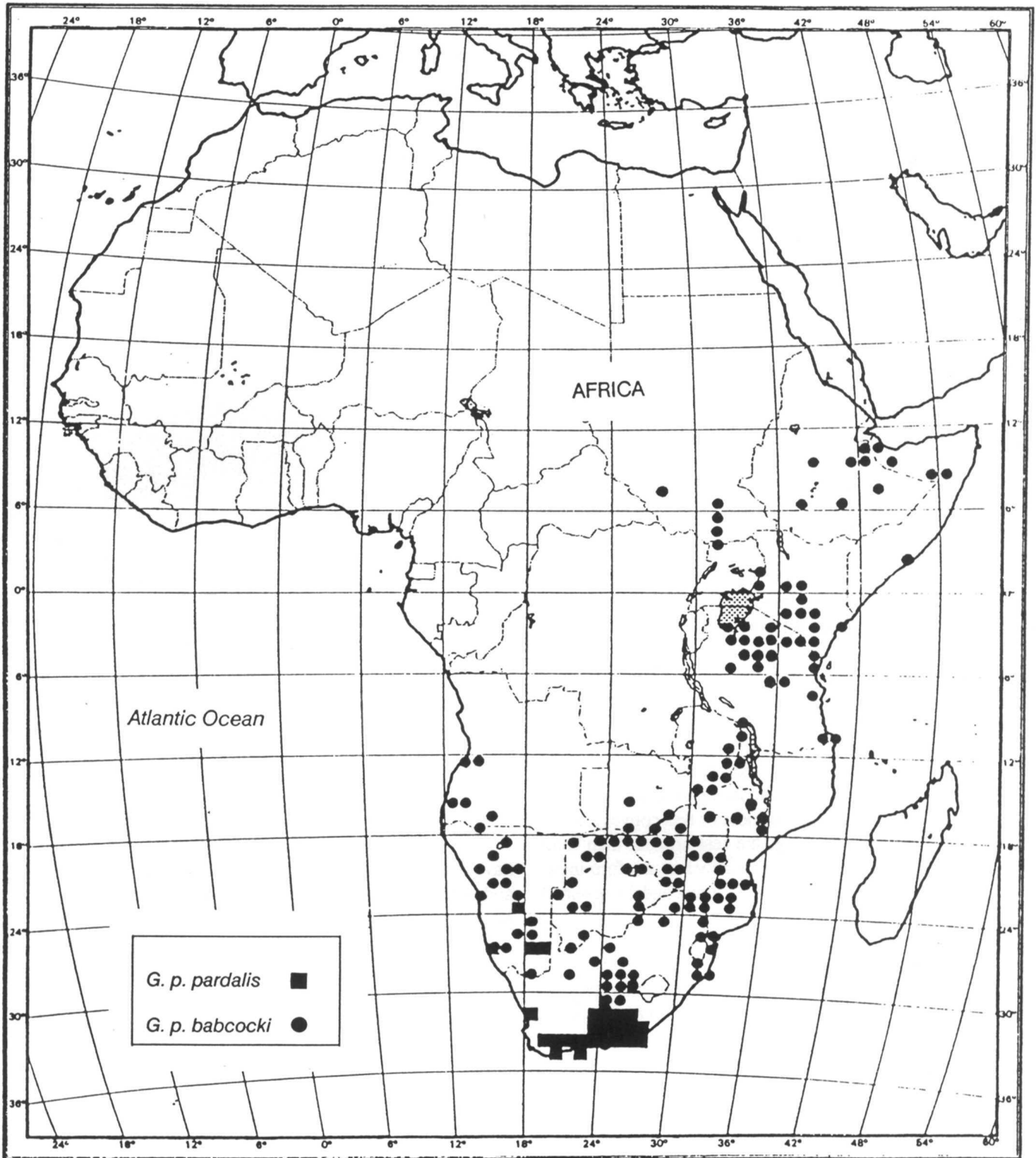


Figure 10. Distribution of *Geochelone pardalis*.

weighted 43 kg (Branch and Braack 1987). The largest female recorded is a specimen captured about 23 km north of Aberdeen, Cape Province in 1929 and kept in captivity in the Transvaal, where by 1941 she had attained a length of 498 mm and a mass of 20 kg (Cairncross 1946). In the typical form, the males apparently attain a slightly larger size than the females.

In the northern race, *G.p. babcocki*, the males are considerably smaller than the females. Loveridge and Williams (1957) record a male from Arusha, Tanzania, with a carapace length of 340 mm and a female from Mount Mbololo, Kenya (MCZ 40004) with a length of 385 mm. Leakey (1944) records two Kenyan females weighing 18.6 and 16.8 kg.

Distribution

The typical form is restricted to the central and southern Cape Province and the southwestern Orange Free State (where it apparently intergrades with *G. p. babcocki*), with relict populations in southern Namibia. Fossil remains from the Middle Pleistocene of Makapansgat in the northern Transvaal appear to represent the typical form (Broadley 1962).

The tropical leopard tortoise, *G. p. babcocki*, ranges from southern Sudan and southern Ethiopia south to Namibia, the northern Cape Province, western Orange Free State and northern Natal.

Habitat

In the south portion of its range this species occupies a wide range of habitats, from semi-desert bushy Karoo-Namib shrubland (annual rainfall below 100 mm) to woodlands and savannas of the highland Sourveld (annual rainfall of up to 1400 mm) in the Amatola Mountains of the eastern Cape Province (Greig and Boycott 1978).

Behaviour

This tortoise is active during the daytime, but avoids excessive heat at midday by sheltering under bushes (Greig and Boycott 1980). During the cold and dry winter months they often find shelter in unoccupied burrows, especially those of antbears, but also use those of springhares, jackals, and foxes. They may also find shelter under rocks and logs, in termitaria and in dense undergrowth of shrubs (Grobler 1982). This species will usually float in water if its habitat is inundated by floods. Many were found "swimming" in Lake Kariba when it was initially filling.

In the Serengeti National Park in Tanzania, an adult female *G. p. babcocki* was marked and released 8 km away from her capture point, where she remained for three and half months during a dry period. When the rains broke, the tortoise began

to move back to her original capture point by a circuitous route, taking 53 days to cover 12 km. In the subsequent four months she was located 27 times, always within 2.2 km of the original capture point, her home range being calculated as 1.6 sq km (Bertram 1979).

Breeding

Combat between rival males often precedes courtship, consisting of the male thumping the back and sides of the female's carapace with his gular "ram." The male then mounts the female, his concave plastron fitting over the posterior curve of her carapace, while he grips her carapace with the claws of his forelimbs. Copulation is accompanied by peculiar asthmatic "hissing croaks" (Bennefield 1982).

The female selects a nesting site in an open area and excavates a flask-shaped hole (about 20-30 cm deep and of a similar diameter at the bottom) with her hind feet, frequently urinating to soften the ground. The soil is lifted up on each foot in turn and deposited neatly at each side of the hole. The spherical eggs are covered with a thick mucous secretion which helps to protect them as they drop into the hole. As each egg is laid, it is moved to the side of the nest by the female's foot, thus reducing the risk that the next egg may fall on it and break it. The eggs are usually arranged in two or three layers. The hole is then back-filled with the moist excavated soil, tamped down with the hind feet and often camouflaged with sticks and leaves. The typical form has been recorded as laying six clutches totalling 52 eggs between 23 November and 16 May (Cairncross 1946). A Zimbabwean *G. p. babcocki* laid five clutches totalling 48 eggs at Bulawayo between 18 December and 29 May (Bennefield 1982).

The typical form lays clutches of about five to 18 large eggs averaging 43 to 50 mm in diameter which take from eight to 18 months to hatch (Archer 1948). The tropical leopard tortoise usually lays 5-14 eggs, but clutches of 23 (Zululand: Rose 1962), 24 (Transvaal: Archer 1968), and 30 (Kenya: Leakey 1944) have been recorded. The eggs of *G. p. babcocki* usually average 34-40 mm in diameter, but Archer (1968) records a diameter of 25-28 mm for eggs from his Transvaal female, and Poglayen-Neuwall gives diameters of 42-48 mm for eggs of this subspecies laid at Tucson Zoo, Arizona. The tropical subspecies has shorter incubation times, 178-206 days in Zambia (Wilson 1968), 392 days in Zimbabwe (Bennefield 1982) and 378-384 days in Natal (Rowe-Rowe, 1970). Hatchlings are 37-50 mm in carapace length.

Diet

This species is largely vegetarian and seems to prefer succulent vegetation. In the Addo Elephant National Park, it has been observed feeding on *Portulacaria afra*, *Blepharis* sp., *Opuntia*

sp. and *Gazania krebsiana* (Branch and Braack 1987). Hewitt (1937) recorded their diet included grass and various succulents, crassulas, spekboom, thistles, prickly pear, and also pumpkins, watermelons, and beans when available. Bones, dry dog faeces, and owl pellets are also devoured.

The tropical leopard tortoise feeds largely on grass, but succulents, fungi, and ripe fruit of the marula (*Sclerocarya caffra*) are readily consumed. Bones and hyena faeces are eaten for their calcium content. In the Lombard Nature Reserve in the southwestern Transvaal, the diet includes the Devil's Thorn (*Tribulus terrestris*) and the grasses *Cynodon dactylon* and *Themeda triandra* (Van Zyl 1966).

Threats to Survival

This large tortoise is eaten by man throughout its range, and it is usually rare in densely populated areas. The eggs are dug up and devoured by many small carnivores, and others are destroyed by ants. Hatchling tortoises are preyed upon by secre-

tary birds, ground hornbills, and crows, in addition to many small carnivores. Reptilian predators include *Varanus exanthematicus albigularis* and *Bitis a. arietans* (Wilson 1968). Many tortoises are destroyed in bush fires, but others survive the loss of all or most of their epidermal shields, regenerating irregular keratinous scar tissue.

Figures for the international trade in live tortoises for the period 1980-85 are provided by Evans (1988).

Conservation

This species seems to be in no danger, as it is protected in numerous national parks and other reserves throughout its range. There are also good populations in the sparsely inhabited Kalahari. In the Cape Province, the typical form is protected in the Addo Elephant, Bontebok, Karoo, and Mountain Zebra National Parks, as well as another 14 nature reserves (E.H.W. Baard, in litt.).

Geochelone sulcata
Spurred Tortoise (English)
Abu gatta, Abu gefne (Arabic)

Donald G. Broadley

Description

Beak weakly hooked, edge of jaws strongly dentate; prefrontal large, usually divided longitudinally; frontal usually large, rarely broken up; remaining upper head scales small, irregular; forelimb anteriorly with large unequal, juxtaposed or imbricate scales, forming 3-6 longitudinal and 6-7 transverse series from elbow to outer of five claws; posterior side of thigh with 2-3 large conical tubercles; heel with large, conical, spur-like, bony tubercles; claws four; tail without terminal claw-like tubercle.

Carapace flattened dorsally, sides descending abruptly, deeply notched in nuchal region, anterior and posterior margins reverted and serrated, not more than twice as long as deep; dorsal shields concentrically grooved; nuchal usually absent; vertebrals five, rarely four, six, or seven, not convex, the second, third, and fifth much broader than long, broader than the costals; costals four, rarely five, not forming an angle with the marginals; marginals 11, rarely 10, 12, or 13; supracaudal usually undivided.

Front lobe of plastron somewhat produced and bifid; gulars paired, deeply forked in males; pectorals very narrow, their anterior border usually straight, widening abruptly towards the axillary notch; axillaries two, outer moderate to small, inner minute; inguinals two, outer large to moderate, inner small, meeting femoral; hind lobe deeply notched posteriorly, angular or crescentic. Posterior half of plastron deeply concave in adult males.

Coloration

Carapace of juvenile (50 mm) pale yellow, the scutes with narrow brown sulci. Plastron yellowish white. Carapace of adult brownish to horn colour, uniform. Plastron, head and limbs yellowish, uniform.

Size

Maximum carapace length 830 mm. Carapace length of female (MCZ 19975) from Kastina Emirate, 670 mm, breadth 470 mm, height 270 mm. Apparently exceeded by that of a specimen mentioned below.

Growth

On hatching, the young are 50 mm long and 47 mm wide. The margins of the carapace are strongly lobed. An 18-year-old tortoise measured 750 mm in carapace length and had a mass of over 60 kg. Growth in captivity can be very rapid. In twelve years, an individual increased its mass from 43 kg to 105 kg (Flower 1925).

Distribution

The Sahel region from southern Mauritania and northern Senegal eastward to northern Ethiopia.

Habitat

The three major vegetational zones occupied by this species are undifferentiated woodland; Sahel *Acacia* wooded grassland and deciduous bushland; Sahel semidesert grassland and shrubland.

Behaviour

During the dry season, these tortoises retire into burrows or "pallets" which they excavate using the forelimbs as shovels. Reports of the depth of these burrows vary between 75 cm and 3.5 metres (Villiers 1958).

Breeding

During the rainy season copulation occurs repeatedly over the course of about a week, each coupling lasting about 15 minutes and repeated several times a day. The male mounts the female, leaning heavily on his forelegs, which rest on the flared anterior edge of the female's carapace. Throughout the duration of the coupling, the male intermittently holds his head vertically and at regular intervals makes a muffled hoarse cry like a deep rattle (Villiers 1958).

Diet

This species, the largest African tortoise, frequents very arid regions lacking permanent water supplies and areas where rainfall is scanty and erratic. Its diet consists largely of succulent plants, but in captivity it shows a preference for *Ipomaea* leaves (Villiers 1958).

Threats to Survival

It is not known whether the degradation of habits in the Sahel during the recent severe droughts has adversely affected the populations of *G. sulcata* or whether it has increased the utilization of tortoises as a source of human food. As most of the area occupied by these species is inhabited by Moslems, it is probably less exploited for its meat than *G. pardalis*.

Conservation

This species occurs in arid regions which are not often selected for proclamation as national parks or reserves. However, the recently created Air and Tenere Reserve in Niger should shelter some populations of *G. sulcata*.

Current Research

None known.

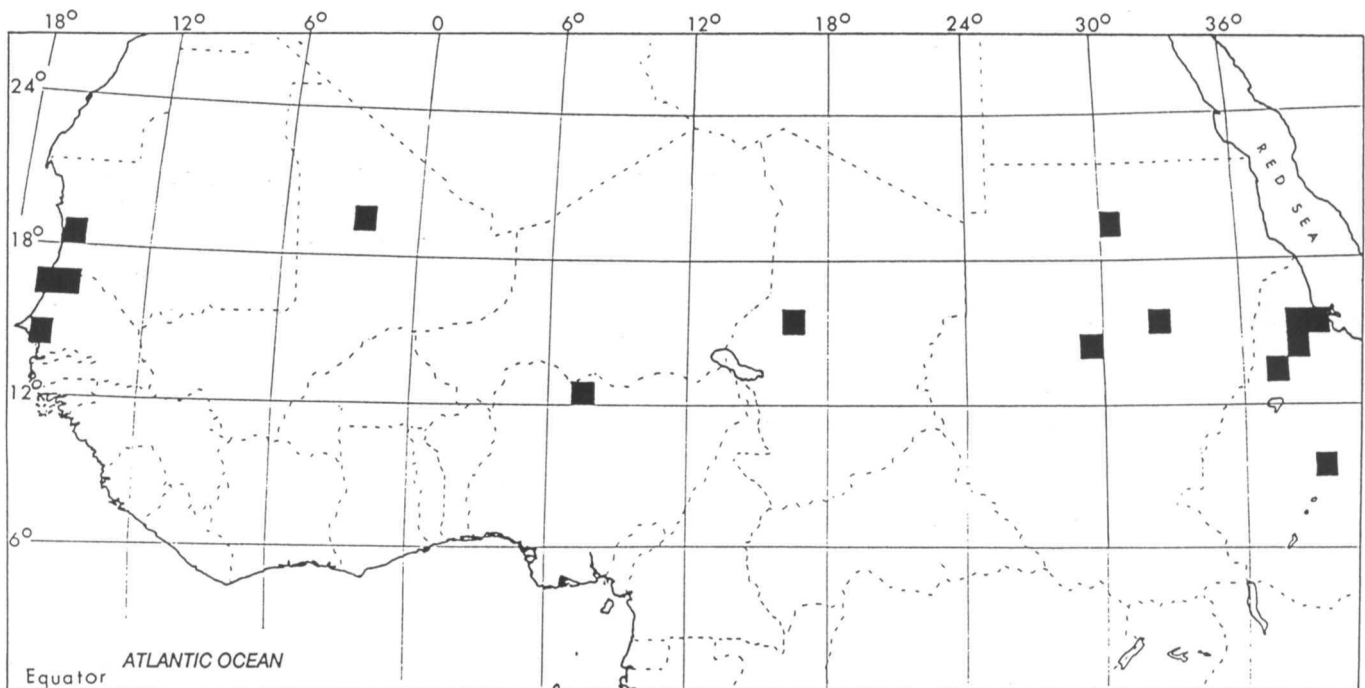
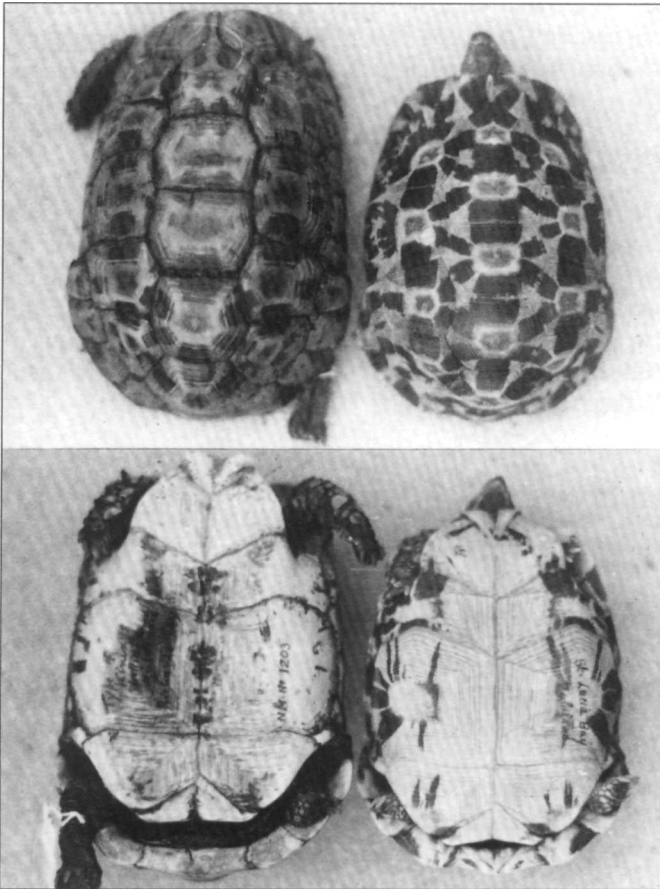


Figure 11. Distribution of *Geochelone sulcata*.

Kinixys belliana Bell's Hinged Tortoise

Donald G. Broadley



Bell's hinge-back tortoise (*Kinixys belliana zuluensis*); left, male (type specimen), Richards Bay, Zululand; right, female, St. Lucia Bay, Zululand. (Photo by D.G. Broadley.)

Editorial Note

In his *Kinixys* species accounts, Dr. Broadley has elevated *Kinixys belliana spekkii* to specific status and has resurrected *Kinixys lobatsiana* as a valid species. Dr. Broadley is a leading authority on the taxonomy of *Kinixys* and undoubtedly has carefully researched this problem. However, we strongly feel that this publication is primarily concerned with conservation and ecology, and will be peer reviewed by conservationists and ecologists. Therefore, it is not an appropriate forum to propose changes in nomenclature. We have however included these species accounts as an addendum to *Kinixys belliana*, thereby retaining the valuable information contained in them, while not transcending the scope of this publication.

Description

Beak not or but weakly to moderately hooked, unicuspid; edge of jaws not serrated; prefrontal large, entire, semidivided or divided longitudinally, rarely broken up; frontal small (occasionally divided longitudinally), moderate or broken up; upper head scales small, irregular; forelimb anteriorly covered with few or many, large, unequal, scattered or juxtaposed, strongly imbricate or non-imbricate, more or less pointed (subcircular or pointed in young, subacute in adults) scales, which on anterior edge form a longitudinal series of 5-9 from elbow to outer of five claws, rarely four (except in the western race *nogueyi*, which always has four); posterior side of thigh without enlarged tubercles; heel with or without well defined spur-like tubercles, claws four, very rarely three; tail terminating in a more-or-less distinct horny tubercle that may be much larger in males.

Carapace moderately convex or slightly flattened dorsally (shell length/height ratio 1.82 to 2.37), sides sloping, not or but feebly notched in nuchal region; anterior margin not or but slightly expanded not or but slightly reverted, not spinose in young, posterior margin expanded, not or but slight reverted, not or but slightly serrated, not spinose in young; rear end in young sloping more or less steeply, in adults even more so; dorsal shields with well marked growth annuli and deep sulci except in aged specimens, sometimes swollen, not convex. Nuchal usually elongate, though as broad as, or much broader than long in very young (occasionally divided, minute or absent); vertebrals five, rarely four, six or eight, not or but slightly convex, first broader than long in young, broader than long, as broad as long, or longer than broad in adults; second to fifth as broad as, or broader than long; second broader, subequal to, or narrower than, fifth in young, narrower in adults; fifth flat in young, more or less convex in adults; costals four, rarely three or five, usually not forming an angle with marginals; marginals 9-12, usually 11; supracaudal undivided, very rarely divided with or without a tendency to be incurved in males, otherwise not or slightly reverted in both sexes.

Front lobe of plastron anteriorly truncate, very thick, usually slightly or moderately projecting beyond the anterior border of the carapace (especially in males), not or very feebly notched; gulars paired, usually less than twice as broad as long; pectorals with a moderate median sulcus (in short contact or separated in the form *mertensi* Laurent); axillaries 2-4, the innermost small, inconspicuous or absent, the outermost more or less concealed; inguinal large, usually in contact with the sixth marginal, in contact with the femoral; hind lobe very short and truncate, not or but slightly notched posteriorly.

Coloration

Carapace buff, yellowish brown, olive brown or reddish brown; in young uniform, or the areolae deep brown, surrounded by zone of yellow which may extend to the margins of each scute or be interrupted by fine black radiations from the darker areolae or be entirely replaced by black edging. The juvenile colouring may persist in adults, though usually with the modification that the black edging of the shields is irregularly or symmetrically broken up by yellow pigment, or only the black areolae of the juvenile pattern persists, in which case it is frequently interrupted by a median, longitudinal, yellow streak. In some old individuals, usually males, the colouring may be uniform horn coloured.

Plastron horn coloured, uniform or patterned with black (irregularly blotched with black in *nogueyi*), the latter sometimes in the form of rings or radiations from around the areolae.

Size

Largest male (NM 1203 Richards Bay, Zululand [type of *K. b. zuluensis* Hewitt]) carapace length 206 mm, breadth 140 mm, height 89 mm; largest female (NMZB-UM 32977 Mutare, Zimbabwe) carapace length 217 mm, breadth 142 mm, height 103 mm.

Subspecies

When Laurent (1956) described *AT. b. mertensi*, the sample of "*K. belliana*" that he used for comparison consisted of 8 *K. spekii* and the "false type specimen" of *K. belliana*, which is a *K. b. nogueyi* (Broadley 1981:196). In his 1962 paper, three quarters of Laurent's enlarged sample of "*belliana*" were *K. spekii*, whereas I believe his "*schoensis*" sample to represent typical *belliana*.

The true type specimen of *K. belliana* Gray, which I identified in 1979, soon after it had been removed from display in the Reptile Gallery at the Natural History Museum, has no locality data, but in the ratios used by Laurent it comes closest to Ethiopian material, although it also just falls within the range of variation for *mertensi*. With the limited material available from this area, it seems best to place *mertensi* provisionally in the synonymy of *K. belliana belliana*, which will then have a range extending from northeastern Zaire through southern Sudan and Ethiopia to northwestern Somalia and south to Uganda and western Kenya.

The adult female type of *AT. b. belliana* is devoid of markings and the other material is very variable. The markings may be zonary, radial, speckled or absent. In contrast, adults of the East African coastal form, which ranges from northeastern Tanzania (Tanga) south to Zululand, has well-defined broad black radial markings in both sexes. As it is isolated from the populations of *K. b. belliana* by the belt of desert and semi-desert through Somalia and northern Kenya, the revival of the subspecies *K. b. zombensis* (Hewitt 1931) (with *K. b. zuluensis* Hewitt, 1931, as a synonym) for this east coast form by Bour (1979) seems to be justified. This subspecies has been introduced into northwestern Madagascar (Bour 1979).

Key to the subspecies of *K. belliana*

- 1a. Forelimb always with 4 claws; plastron with irregular dark blotches or uniform; range Senegal east to northern Cameroon.....*K. b. nogueyi* (Lataste)
- 1b. Forelimb usually with 5 claws (occasional specimens have 4); plastron with symmetrical dark patterns or uniform.
- 2a. Adults always with a broad black radial pattern on the carapace; range East African coastal plain from Tanzania south to Zululand.....*K. b. zombensis* (Hewitt)
- 2b. Adults with variable carapace patterns, or uniform, range eastern Cameroon east to western Kenya, Ethiopia and northwestern Somalia.....*K. b. belliana* (Gray)

Distribution

The western race *nogueyi* ranges from Senegal east to northern Cameroon, where it meets the typical form, which then extends eastwards through northeastern Zaire to western Kenya, Ethiopia and northwestern Somalia. The subspecies *zombensis* extends along the East African coastal plain from Tanzania to Zululand, and this form has been introduced into northwestern Madagascar (Bour 1979).

Habitat

Moist savanna woodland and thicket.

Behaviour

These tortoises feed in the early morning and the evening, when it is cool, taking cover during the hottest part of the day. They will emerge as soon as it begins to rain. During the dry season these tortoises aestivate in animal burrows, holes in termitaria, or burrows excavated under tree roots.

When alarmed, this species withdraws its head with a hiss and closes the forelimbs over it, simultaneously curling the tail tightly under the shell and withdrawing the hind legs, so that when the rear portion of the carapace is pulled down only the soles of the hind feet are exposed. If picked up, it will react by defecating copiously and odoriferously. It may also snap its jaws and flail its limbs.

Breeding

Combat between males occurs at the beginning of the rainy season. They fight by ramming one another until the weaker one is overturned or driven off. When mating, the male climbs onto the back of the female, bracing himself with his forelimbs while thrusting his tail beneath the rear edge of her carapace. Copulation is accompanied by continuous wheezing gasps from the male, while the female seems quite disinterested.

Nesting occurs from November to April in the southern part of the species' range. Normally two or three eggs (but up to a

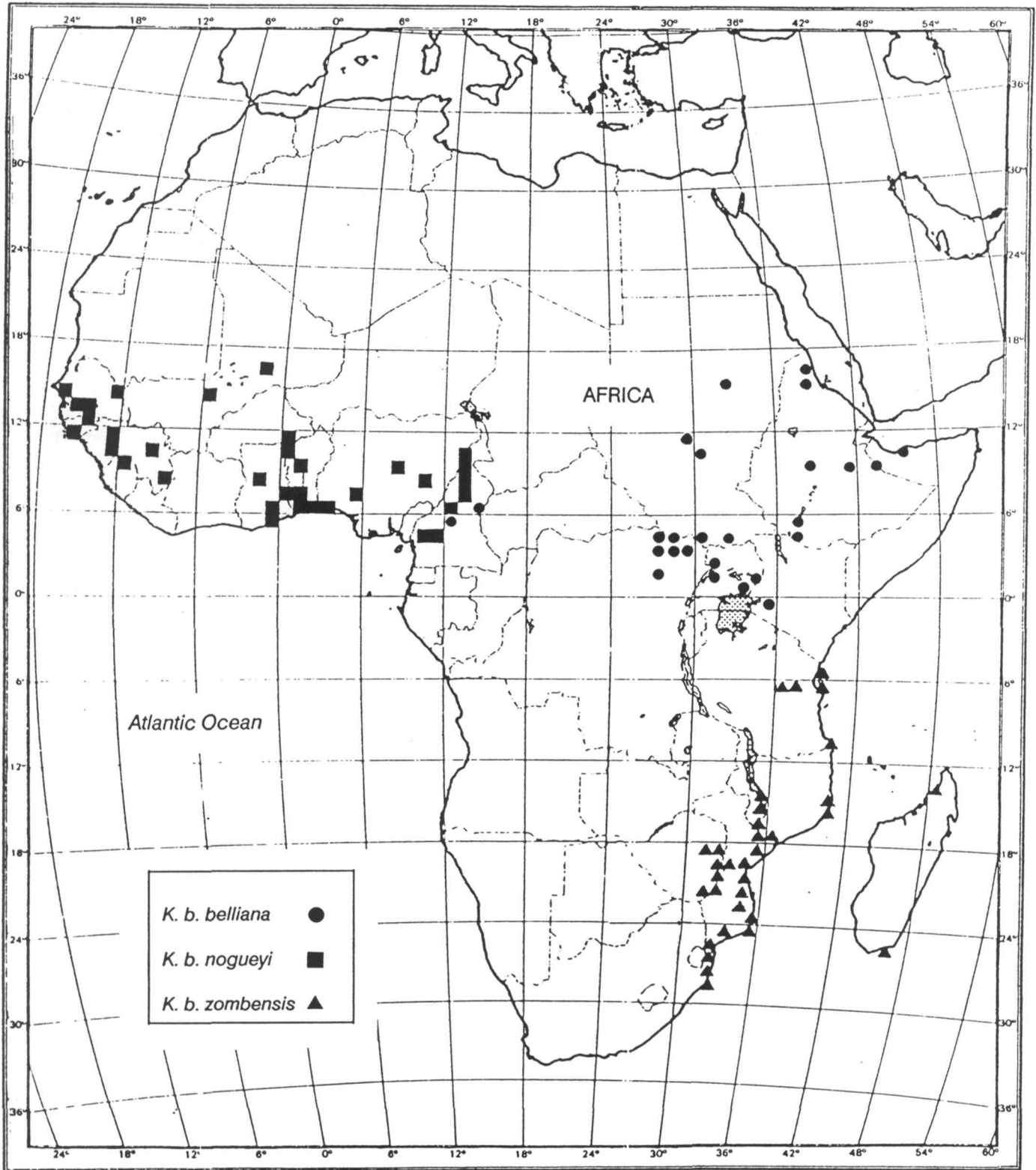


Figure 12a. Distribution of *Kinixys belliana*.

maximum of ten) are laid. They are oval, measuring 38-47 x 30-36 mm, and hatch after about a year. The hatchlings are about 40 mm in carapace length.

Diet

This tortoise has a very catholic diet. It eats a wide range of vegetation and fruit, succulents and fungi being particularly favoured. The most popular foods are millipedes, which are chased and torn to pieces. Snails (small *Achatina* and introduced *Helix*) are eaten after the shells have been broken. This species also scavenges, devouring dried corpses of amphibians and other small animals, as well as small bone fragments.

Threats to Survival

This tortoise is eaten by man throughout most of its range. Of its other enemies, the most formidable is the ground hornbill, which can smash a hole through the thick bone of the carapace with its powerful bill.

Conservation

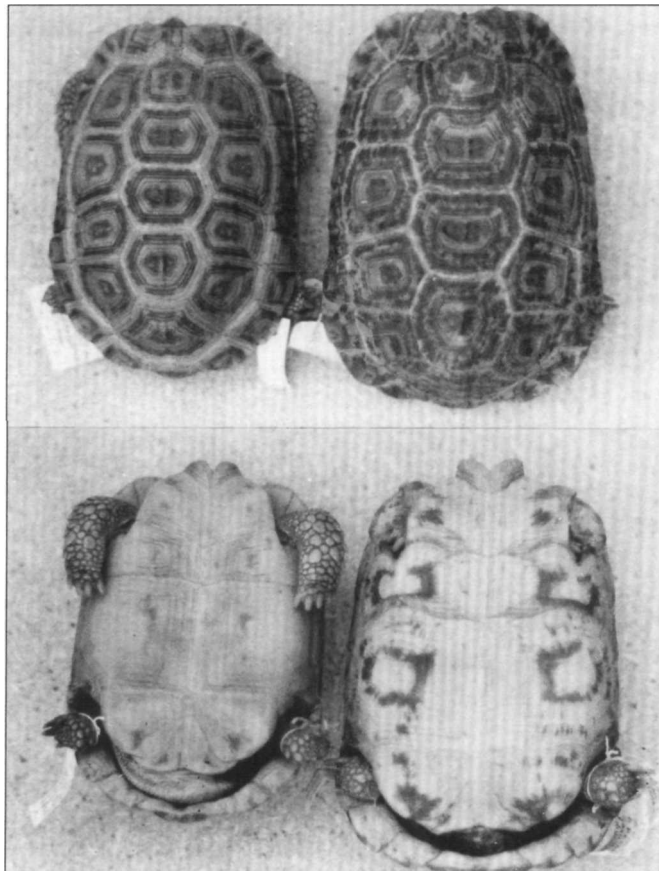
This species is protected in many national parks and game reserves throughout its range. Due to its small size, cryptic coloration, and preference for a moist savanna habitat, it often escapes observation and remains common in densely populated areas (e.g., Mutare District in eastern Zimbabwe).

Addendum

In the last comprehensive revision of this genus, Loveridge and Williams (1957) recognized a single savanna species, *K. belliana*, with a West African subspecies *nogueyi*. In my 1981 review of the southeast African populations, I was able to demonstrate that *K. natalensis* (Hewitt) is a valid species, sympatric with *K. belliana*. The latter species was divided into two subspecies, the typical form restricted to the coastal plain and *K. b. spekii* (Gray), a depressed form on the interior plateau, but also descending onto the coastal plain in some places.

Subsequent examination of more material from throughout the range of *K. belliana* (including all the specimens in the major U.S. museums) has convinced me that *K. spekii* is a valid species, which is sympatric or parapatric with *K. belliana* in several areas in southern Malawi (Shire Valley west of Zomba and Mangochi), eastern Zimbabwe (Mutare and Chipinge Districts), southern Mozambique (Maputo Elephant Reserve), and northern Zululand (Ndumu Game Reserve). There seem to be no hybrid populations, except perhaps for a few specimens from the southern coast of Somalia.

K. lobatsiana (Power 1927) of southeastern Botswana and the Transvaal middleveld also appears to be a valid species, and its status is now being investigated.



Bell's hinge-back tortoise (*Kinixys belliana spekii*), 10 km. SSE of Ressana Garcia, S. Mozambique; left, male; right, female. (Photo by D.G. Broadley.)

"*Kinixys spekii*" Speke's Hinged Tortoise

Description

Beak not or but weakly to moderately hooked, unicuspid; edge of jaws not serrated; prefrontal large, usually divided longitudinally; frontal large, entire; upper head scales small, irregular; forelimb anteriorly covered with large, unequal, juxtaposed, more or less imbricate, more or less pointed scales, which on anterior edge form a longitudinal series of 7-10 from elbow to outer of five claws; hinder side of thigh without enlarged tubercles; heel with or without well defined spur-like tubercles, claws four; tail terminating in a more or less distinct horny tubercle, that may be much larger in males.

Carapace depressed (shell length/height ratio 2.24 to 2.93), highest point frequently on vertebral one or two; scarcely or not notched in nuchal region (rarely deeply notched, when the nuchal is absent); anterior margin not or but feebly expanded, not reverted, not spinose in young; posterior marginals not

expanded, weakly reverted, not serrated, not spinose in young; rear end in young sloping more or less steeply, in adults even more so; carapace scutes relatively flat, with well-defined growth annuli (except in old males, which usually have very worn shells). Nuchal moderate to elongate in adults (rarely divided or absent); vertebrals five, rarely four, six, or eight, not or but slightly convex, first broader than long in young, broader than long, as broad as long, or longer than broad in adults; second to fifth as broad as, or broader than long; second broader, subequal to, or narrower than, fifth in young, narrower in adults; fifth flat in young, more or less convex in adults; costals four, rarely five usually not forming an angle with the marginals; marginals 10-13, usually 11; supracaudal undivided, with the underside narrowed or proximally excavate in both sexes.

Front lobe of plastron truncate anteriorly; thick, projecting well beyond the anterior border of the carapace in both sexes, not or but moderately notched; gulars paired, usually less than twice as broad as long; pectorals with a moderate median sulcus; axillaries 2, of moderate size; inguinal large, usually in contact with sixth marginal, in broad contact with the femoral; hind lobe short and truncate, with a very shallow posterior notch. Plastron usually concave in adult males.

Coloration

Carapace with a zonary pattern in juveniles and subadults. This may persist in adult males, but they often become uniform olive-brown or yellow-brown. In females, the dark brown to black zones tend to break up into short ragged radiations. In adult males the plastron is uniform yellow or may show vestiges of this pattern. The head, limbs, and tail are usually uniform yellow, but may be speckled with black.

Size

Largest male (TM 41761 Maputo Elephant Reserve, Mozambique) carapace length 181 mm, breadth 124 mm, height 79 mm; largest female (TM 39412 10 km south of Kongola Ferry, Caprivi, Namibia) carapace length 198 mm, breadth 126 mm, height 79 mm. Archer (1967) recorded a specimen which was 200 mm long after 22 years in captivity.

Taxonomy

The following forms are regarded as synonyms of '*K. spekii*': *darlingi* (Boulenger 1902); *australis* (Hewitt 1931); *jordani* (Hewitt 1931); *youngi* (Hewitt 1931); and *mababiensis* (FitzSimons 1932).

I have examined the unique type specimen of *Testudo procterae* (Loveridge 1923), and am satisfied that it is a subadult '*Kinixys spekii*' and not a synonym of *Malacochersus tornieri*.

Distribution

The central plateau areas of Africa south of the equatorial forests, extending from Kenya south to the northern Transvaal, Swaziland and southern Mozambique, westward to southern Zaire, Angola, and northern Botswana.

Habitat

Moist savanna woodlands, especially miombo and mopane, but extending into drier *Acacia* and *Commiphora* deciduous woodland and thicket in the northeastern part of its range.

Behaviour

These tortoises feed in the early morning and the evening, when it is cool, taking cover during the hottest part of the day. They will emerge as soon as it begins to rain. During the dry season they aestivate in rock crevices, inside hollow logs, holes in termitaria, or in burrows excavated under tree roots or rocks. They tend to spend the dry season in the woodland (which provides more cover), but move into the woodland/grassland ecotone (which provides more food) during the rains (Scoones 1986).

When alarmed, this species withdraws its head with a hiss and closes the forelimbs over it, simultaneously curling the tail tightly under the shell and withdrawing the hind legs, so that when the rear portion of the carapace is pulled down only the soles of the hind feet are exposed. If picked up, it will react by defecating copiously and odoriferously. It may also snap its jaws and flail its limbs.

Breeding

Combat between males occurs at the beginning of the rainy season. They fight by ramming one another until the weaker one is overturned or driven off. When mating, the male climbs onto the back of the female, bracing himself with his forelimbs while thrusting his tail beneath the rear edge of her carapace. Copulation is accompanied by continuous wheezing gasps from the male, while the female seems quite disinterested.

Nesting occurs from November to April in the southern part of the species' range. Normally two or three eggs (but up to a maximum of six) are laid. They are oval, measuring 38-47 x 30-34 mm, and hatch after about a year. The hatchlings measure 30-50 mm in carapace length.

Diet

This tortoise has a very catholic diet. It eats a wide range of vegetation and fruit, succulents and fungi being particularly

favoured. The most popular foods are millipedes, which are chased and torn to pieces. Snails (small *Achatina* and the introduced *Helix*) are eaten after the shells have been broken. This species also scavenges, devouring dried corpses of amphibians and other small animals, as well as small bone fragments.

Threats to Survival

This tortoise is eaten by man throughout most of its range. Of its other enemies, the most formidable is the ground hornbill, which can smash a hole through the carapace with its powerful bill. The bones of the shell are much more fragile than those of *K. belliana*.

Conservation

This species is protected in many National Parks and Game Reserves throughout its range. Due to its small size, cryptic coloration and preference for a moist savanna habitat, it often escapes observation and remains common even in densely populated areas.

"Kinixys lobatsiana" Lobatse Hinged Tortoise

Description

Beak weakly to moderately hooked, unicuspid; edge of jaws not serrated; prefrontal large, semidivided or divided longitudinally; frontal moderate, often fragmented; upper head scales small, irregular; forelimb anteriorly covered with a few large more or less pointed (pointed in young, subacute in adults) scales, set in matrix or smaller flat scales, claws five; thigh without enlarged tubercles; heel without well defined spur-like tubercles, claws four; tail terminating in a distinct horny tubercle that is much larger in males.

Carapace moderately convex (shell length/height ratio 2.41 to 2.49 in three males; 2.06 to 2.20 in five females), sides sloping, feebly notched in nuchal region; anterior margin not or but slightly expanded, not reverted; posterior margin not expanded, usually moderately reverted; rear end sloping more or less steeply; carapace scutes with well marked growth annuli and deep sulci, except in aged specimens, sometimes swollen, not convex. Nuchal usually elongate, sometimes minute; vertebrals five, first as long or longer than broad in adults, second to fifth broader than long, second narrower than fifth in adults

(subequal in young), fifth flat in young, more or less convex in adults; costals four, not forming an angle with the marginals; marginals 11, supracaudal undivided, usually reverted, inferiorly not narrowed mesially, but often with a median groove.

Front lobe of plastron anteriorly truncate, very thick, usually slightly projecting beyond the anterior border of the carapace (especially in males), notched strongly in males, feebly in females; gulars paired, usually less than twice as broad as long; pectorals with a short median sulcus; axillaries 2-3; inguinal large, in contact with or separated from sixth marginal, in contact with the femoral; hind lobe very short and truncate, feebly notched posteriorly.

Coloration

Carapace buff to dull yellow, areolae brown, with irregular black radiations which become worn away from the centre of the scute, so that old specimens are often devoid of markings. Plastron buff with a brown border to the areolae and sometimes some narrow black rays, these markings fading with age.

Size

Largest male (AM/cotype Lobatse, Botswana) carapace length 162 mm, breadth 103 mm, height 65 mm; largest female (TM 49863 Kromdraai, Transvaal) carapace length 167 mm, breadth 116 mm, height 79 mm.

Distribution

Southeastern Botswana at Lobatse and Gaborone, eastward into the central Transvaal middleveld.

Habitat

Mixed *Acacia* and *Combretum* woodland on the southeast Botswana hardveld, extending into tropical bushveld in the Transvaal. It extends onto the high veld only in rocky areas that provide adequate protection from low winter temperatures, as along the Magaliesberg range (Boycott and Bourquin 1988).

Threats to Survival

This species is undoubtedly eaten by man throughout its range.

Conservation

This tortoise is protected in the Loskop Dam Game Reserve in the Transvaal.

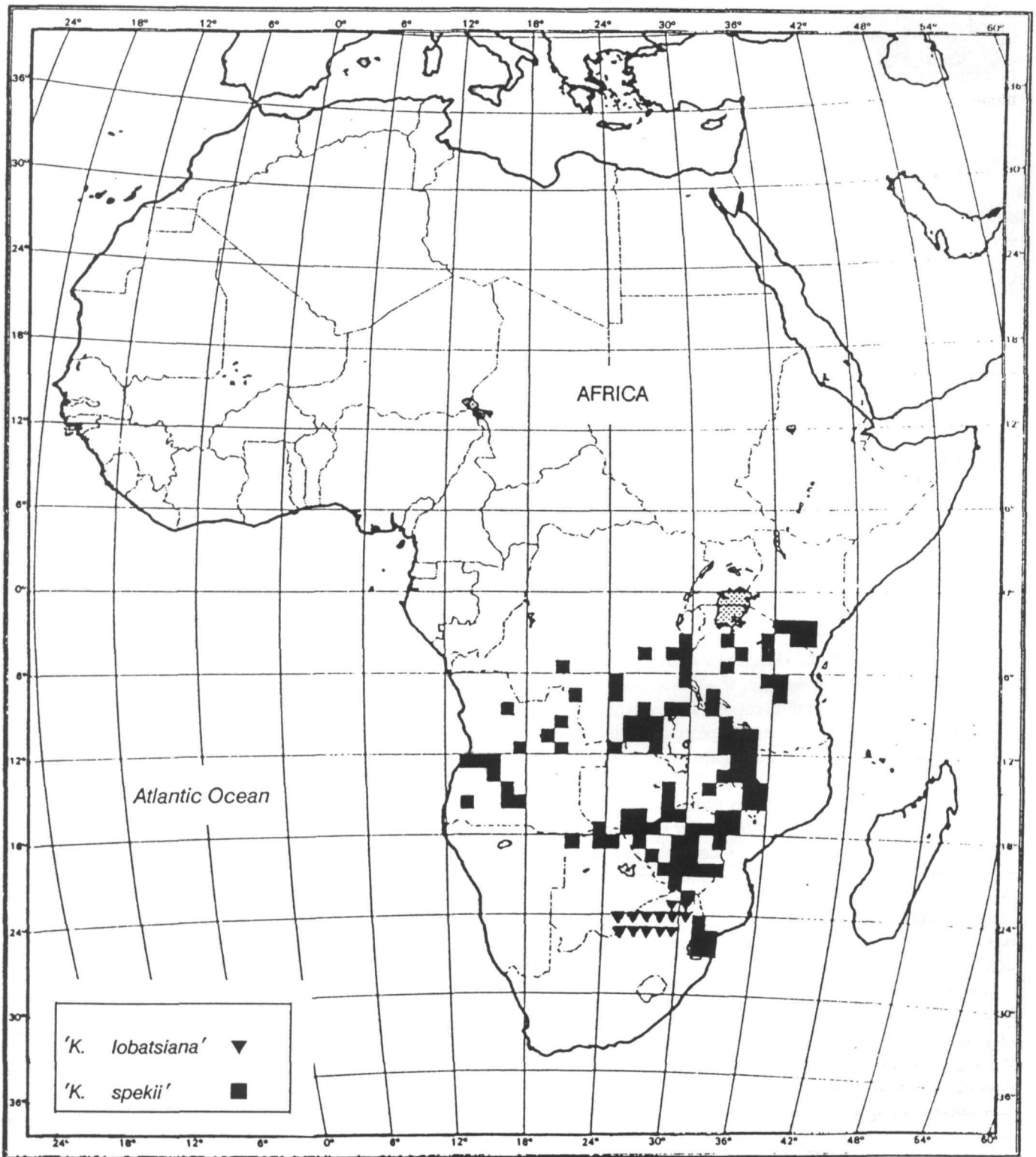


Figure 12b. Distribution of "*Kinixys lobatsiana*" and "*Kinixys spekii*."

Kinixys erosa

Serrated Hinged Tortoise

Donald G. Broadley

Description

Beak weakly to moderately hooked, unicuspid; edge of jaws not dentate; prefrontal divided longitudinally; frontal large or fragmented; upper head scales small and irregular; forelimbs anteriorly covered with a few scattered, extremely large, unequal or non-imbricate, more or less pointed scales, which on the anterior edge form longitudinal series of four to five from elbow to outer of five claws; posterior side of thigh without enlarged tubercles; heel usually without any spur-like tubercle, if present situated low on the heel, claws four; tail terminating in a horny, claw-like tubercle that is much larger in males.

Carapace flattened dorsally, sides sloping, not or but scarcely to moderately notched in nuchal region; anterior margin strongly expanded and slightly to strongly reverted, spinose in young; posterior margin not expanded, more or less reverted and strongly serrated, spinose in young; rear end in young sloping gradually, in adults more steeply, if vertical only from the middle of the fifth vertebral; carapace scutes concentrically striated, neither swollen nor convex (except as noted below); nuchal absent or rarely present, elongate, occasionally developed on the underside only; vertebrals five, first broader than long in young, broader than long, as broad as long, or longer than broad in adults, second to fifth broader than long, second broader or subequal to fifth in young, narrower in adults, fifth flat in hatchlings, more or less convex in adults, broader than the costals; costals four, rarely three, not or but rarely forming an angle with the marginals; marginals 11, rarely 12, the anterior much longer than the posterior ones; supracaudal undivided, more or less reverted in both sexes.

Front lobe of plastron very thick, projecting beyond the anterior border of the carapace, openly or deeply notched, bifid; gulars paired; axillaries three to four, the innermost small, the one or two outermost more or less concealed; inguinal large, in contact with the femoral; hind lobe very short, truncate, not or very broadly notched posteriorly.

Coloration

Head light yellow, limbs dull yellowish. Carapace of hatchlings nearly uniform pale red-brown, darkening with age until almost black in old individuals, while the centres of the scutes remain somewhat lighter; in older juveniles and all adults irregularly stellate patches of light yellow appear on the outer margins of the costals, also in smaller areas on the vertebrals, upper portions of the costals and the anterior and posterior marginals (well-illustrated in Laurent 1964: fig. 2).

Plastron black with yellow on the outer margins of the gular and humeral scutes and narrow zones of yellow along the sutures, or with a broader midplastral yellow zone.

Size

Largest male (AMNH 10023 from Banalia, Zaire) carapace length 323 mm, breadth 236 mm, height 122 mm (Schmidt 1919); largest female (MCZ 52169, from Inferri Chiefdom, Sierra Leone) carapace length 260 mm, breadth 172 mm, height 106 mm.

Distribution

Gambia eastward to Zaire and Uganda, south to Cabinda, northern Angola (Laurent 1964) and the northwestern shore of Lake Tanganyika. Fossil material is known from the lower Miocene deposits at Songor Hill, near Lake Victoria, Kenya (Meylan and Auffenberg 1986).

Habitat

Evergreen forest, especially marshy areas. During the day it hides beneath logs, roots, and heaps of dead and living vegetation, sometimes completely covering itself with debris (Lang in

Schmidt 1919: 405). These tortoises may be found living in streams, where they can swim and dive to obtain food.

Diet

Omnivorous.

Breeding

In northeast Zaire, a captive specimen laid four eggs in November; they measured 40 x 36 x 31 mm (Schmidt 1919: 404). Eggs laid by captive specimens at Dakar averaged 45 x 37 x 31 mm (Villiers 1958).

Threats to Survival

Probably eaten by man throughout its range. In Zaire, dogs are used to track the tortoises by scent (Schmidt 1919: 405). It is presumably threatened in the long-term by the continual clearance of its rain-forest habitat.

Conservation

This species appears to be protected in the Sapo National Park in Liberia; the Tai, Marahoue, Banco, and Azagny National Parks in the Ivory Coast; the Campo and Dja Nature Reserves in Cameroon; the Okanda National Park in Gabon; and the Odzala National Park in the Republic of the Congo.

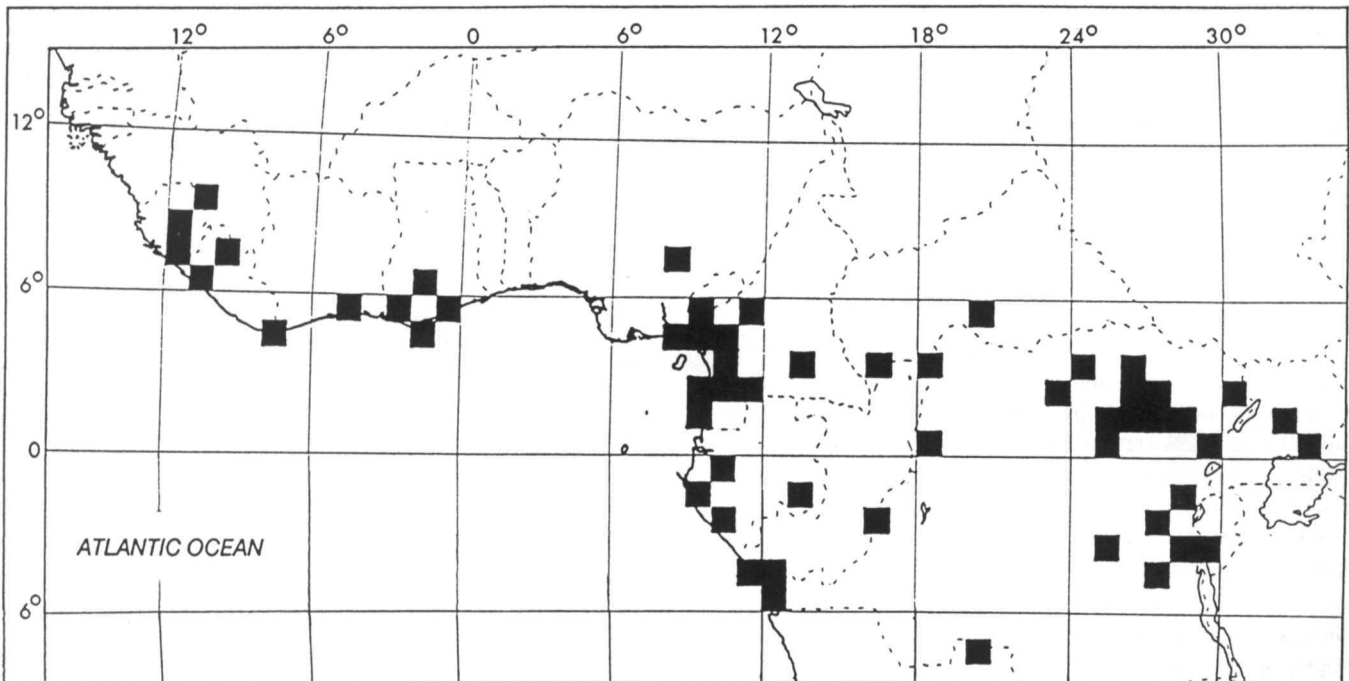


Figure 13. Distribution of *Kinixys erosa*.

Kinixys homeana

Home's Hinged Tortoise

Donald G. Broadley

Description

Beak moderately to strongly hooked, unicuspid; edge of jaws not dentate; prefrontal divided longitudinally; frontal large, small, or fragmented; head scales small and irregular; forelimb anteriorly covered with a few scattered, large, unequal, strongly imbricate, more or less pointed scales, which on the anterior edge form a longitudinal series of five to eight from elbow to outer of five claws; posterior side of thigh without enlarged tubercles; heel with or without a spur-like tubercle, claws four; tail terminating in a small, somewhat claw-like tubercle that is larger in males.

Carapace flattened dorsally, sides sloping, not or but openly notched in nuchal region; anterior margin strongly expanded and not or but slightly reverted, spinose in young; posterior margin not expanded; more or less strongly reverted and strongly serrated, spinose in young, rear end in young sloping gradually, in adults vertically from the anterior part of the fifth vertebral. Carapace scutes concentrically striated, though sometimes scarcely distinguishable, through wear, in aged specimens, neither swollen nor convex (except the fifth vertebral). Nuchal elongate, very rarely absent; vertebrals five, with a slight median keel, first broader than long in young, as long as, or longer than, broad in adults, second to fifth broader than long, the third broader than the third costal; costals four, rarely five or seven, not or but rarely forming an angle with the marginals; marginals 11, rarely 12, the anterior much longer than the posterior ones; supracaudal undivided, rarely divided, more or less strongly reverted in both sexes.

Front lobe of plastron very thick, not or but slightly projecting beyond the anterior border of the carapace, openly notched; gulars paired; axillaries 2-4, the innermost, if present, small, the outermost more or less concealed; inguinal large, in contact

with femoral; hind lobe very short, rounded, truncate, notched posteriorly.

Coloration

Head and limbs pale yellow. Carapace of hatchlings pale brown, nearly uniform, darkening with age until almost black, while the centres of the scutes remain somewhat lighter; in older juveniles and all adults irregularly stellate patches of light yellow appear on the outer margins of the costals also in smaller areas on the vertebrals, upper portions of the costals and the anterior and posterior marginals.

Plastron yellow, frequently uniform on the gulars, whereas the remaining scutes have black centres, sometimes very extensive, reducing the yellow to narrow lines along the sutures and sometimes a midplastral yellow zone.

Size

Largest male (NMZB-UM 33496 from Ghana) carapace length 211 mm, breadth 146 mm, height 90 mm; largest female (USNM 109685 from Zorzor, Liberia) carapace length 223 mm (Loveridge: 1941:115).

Distribution

Zaire westward to Liberia.

Habitat

Lowland evergreen forest.

Behaviour

When rain is falling and the animal is thirsty, it fully extends its rather long hind limbs, so that the hind part of the shell is well elevated. The forelimbs are bent sharply at the elbows, so that the distal sections are more or less vertical. Water falling onto the carapace is conducted along the "gutters" formed by the reverted shell margins, while the arrangement of the forearm, wrist and foot assures that the water spilling off the front of the carapace is funnelled to the mouth (Auffenberg in Pritchard 1979).

Breeding

The eggs average 46 x 35 x 32 mm in size.

Diet

Omnivorous.

Threats to Survival

Clearance of the forest for cultivation.

Conservation

This species appears to be protected in the Sapo National Park in Liberia; the Tai, Marahoue, Banco, and Azagny National Parks in the Ivory Coast; the Campo and Dja Nature Reserves in Cameroon; and the Okanda National Park in Gabon.

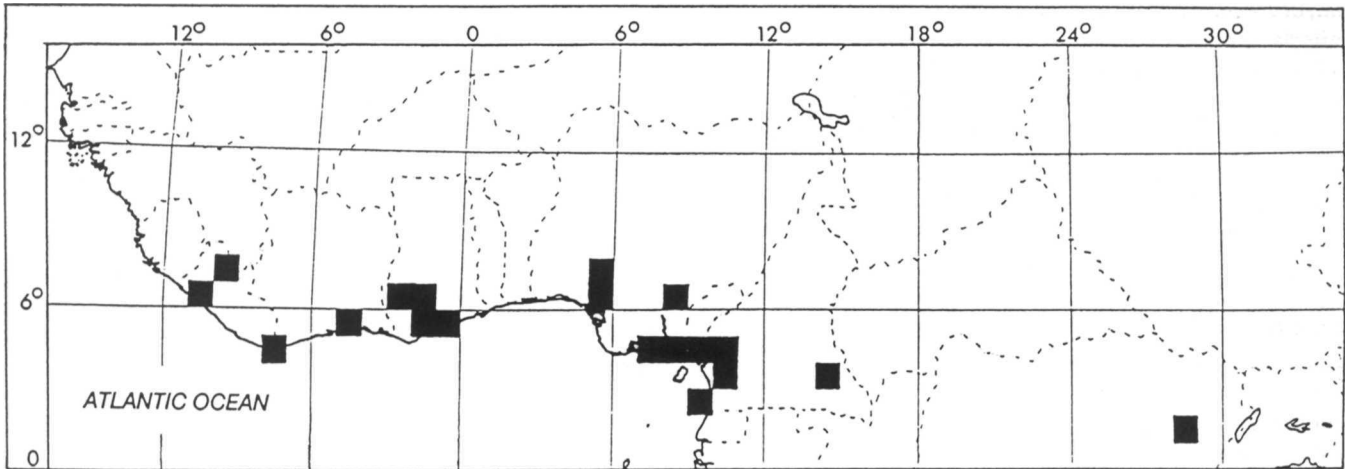
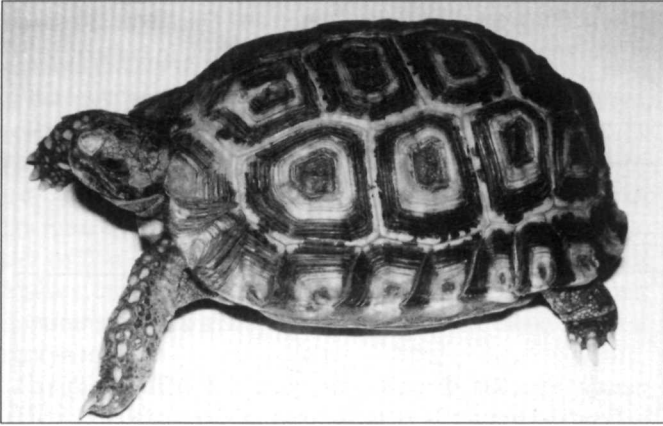


Figure 14. Distribution of *Kinixys homeana*.

Kinixys natalensis

Natal Hinged Tortoise

Donald G. Broadley



Natal hinge-back tortoise (*Kinixys natalensis*). (Photo by R. Boycott.)

Description

Beak tricuspid; prefrontal longitudinally divided; frontal entire; forelimb covered with more or less imbricate scales, some enlarged and pointed, forming on anterior edge a longitudinal series of 7-8 from elbow to outer of five claws; hind foot with four claws.

Carapace moderately convex (shell length/height ratio 1.97 to 2.41), often with flat-topped protuberances on vertebrals four and five, with end of carapace more or less vertical from top of posterior knob; anterior margin not or but slightly expanded; posterior marginals slightly reverted, forming a distinct "gutter," and feebly serrated in adults (serrated in juveniles); carapace scutes often raised, and with well marked concentric growth annuli; nuchal elongate in adults, often minute exter-

nally; vertebrals five, rarely six; costals four, rarely five; marginals 11-12, with supracaudal usually partially or completely divided.

Front lobe of plastron truncate anteriorly, not or but slightly projecting beyond anterior border of carapace; gulars paired, wider than long; pectorals with a rather narrow median sulcus; axillaries small (approx. three); inguinal large (very rarely absent), in contact with or separated from sixth marginal, in contact with femoral; hind lobe short and truncate, with a very shallow posterior notch. Adult males without a distinctly concave plastron.

Coloration

Carapace with a concentric pattern on each scute, the areolae light to dark brown, followed by a broad orange/yellow zone, then a black zone that may be broken up into short rays, it may extend almost to the margin of the scute or may be followed by another orange/yellow zone. The scutes of the plastron have extensive roughly symmetrical black figures, with yellow centres and margins. Two black rings on the abdominals are particularly prominent. The colour patterns become broken up and poorly defined in large adults. An old female from near Ressano Garcia (NMZB-UM 30453) is uniform brown above and uniform yellow below.

Size

Largest male (AM 6975A [lectoallotype]) carapace length 125 mm, breadth 94 mm, height 56 mm, largest female (AM 6975B) carapace length 155mm, breadth 113 mm, height 70 mm. Both specimens are from Jameson Drift, Natal.

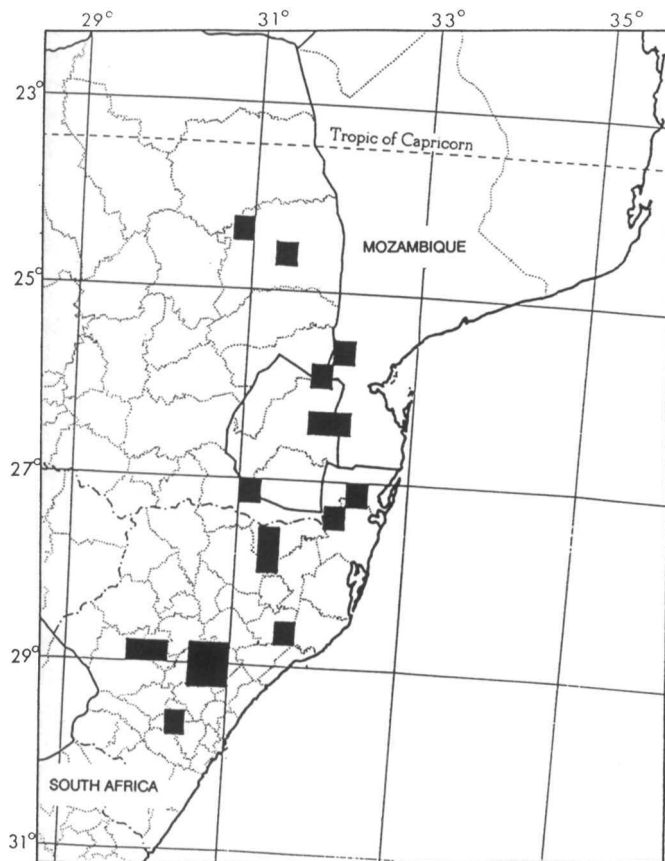


Figure 15. Distribution of *Kinixys natalensis*.

Distribution

The eastern Transvaal (Boycott and Jacobsen in press) and adjacent Mozambique, south through Swaziland to the Natal midlands at Pietermaritzburg (Lambiris 1988).

Habitat

Dry rocky areas at altitudes from 300 to 1,000 m. In Natal and Swaziland the species occurs in valley and mountain bushveld and in mountain thornveld (Boycott 1988). Its distribution in the Transvaal is associated with granitic outcrops and ridges with tropical arid bushveld vegetation (Boycott and Jacobsen in press).

Behaviour

During the day, tortoises have been found under rocks on top of the Lebombo range in Swaziland (Boycott 1988). In captivity this species hibernates from May to September, and mating behaviour has been observed in February.

Diet

Apparently similar to that of other species of *Kinixys*, including insects. Captive specimens have been observed to eat snails.

Threats to Survival

The species is threatened by habitat degradation over parts of its range, such as the Tugela River valley and the Ubombo District, as a result of human pressure. In parts of its range shifting cultivation is practiced, with disastrous consequences to the habitat. In other areas silviculture is also responsible for loss of habitat. Throughout its range the species is threatened by uncontrolled veld fires, which in many areas occur with regularity (Boycott 1988).

Conservation

This species is protected in the Itala and Weenen Nature Reserves in Natal (Bourquin in litt.), the Mbuluzi, Mlawulu, and Ndzinda Nature Reserves in Swaziland, and Manyeleti Game Reserve in the Transvaal.

Malacochersus tornieri

Pancake Tortoise; Soft-shelled Tortoise

Donald G. Broadley

Description

Beak weakly or moderately hooked, bi- or tricuspid, edge of jaws minutely denticulate; a pair of supranasals in contact, very rarely separated; prefrontal entire or divided longitudinally or somewhat broken up; frontal large, small, or broken up; remaining upper head scales small, irregular; anterior edge of forelimb with some moderately enlarged, more or less imbricating scales forming about 5-10 (rarely 12) transverse series from elbow to outer of five claws; on inner aspect of forelimb are 2-4 prominent, enlarged, separated or juxtaposed pointed scales; posterior side of thigh with a rosette of enlarged scales surrounding a somewhat large subconical tubercle; heel sometime with trace of a spur-like tubercle, claws four; tail without terminal claw-like tubercle.

Carapace very much flattened dorsally, flexible, its sides either straight and parallel or oblique, perpendicular or steeply sloping, scarcely notched in nuchal region, anterior margin flat and weakly serrated, lateral margins sometimes reverted, gutterlike, posterior margin flat, rarely reverted, slightly serrated; carapace scutes concentrically striated, rarely swollen; nuchal somewhat broader than long in young, usually elongate in adults, anteriorly indentate and projecting, usually broader posteriorly, rarely completely divided; vertebrals five, rarely four, six, or seven, sometimes flat, very rarely divided longitudinally or transversely, the contact between fourth and fifth frequently very narrow, first vertebral slightly broader than long or as broad as long and smaller than the second to fifth, which are much broader than long, as broad as, or broader than the costals; costals four, rarely five, sometimes forming an angle with the lateral marginals; marginals 11, sometimes 12; supracaudal divided, sometimes above only, rarely undivided, downwardly directed or outwardly flared irrespective of sex.

Front lobe of plastron anteriorly truncate, more or less produced openly notched; gulars paired, as wide as, or wider than, long; exceptionally an intergular; pectorals moderately broad, not or but slightly narrowed medially, their anterior border usually straight, widening gradually towards the axillary notch; axillaries two, rarely three, small; inguinals two to four,

outermost normally triangular, the others transverse, the innermost in contact with femoral; hind lobe more or less deeply notched posteriorly.

Coloration

Colour of a hatchling (MCZ 18167)

Ground colour of carapace pale yellow; sutures between dorsal scutes irregularly, but broadly bordered with dull brown, though frequently interrupted at one or more points on each shield; vertebrals two to four have a median brown spot, which the first and fifth vertebrals and each of the costals have a fainter, less regular, brown spot; dorsal edge of marginals with a less well defined brown border, tending to extend downwards between each marginal, free edge of marginals without markings. Plastron pale yellow, immaculate.

Colour of juveniles

Ground colour of carapace pale yellow; brown borders covering the sutures become black, and both these and the inner brown borders tend to be interrupted to a varying extent by yellow rays. The brown spots on the vertebrals and costals may or may not persist. Plastron pale yellow, all the sutures, except those between the gulars and anals, dark brown crossed by light rays, while the gulars and anals may show a trace of such pigmentation. Plastron substantially as described below for adults.

Colour of adults

Ground colour of carapace pale yellow to horn with variable markings; dorsal pattern almost always more or less distinctly rayed, with the rays tending to be irregular, centre of areola yellow surrounded by very irregular traces of brown, while immediately outside the areolar area is a narrow zone of yellow, beyond which to the periphery of the shield is a broad black boarder, broken by fine or broad yellow rays, sometimes one colour, sometimes the other predominating, depending whether the light rays are broad or narrow, heavy or faint. Plastral scutes with yellow areolae which may be smudged with brown; around the areola a broad zone of black, broken to greater or lesser extent by yellow rays, in some cases extends to the

periphery of the shield, while in others it is separated from the periphery by a narrower or wider zone of yellow. In certain extreme cases the plastral scutes appear almost black, in others mostly yellow. Very rarely, an old specimen may be almost uniformly horn-coloured both above and below.

Size

Largest male (NMZB 7988 Kitui District, Kenya) carapace length 167 mm, breadth 111 mm, height 36 mm; largest female (MCZ 23024) carapace length 177 mm, breadth 131 mm, height 40 mm.

Synonymy

I have examined the subadult holotype of *Testudo procterae* (Loveridge 1923) (BM 1946.1.22.59) from Ikikuyu, Tanzania, subsequently placed in the synonymy of *M. tornieri*, and I am satisfied that it is actually a synonym of '*Kinixys spekii*.'

Distribution

Central Kenya, from as far north as 29 km west of Isiolo in Samburu District (Wood in Evans 1988), south to central Tanzania, i.e. from Busisi, Lake Victoria, south to the Ruaha National Park and Lindi.

Soft-shelled tortoises were reported from the former Northern Frontier District of Kenya by the late R.B. Woosnam in 1914 (Loveridge and Williams 1957: 286), but no material is available from that area.

Habitat

Small hills with rocky outcrops in arid thornbush or savanna, at altitudes from about 30 to 1,800 metres. They have been found gathered under a flat stone topping a large two and a half metre high boulder. Some have been found in such unlikely places as fissures located high up in towering rocks and in vertical clefts in boulders, the tortoises having to climb the rock and slide down the cleft. Their flat shells enable them to flip over easily should they fall on their backs in their clambering (Eglis 1967).

The most unusual habitat recorded is that of a young tortoise taken by a farmer when "cleaning round his rice plants about a hundred yards from Allen Turner's camp at Mida Creek, near Malindi" (Loveridge 1936:221). This record requires verification.

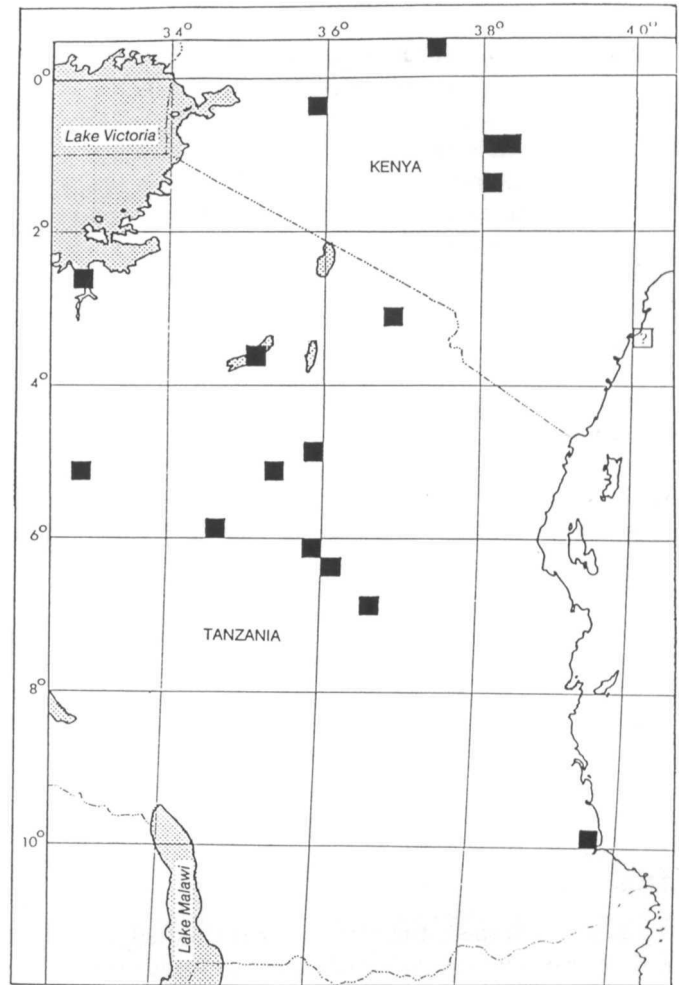


Figure 16. Distribution of *Malacochersus tornieri*.

Behaviour

At 09:00h some young were found basking on a rock slab, though usually during daylight these tortoises spend their time in rock crevices. Their depressed shells enable them to push their way farther into such retreats than if they were convex. When suddenly surprised, the reptiles may be removed with ease, but if warned by a shadow falling across the entrance, they inflate their lungs so that their shells press upon the rock both above and below as they brace their legs like struts. Under these conditions it frequently took a much as an hour to work a single tortoise loose (Loveridge and Williams 1957).

Eleven were found beneath one flattish slab of rock in January, possibly aestivating, as January and February are the hottest months at Dodoma. In conformity with their structure, these tortoises are far more active than members of the genus *Geochelone*, while their predilection for clambering up and falling off rocks calls for rapid recovery in turning over should they land on their backs. In captivity they displayed surprising agility in climbing up vertical wire netting two feet in height, and many escaped. At night, shelter was sought beneath the rockery, where they would pile up on top of one another (Loveridge and Williams 1957). Juvik (1971) describes how one of these tortoises inched its way slowly up a 50 mm vertical crevice by the application of pressure and friction on the opposing walls.

Mertens (1942) found that his captive specimens, though not nocturnal, spent most of the daylight hours in their hiding place. Even when feeding they did not venture more than nine metres from their retreat, which is definitely selected and constantly used thereafter. When surprised in the open the tortoise hastens to its retreat. *M. tornieri*, unlike most tortoises, only momentarily withdraws its head inside its shell, preferring to make a dash for its "home". It locates its retreat in a matter of minutes if moved to a distant corner of the enclosure and then released. Also, after being removed to winter quarters, it readily located its "home" when liberated in the spring.

Diet

Apparently soft-shelled tortoises emerge to feed only during the early morning hours. At Tabora, one was found nibbling dry grass. In captivity, they thrive on lettuce and tender cabbage leaves. They also have been fed on bread soaked in jam (Loveridge and Williams 1957). Bread soaked in milk was taken, as were clover, dandelion, and lettuce, but fruit was accepted only sparingly, and bananas refused altogether. The species is exclusively vegetarian (Mertens 1942).

Breeding

Courtship consisted of the male snapping at the limbs of the female as he followed her about, at times clambering onto her back and biting viciously at her head whenever she ventured to thrust it out. Two males seized the edges of the females'

carapaces in their jaws, dragging them along, eventually pushing beneath them in apparent attempts to overturn them. One male persistently, though unsuccessfully, endeavoured to mate with a female *Kinixys belliana* sharing the enclosure. Pairing took place in January and February, as early as 09:00h and as late as 16:30h.

Females appeared gravid in April. A single elongate egg is laid July or August in East Africa. Two eggs removed from the enclosure at Kilosa, where they had been buried beneath a rockery, measured 26 x 42 mm and 28 x 44 mm. The mean measurements for 27 eggs laid at San Diego Zoo were 47 x 29 mm and the incubation period varied between 113 and 221 days (Shaw 1970).

Threats to Survival

Collection of live specimens for export with possible consequent destruction of habitat by removal of boulders may pose a threat. Evans (1988) provides figures for the international trade in live tortoises for the years 1980-85.

"The collection of pancake tortoises for export is now apparently totally prohibited by the Kenyan government, and the Kenyan people do not appear to eat or have any other kind of active interest in the species. In this sense the existing populations are not obviously threatened. However, in our study area and probably elsewhere within the Kenyan range of pancake tortoises, land is being cleared at a rapid pace for agricultural purposes. Disruption or elimination of the indigenous thorn scrub vegetation characteristic of the region may, in fact, be the most serious threat to the continued existence of pancake tortoises in Kenya" (Wood in Pritchard 1987).

Conservation

Populations of this species are protected in the Serengeti and Ruaha National Parks in Tanzania.

Current Research

Roger C. Wood (Stockton State College, Pomona, New Jersey) and Alex Duff MacKay (National Museum of Kenya) began a preliminary survey of this species in Kenya in 1987 (Pritchard 1987).

Regional Introduction

William Branch

General Introduction to Biogeographical Region

Southern Africa is a region rich in geological diversity, climatic variability, and topographic complexity. As befits its location at the southern tip of the African continent, it has a mainly temperate climate, with wide seasonal contrasts in rainfall and temperature. The following summary is taken from Branch (1988).

The rainfall is strongly influenced by the cold Atlantic Ocean (Benguela) and warm Indian Ocean (Agulhas) currents that sweep up and down the west and east coasts respectively. The annual rainfall increases considerably in the north and east, whereas the west coast and adjacent regions are the driest parts. Rainfall is largely dependent on the prevailing winds, which in summer sweep anticlockwise across the continent, carrying moist air in the form of thunderstorms from the Indian Ocean across the eastern regions. Because of the high altitude of the interior, little rain remains to fall in the west where the Kalahari and Namib deserts lie. In winter, the winds bring rain to the west and southern coast, whereas the rest of the country is dry.

The temperature is affected by both the position (between 17°S and nearly 35°S) and the high altitude (1,000-2,000 m) of much of the interior. The cold Benguela sea current sweeping up the west coast keeps the air temperatures cool, and causes local fogs that sweep across the Namib Desert, and on which many of the region's unique reptiles (e.g., *Homopus bergeri*) depend for their water. Summer temperatures are highest in the Kalahari and surrounding regions, becoming less intense with altitude on the highveld of the Transvaal and Orange Free State and the Zimbabwean and Namibian plateaus. Coolest areas during the summer are the high mountains of the eastern escarpment and the southwestern Cape Fold Mountains. Winters are mild along the east coast (the Mozambique Plain and adjacent lowveld of the eastern Transvaal and the Limpopo and Zambezi river valleys). The coldest winter regions are the highveld and mountains of the Great Escarpment, which regularly have night frosts and where (with the exception of the Namibian escarpment) heavy snowfalls are frequent. The rest of the region has warm, sometimes pleasantly sunny, winter days with cool, occasionally cold, nights. The region is covered

by a complex mosaic of different vegetation types. Seven major categories, called biomes, are recognized. In terse summary, these include:

1. Fynbos is a local name for the Mediterranean-type heathlands that cover the southwestern and southern Cape, from the Cederberg to Port Elizabeth. It comprises the richest, and yet smallest, of the world's floral kingdoms, and contains an amazing diversity of plants, dominated by heathers, proteas, and restios, which grow on acidic, nutrient-poor soils. Receiving mainly winter rain (300-2,500 mm per acre), it forms a low (1-3 m), woody scrubland that is adapted to frequent, lightning induced, summer fires. There are various subdivisions, of which here the most important is rhenosterbosveld, that occurs on the coastal lowlands and has more grass and fewer heathers and proteas. More than 90% has been cleared for agriculture.
2. Afromontane vegetation is restricted to the upper slopes of the eastern mountains of the Great Escarpment, but extends down to sea level in the temperate southern Cape, and forms an "archipelago" of relict habitats. Due to its closed canopy and cool interior it contains few reptiles, and rarely has tortoises.
3. Desert occurs as a narrow strip along the west coast. The Namib is an ancient desert, composed of shifting sand dunes along the coast and hard gravel plains and barren, rocky mountains inland. Plant cover is sparse, with scattered grasses and specialized succulent plants on the sand and gravel plains, and stunted acacia trees along the river courses. It is not unusual for less than 10 mm of rain to fall in a year, and droughts of 3-4 years may occur. The offshore Benguela current is responsible for the cold, moisture laden fogs that may extend up to 50 km inland on over 100 days per year.
4. Karoo and semidesert covers the central and western Cape, extending through Namibia, inland of the Namib Desert. This biome ranges from sea level to 2,700 m, with numerous mountainous regions and a complex geology. In the north it merges into the arid savannah of the Kalahari. Rainfall (occurring mainly in the winter in the west, and in summer in the

east) rarely exceeds 250 mm per acre. The soils are poor, shallow, and rocky, and support a sparse, woody scrub. A succulent karoo scrubland occurs on the sandy coastal plain of Namaqualand (northwestern Cape), with outlying pockets in the rain shadow valleys behind the Cederberg (the Tanquwa Karoo) and within the Cape Fold Mountains (the Little Karoo).

5. Grassland occurs on the interior plateau from 1,200-2,100 m, covering the highveld of the southern Transvaal, Orange Free State and northeastern Cape. The growth of trees is inhibited by dry, extremely frosty winters and possibly by regular winter fires. Rainfall ranges from 250-500 mm per year and occurs mainly in summer. Grassland merges into the next biome in the northeast, via the hardveld of eastern Botswana (the Kalahari-Highveld transitional zone).
6. Savanna covers much of the northern area of the subcontinent. Two main types occur. Arid savanna is open and grassy, and adapted to low rainfall and cold, dry winters. As flat, open acacia woodland it covers the Kalahari sands of southern and central Botswana, extending into northern Namibia as the sandveld.
7. In the extreme north, with its higher rainfall and warmer winters, a mesic savanna of open *Brachystegia* woodland covers much of the Zimbabwean plateau, the Caprivi Strip and adjacent northern Botswana.

Brief History of the Species

With the exception of European *Testudo*, some of the first tortoises in the world to be described originated from the Cape. The lectotype of *Psammobates geometricus* is based on an illustration in Piso (1658), while the descriptions of both *Homopus areolatus* and *H. signatus* date from the late eighteenth century. A number of other species were described during the nineteenth century (e.g., *Homopus femoralis*, *Psammobates oculifer*.) The studies of Hewitt (1934, 1935) led to the description of numerous new species and races of southern African tortoises, many of which are now considered invalid. Recent studies (e.g., Broadley 1981) have led to the reinstatement of some taxa, and continuing studies are required.

In the early 1970s, Greig and Burdett (1976) undertook a detailed survey of the distribution of tortoises in southern Africa, and their study remains the baseline for modern studies. Ecological investigations on the subcontinent's chelonians have been almost completely neglected, and only in this decade have detailed studies been initiated (e.g., Branch 1984; Els 1989; Baard in prep.). There is no doubt that more detailed and specific studies on the taxonomy and ecology of the subcontinent's tortoises are desperately needed. Some of the species, although found over wide ranges, occur in low densities and are

noteasily amenable to simple mark and recapture studies. None the less they can be studied with the aid of radiotelemetry. The most obvious and needed studies include:

1. A taxonomic reappraisal of the *Psammobates tentorius* complex.
Ecological studies on the genera *Homopus* and *Kinixys*. Possible candidates are *K. b. spekii* in Zimbabwe, where preliminary observations were made on a population at the Atlanta Research Station (Lambiris, unpubl. obs); and either
2. *H. areolatus* in the southwestern Cape, or *H. s. signatus* on the granite koppies around Springbok, Little Namaqualand. All species are found in relatively high densities.

An investigation of resource partitioning between sympatric tortoises. The most feasible projects include comparative studies on *Homopus areolatus*, *Psammobates geometricus*, and *Chersina angulata* in the southwestern Cape geometric

3. tortoise reserves. Preliminary investigations are already underway (Baard in prep.). Comparative studies should also be conducted on *Homopus areolatus* and *Chersina angulata* in the southern and eastern Cape; e.g., the Bontebok National Park (Rowlands 1988) or Addo Elephant National Park (Branch and Braack 1987).

Current Importance in Terms of Diversity, Numbers, and Conservation

Southern Africa has the distinction of having the richest diversity (both generic and specific) of tortoises in the world, with nearly a third of the world's species occurring on the subcontinent. No less than 13 species in five genera are recorded from the subcontinent, and it is possible that other species remain to be described. In addition, at least three species have recognized geographical races within the region. *Psammobates tentorius* occurs in such a bewildering array of shapes and colour patterns that its taxonomy continues to be confused.

The species range in size from very large to minute. The leopard tortoise (*Geochelone pardalis*) reaches a maximum size of 750 mm and 48 kg, and is thus one of the largest mainland tortoises. In contrast, at a maximum size of 95 mm and weighing 140 gm, the Namaqualand speckled padloper, *Homopus s. signatus*, is the world's smallest tortoise. In some parts of the Cape Province tortoises are very common. *Chersina* may reach densities of 20-40 tortoises per hectare in the Eastern Cape, and possibly 100 per hectare on Dassen Island. Many regions have a number of species in sympatry. Throughout most of the Cape coastal region *Chersina angulata* and *Homopus areolatus* are sympatric, together with *Geochelone pardalis* in the eastern and southern Cape, *Psammobates geometricus* in the southwestern Cape, and *Homopus signatus* along the Cape west coast. Certain inland localities may have five species occurring in the same quarter-degree grid square such

as the Karoo National Park, Beaufort West (Branch 1985), and the Pearston district in the eastern Cape (Greig and Burdett 1976). These species may not always be microsympatric, and some species are found at different altitudes. These localities offer exciting prospects for studies on resource partitioning among tortoise species.

Most of the species have relatively large ranges and still occur in high population densities. *Chersina angulata* was exploited for thousands of years as a food resource by primitive man (Klein and Cruz-Urbe 1983), but there is no evidence of range contraction. It is no longer significantly exploited for food. The status of leopard tortoise populations on the subcontinent is still problematic. Whether they occurred naturally in the southwestern Cape is doubtful. No material referable to this species has been found in the extensive archaeological investigations in the region, and most modern records are attributed to escaped pets or other introductions. Similarly, the modern absence of this species from the Transkei may be due to extermination by early settlers, but whether the species was ever found there is not confirmed by the region's poor archaeo-

logical data. A complication in unravelling the distribution of tortoises in the subcontinent is the regular transport and release of "pet" tortoises that can lead to spurious distribution records (e.g., Pooley 1965).

Tortoises are well protected in southern Africa. Within the Republic of South Africa, tortoises are protected by provincial legislation in all provinces; none may be captured, kept, transported, or exported without permission. This is rarely granted unless a detailed and valid application is made. Within the region, only one species is threatened. The geometric tortoise, *Psammobates geometricus*, is seriously threatened by habitat destruction. Its plight is well known, and active steps have been undertaken to investigate the causes for its decline, to collect basic data on its ecology, and to conserve remaining suitable habitat (Baard 1988). Only two other tortoises are listed in the recently revised South African Red Data Book (Branch, 1988). These are the natal hinge-back tortoise, *Kinixys natalensis*, which is listed as "Rare," and the southern speckled padloper, *Homopus signatus cafer*, which is "Restricted." Neither is seriously threatened at the moment.

Chersina angulata
Angulate Tortoise; Bowsprit Tortoise (English)
Rooipensskilpad; Bontskilpad (Afrikaans)

William Branch

Taxonomy

No subspecies have been described, and there is little significant regional variation. The intense red coloration of the western "rooipens" form is occasionally found in the Eastern Cape, and possibly reflects a diet high in carotene. The junior synonym *Chersina* (Merrem 1820) is occasionally used following FitzSimons' (1938) belief that *Chersina* (Gray 1831) was preoccupied by *Chersina* Humphreys 1797 (proposed for a gastropod). However, Loveridge and Williams (1957) note that the latter name has been outlawed by a ruling of the International Commission on Zoological Nomenclature (Decision 51). The specific status of Pliocene and Miocene fossils currently assigned to *Chersina* is under investigation (Meylan and Auffenberg 1986).

Description

A medium sized tortoise; males are larger than females; tortoises grow larger in the western regions than in the eastern part of the range; maximum size in Eastern Cape: males TL (straight) 225 mm, mass 1,000 g; females TL 185 mm, mass 900 g (Branch 1984); in Western Cape: males TL 285 mm, mass 2,600 g; females TL 225 mm, mass 1,820 g. The largest recorded specimen is of indeterminate sex from near Wydgelee in the southern Cape: TL 300 mm, mass 3,250 g (Branch and Baard 1989).

The shell is elongate, more or less convex and with steep sides, and without hinges. There are 5 vertebrals, 4 costals, 10-13 (usually 11) marginals, a single supracaudal and a narrow nuchal. A distinguishing feature is the large, undivided gular. The anterior and posterior marginals of adult males are flared, giving them a characteristic "violin" shape; mature males also have a pronounced plastral concavity, a more elongate gular, a rounded and incurved supracaudal, and a longer tail. The front feet have five toes, the hind feet four toes, and there are no buttock tubercles or terminal spine on the tail. Various abnormalities have been described by Cairncross (1958) and Branch (1982). Coloration is relatively constant. Typically the marginals are horn-coloured, each with a distinct black triangle. The vertebrals and costals are black edged with light centres and a small black central spot. The plastron is usually horn-coloured with a dark mahogany brown centre that may be streaked and

disrupted along the midline in old adults. The plastrons of some specimens, particularly from the western Cape coastal regions, are orange to bright red, extending on to the carapace (the "rooipens" form). Old adults often become worn and a uniform horn colour. Occasional specimens are predominately dark grey to black.

Distribution

Found throughout the Cape coastal regions from East London in the east, around to the Orange River Mouth, and extending peripherally into southern Namibia. Isolated records from Luderitz and southern Namibia may represent isolated, relict populations, or escaped captive specimens. A population in the Karoo National Park and adjacent farms at the base of the Nuweveldberg may similarly represent a relict population or one derived from early escapees.

Status

Chersina is a common species, and in certain regions can reach very high densities. A study site in partially cleared dune thicket near Port Elizabeth has over 400 tortoises marked in 17 hectares. Much of this site comprises open pasture (Branch 1984). A similar high density of tortoises occurs on Dassen Island off the Cape west coast. Preliminary transects on this flat, sand covered granite island (19 m high, 220 hectares) indicate that as many as 10-20,000 tortoises may be present (Curlpers, comm.; Branch and Els unpubl. obs.; Crawford pers. comm.). Stuart and Meakin (1983) obtained an estimate of 6-7 tortoises per hectare for the Pearly Beach coastal resort in the southern Cape following a severe fire in the reserve. *Chersina* is tolerant of disturbed habitats and occurs through a wide range of habitats. Due to its wide distribution and high population densities it is not threatened.

It was collected for the pet trade (Anon. 1950), but this was halted by provincial legislation. Now fully protected, illegal exports are rare. Utilized as food by Stone Age peoples, its remains are extremely abundant at many archaeological sites. Klein and Cruz-Urbe (1983) interpret changes in average tortoise size at different strata in two southern Cape archaeological sites as reflecting changes in human utilization of

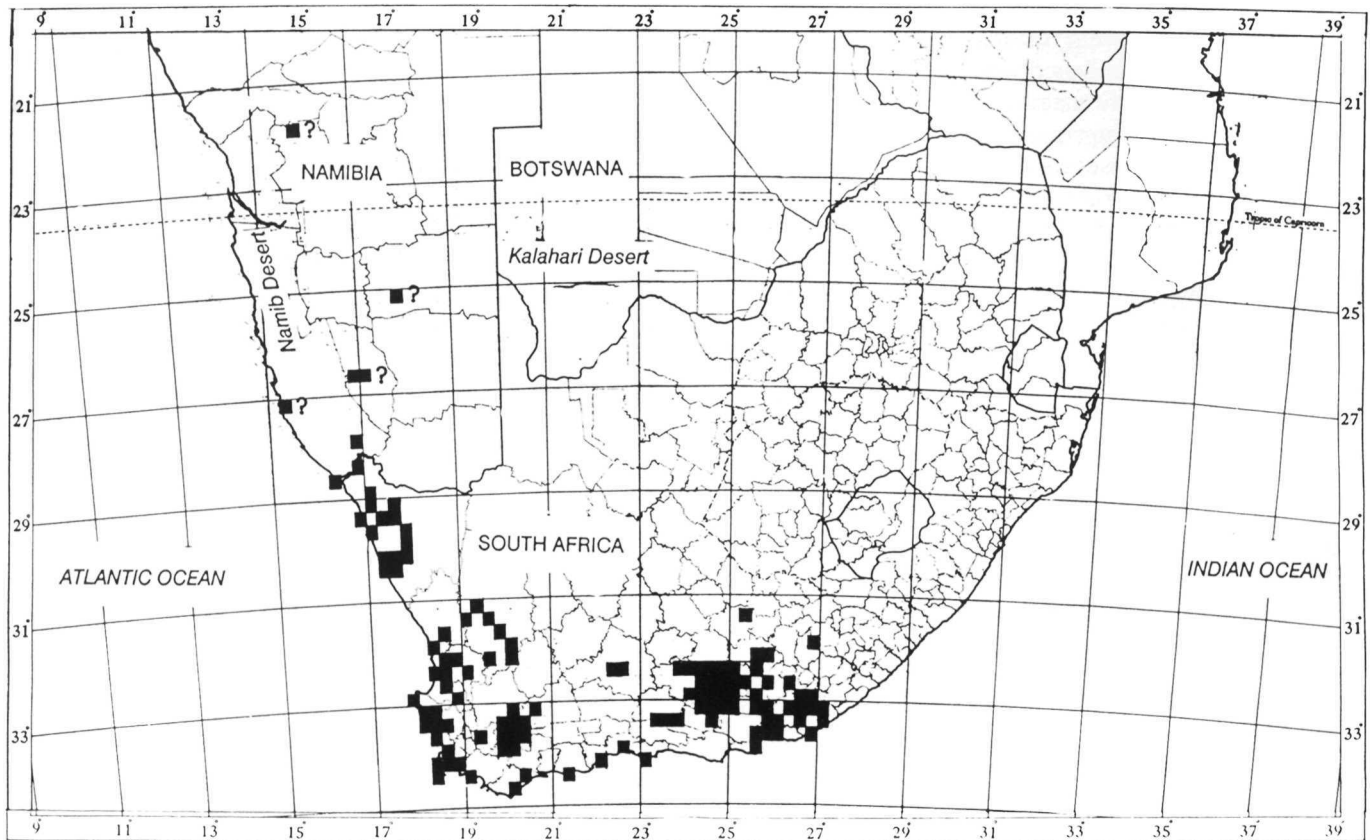


Figure 17. Distribution of *Chersina angulata*.

tortoises. Although it is probable that *Chersina* is occasionally eaten by humans, there is no evidence this makes any significant impact on present populations.

Habitat

This species occurs in a wide range of habitats. Throughout most of its range, *Chersina* occupies a Mediterranean type climate, with hot, dry summers and cool winter rain. In the southern and western Cape it is found on sandy, acidic, nutrient-poor soils with low shrub coastal fynbos vegetation composed of grasses, *Restio*, and *Erica* elements. In the northern regions of the western Cape coast, the decreasing rainfall gives rise to a succulent karroid vegetation. In the Eastern Cape, with a transition to higher summer rainfall, *Chersina* is found in dune thicket, composed of small, evergreen trees, particularly *Mimusops caffra*, *Sideroxylon inerme*, *Rhus* sp. and succulent, thorny scrub, spekboom (*Portulacaria afra*), and *Aloe* spp. At its climax this vegetation excludes tortoises, although they can occur at the ecotone between thicket and adjacent vegetation types. Partial clearing of thickets for agricultural purposes can lead to an explosion in tortoise populations, associated with an increase in ecotone. However, tortoises are obviously excluded following total bush clearance for crop farming.

Ecology

Much of the following discussion is based on ecological studies undertaken in the Eastern Cape. Branch (1984) published preliminary observations on this population, but these have been refined, extended, and in some cases amended by the radiotelemetry and ecophysiological studies of Els (1989). Given the different habitats and climatic regimes experienced by *Chersina* in the Western Cape, it is probable that there will be subtle, but important, differences between the populations. *Chersina* is active throughout the year, sheltering within its retreat in cool, rainy weather. Food intake is reduced in cool weather. Retreats are simple tunnels ("forms"), rarely longer than 40 cm, formed by the tortoise pushing into thick vegetation at the base of shrubs. In the Eastern Cape "forms" are usually situated on the northeast side of shelter, allowing them to obtain maximum heat from the early morning sun, and protecting them from the prevailing WSW winds. Tortoises move into their forms long before sunset, when their body temperatures are still higher than 20-25°C.

Home range is relatively small, not differing significantly between females and males, with mean areas of 2,452 and 2,799 sq m respectively. There is considerable variation in home range size (704-7,455 sq m), and, to a large extent, home ranges overlap. Tortoises rarely forage more than 10m from cover, the

distance from cover being directly related to the tortoise's size. Only adult tortoises are willing to forage in open pasture, as they are better able to withstand predation and high temperatures.

They are seldom active at ambient temperatures lower than 17°C, while the upper temperature limit for activity is approximately 28°C. Most tortoises are active in the late morning, with activity generally occurring between 06:00h and 18:00h in summer, and 08:00h and 17:00h in winter. *Chersina* only become active once their body temperature reaches 17°C, and they cannot maintain their body temperature at a level higher than ambient temperature on rainy, overcast days. They seldom bask, body temperature generally increasing with that of the environment. When they move out of their forms into the sun, their body temperatures show a rapid increase due to direct insolation. Shelter from the sun is sought when their body temperature reaches approximately 30°C.

Their diet consists mainly of grasses and annuals, although small fragments of snail shell are also ingested, presumably as a source of calcium. Faeces from horses and rabbits are also eaten. Compared to other plants in the study area, the electrolyte levels in the food plants are low, but the potassium levels in these plants are still higher than those in the tortoise's plasma. This excess ingested potassium must be excreted. The plants they eat have a high moisture content (mean 79%), which is important, as they rarely have access to standing water in large parts of their range, and are dependent upon food plants and rain for water. In the western Cape (e.g., Dassen Island), *Chersina* have to survive long periods without water. Therefore, they are under water stress by the end of the summer drought and potassium accumulates in their plasma while they void urine hyperosmotic to their plasma. In the Eastern Cape rainfall occurs throughout the year, therefore, tortoises are seldom water stressed. Where rain pools form, tortoises drink by sipping water, emptying the contents of their cloacal bursae. On sandy soils, the tortoise adopts an unusual drinking posture. The hindlegs are fully extended so that the carapace is steeply angled, the neck fully stretched out, with the head pushed into the sand past eye level. Water drains down the carapace and neck, forming a pool in the sand around the tortoise's head, from which the water is sucked through the nose.

Chersina is unusual among tortoises in that males grow larger than females. Mature males actively enter into combat with other males, despite having overlapping territories. Large tortoises entering a male's range are visually inspected, and, if they are adult males, are often attacked. Attack takes the form of active butting and attempts to overturn the opponent using the greatly enlarged gular. Combat lasts for 10-30 minutes, and often terminates when the defeated male retreats quickly to cover. Overturned males usually right themselves and then retreat. Fatalities from overheating have been observed in overturned males unable to right themselves. Adult females are actively courted by males. This involves persistent pursuit by the male, even into an adjacent male's territory, in which case combat between males may ensue. The male bobs his head and may nudge and bite the female, emitting soft grunts. Copulation

follows the typical laboured tortoise fashion and is vociferous.

Mating occurs throughout the year, dependent upon temperature, but is most common between September and April. Egg laying occurs throughout the year, depending as much on rainfall as temperature. Females lay a single egg (very exceptionally two) in a shallow pit dug in sandy soil, in a well drained, sunny position. As suitable sites may be limited, females move to them specifically for egg laying. The eggs are oval and hard-shelled (34-43 mm x 24-35 mm, 25-30 g). The interval between egg laying varies from 1-6 months. Adult females lay from 6-7 times in a year. Egg laying occurs following rain. Females may delay oviposition until rain occurs. Depending upon the frequency of rainfall, a variable number of females may begin to nest. Construction of the egg pit and egg laying takes several hours. Incubation periods range from 94-198 days depending upon incubation temperature (i.e., whether the egg is laid in winter or summer). Egg shells crack 6-7 days before hatchlings emerge. Hatchlings are rounded in shape (and have a greater over the curve width than length), measuring approximately 30-39 mm in length and weighing 12-18 g. Growth is relatively slow, with sexual maturity probably not reached until 10-12 years in the wild (but has occurred in seven years in captivity). Longevity probably exceeds 30 years.

It is tempting to postulate that the various unusual aspects of reproduction in *Chersina* (i.e., the greater male size, male-male combat, and the single egg clutch) form a co-adapted strategy. As females lay only single eggs at frequent intervals, there is selective advantage in males trying to maintain "harems" as they need to continually inseminate females. This leads to selection for increased male size and combat behaviour. Given the length and noisy nature of tortoise copulation, it may not be necessary for dominant males to maintain exclusive territories providing they command a majority of successful matings.

Predators on juveniles and subadults include viverrids, jackals, the rock monitor (*Varanus exanthematicus*), and various birds, including crows, kelp gulls, and black eagles. Predation on egg sites by viverrids has been noted in the Eastern Cape, and probably occurs elsewhere, although their absence on Dassen Island probably results in high hatchling success. However, this is offset by the high subadult mortality from kelp gull predation (Branch and Els in prep.). Adults are usually immune to predation, but are killed by fire and injury from large grazing mammals (particularly shod horses and elephants). Others are killed on roads. Mortality from an unknown respiratory ailment has been noted in the Eastern Cape, and tortoises may die from dehydration following prolonged droughts.

Threats

There is no evidence that *Chersina* is threatened, other than on a minor local level. Numbers may have declined in heavily urbanized areas (e.g., the Cape Flats), but it occupies a large range and varied habitats. It is generally tolerant of habitat disturbances and may even undergo population increases in

association with certain agricultural developments. There is no evidence of range contraction. Stuart and Meakin (1983) noted high mortality (24 of 31 tortoises) caused by fire in a reserve of coastal fynbos in the southern Cape. They note that some tortoises were observed burrowing into sand ahead of the fire emerging from 10 minutes to one hour after the fire had passed. It is not known whether they subsequently survived. This particular fire occurred in a region dominated by the Australian acacia "rooikrans" (*Acacia cyclops*), which causes fires of greater frequency and intensity than usually encountered in coastal fynbos. Encroachment by Australian acacias into coastal fynbos and dune thicket threaten *Chersina* by canopy closure and frequent, intense fires associated with this vegetation.

Conservation

The species has been recorded from numerous conserved areas. Large populations occur in the Addo Elephant National Park (Branch and Braack 1987), Bontebok National Park (Braack 1981; Rowlands 1988), Langebaan National Park, Cape Peninsula Reserve, etc. It is well protected by provincial legislation prohibiting the collection, export or killing of most indigenous

reptiles, including all tortoises. Permits to keep tortoises in captivity may be obtained by the public from the Chief Directorate of Nature and Environmental Conservation, Cape Province, and are generally awarded for *Chersina* where facilities for captive maintenance are considered adequate.

Current Research

Being common and widely distributed, *Chersina* is the best studied of the southern African tortoises. Various aspects of thermoregulation have been studied (Craig 1973; Perrin and Campbell 1981; Els et al. 1988). Preliminary aspects of the ecology and meristics of an East Cape population have been published (Branch 1984), and further detailed studies on the ecophysiology of this population, employing radiotelemetry and laboratory studies, have been completed (Els 1989). Long-term data (8+ years) on home range and growth in this population have also been recorded (Branch and Els unpubl. obs.). Various aspects of osmoregulation between this population and that on Dassen Island in the Western Cape have been compared (Els 1989). High seasonal predation on young tortoises by kelp gulls on Dassen Island has also been documented (Branch and Els in prep.).

Homopus areolatus
**Parrot-beaked Tortoise; Common Padloper;
Areolated Tortoise (English)
Padlopertjie, Papengaaibekskilpad (Afrikaans)**

William Branch

Taxonomy

No subspecies have been described, and there is little significant regional variation. Bour (1988), in a footnote, has indicated that *Testudo areolata* is a junior synonym of *T. pusilla* Linnaeus 1758. Hopefully the latter name will be suppressed in favour of *areolata*, which has had long and frequent usage.

Description

A small, sexually dimorphic tortoise. Females are larger than males, reaching 300 mm in length and weighing up to 300 g. Males rarely exceed 100 mm in length and a mass of 140 g. The shell is dorsally flattened, but rounder in females. The scutes of the carapace are flat on top, often with deep sutures and depressed areolae. There are five vertebrals, four costals, 11 (sometimes 10 or 12) marginals, a single supracaudal, and a large, often elongate or square nuchal. Supernumerary scutes are frequent, particularly extra vertebrals and costals. The paired gulars are broader than long; there are usually two axillaries not in contact with the humerals; the inguinals are often fragmented or absent and do not contact the femorals. The feet have four toes (although rare specimens are known with five toes on the forefeet). Buttock tubercles are small or absent, and the tail lacks a terminal spine. The beak is strongly hooked (hence the common name), tricuspid, and has a slightly serrated edge. The nostrils are situated high on the snout. Adult males differ from females in being smaller and having a dorsally compressed, narrow shell with slightly flared marginals. They lack an obvious plastral concavity, but have a longer tail, larger head and beak, and longer, more pointed snout than females.

Coloration is relatively consistent and sexually dimorphic. It is more variable than other species of *Homopus*. Typically, the carapace scutes are olive, brown, green, or grey, with

vertebrals and costals having reddish-brown centres and distinct black borders in juveniles and adult females. The marginals are often tinged reddish-brown. In older tortoises, the colour often fades to a uniform orange-brown. The plastron is normally a dirty white (particularly in young tortoises and adult males), sometimes with diffuse dark centres and narrow, dark suture borders. The skin is usually grey to light yellow-brown, sometimes with brown or orange infusions to the top and sides of the head, especially in adult males. Males also tend to be more olive-green, often with orange to light brown areolae and marginals, and lacking the dark border to the vertebrals and costals. In the breeding season some males also develop bright orange nasal scales.

Distribution

Endemic to the Cape Province where it is found throughout the southern coastal regions, east from East London to the Cederberg near Clanwilliam in the west. It is not normally found above 900 m, although an isolated, relict population occurs at 1300 m around Middelpos in the Roggeveldberg on the western edge of the Great Karoo. It extends inland along the valleys of the Cape Fold Mountains, and as far as Craddock in the Eastern Cape.

Status

Homopus areolatus is a common, distinctive species that inhabits a wide variety of habitats. It is well protected by existing provincial legislation. There is no evidence of exploitation, range contraction or severe habitat deterioration, and it is not presently threatened.

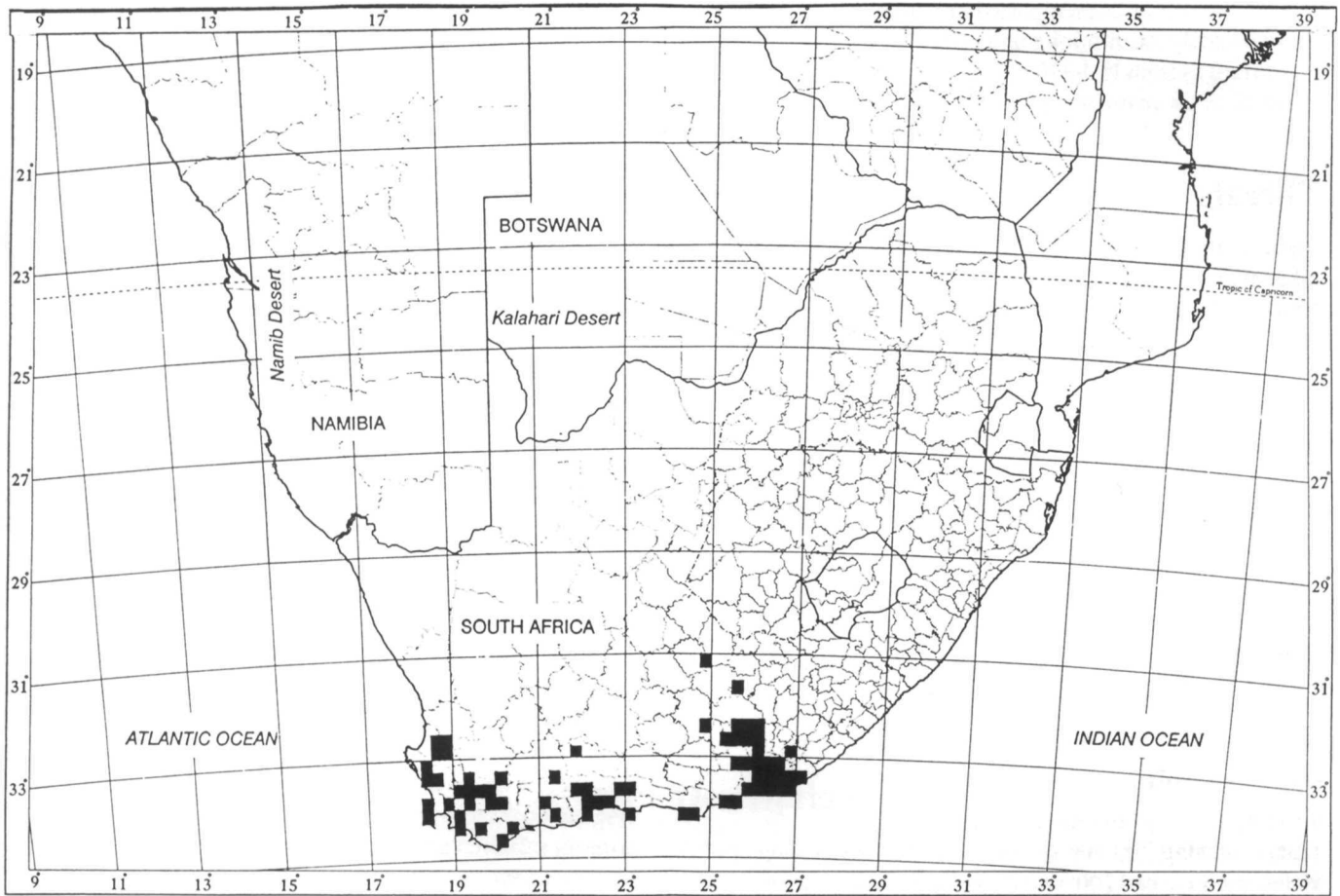


Figure 18. Distribution of *Homopus areolatus*.

Habitat

It is found in a wide range of habitats. Throughout most of its range, *Homopus areolatus* occupies a Mediterranean type climate, with hot, dry summers and cool winter rain. In the southern and western Cape it is found in coastal heathlands (fynbos), and in transitional karroid veld in the drier inland valleys of the Cape Fold Mountains. In the Eastern Cape it enters coastal thicket and bushveld. The habitat becomes increasingly thorny and succulent in the Craddock Gap. It is absent from the more arid interior. Throughout much of its range, rainfall exceeds 250 mm per year.

Ecology

Ecological data on this species are largely anecdotal. No detailed ecological studies have been published. Due to its

small size, this species rarely forages far from cover, often sheltering in small tunnels excavated under stones, or within abandoned rodent burrows. No details of diet in the wild are known. They tolerate captivity, accepting a wide variety of foods. This species emerges early in the morning to feed. In coastal regions, it forages throughout the year. Predators are numerous, including baboons, jackals, mongooses, and large birds (e.g., crows, eagles, secretary birds). When handled they struggle wildly, thrashing their head and legs rapidly from side to side, readily ejecting their cloacal contents. In a laboratory study on thermoregulation, Perrin and Campbell (1981) noted the *H. areolatus* appears to have greater physiological control of conductance and a higher maximum preferred temperature (34.8°C) than either *Geochelone pardalis* or *Chersina angulata*. Nesting has been observed in April, August, October, and November, and it is possible that two clutches of eggs are laid each year. Usually two to three (sometimes four, one record of five) small, elongate eggs (27-33 x 20-23 mm) are laid in a

shallow pit. Hatchlings, reported in March and April, measure approximately 28 mm long and weigh 6-8 g. The incubation period ranges from 150-320 days, dependent upon temperature. Survival of 28 years in captivity has been recorded.

Threats

There is no evidence that *Homopus areolatus* is threatened, other than on a minor local level. It may have declined in heavily urbanized areas (e.g., the Cape Flats), but it occupies a large range and varied habitats.

Conservation

The species has been recorded from numerous conserved areas. Large populations occur in the Addo Elephant National Park (Branch and Braack 1987), Bontebok National Park (Braack

1981; Rowlands 1988), Langebaan National Park, Cape Peninsula Reserve, etc. It is well protected by provincial legislation (which prohibits the collection, export or killing of most indigenous reptiles, including all tortoises). Permits may be obtained by the public to keep tortoises in captivity from the Chief Directorate of Nature and Environmental Conservation, Cape Province.

Current Research

No detailed, specific studies are currently in progress on this species. Basic ecological data (growth, home range, etc.) are being collected on marked and recaptured tortoises living sympatrically with geometric tortoises, *Psammobates geometricus*, in the southwestern Cape (Baard unpub. obs). Rowlands (1988) has initiated a study of sympatric *Homopus areolatus* and *Chersina unguolata* in the Bontebok National Park in the southern Cape.

Homopus bergeri

Nama or Berger's Padloper (English)

Bergerse Skilpad (Afrikaans)

William Branch

Taxonomy

For a species known from less than 30 specimens, *H. bergeri* has a confused and complicated taxonomic history, aspects of which still have to be resolved (Branch et al. in prep.). The confusion stems, in part, from the fragmented condition of the type specimen. The description is based on a bushman's "buchu" pouch that, as is usual, lacks the anterior plastron, the head, and forelimbs. In addition, this specimen has a thin, worn carapace. Although obtained in Gibeon, Namibia, Lindholm (1906) noted in the species description that it may have originated "deeper in South Africa." Soon after its description, Siebenrock (1909) placed it in synonymy with *H. boulengeri*, but within the same year transferred it to the *tentorius* group of *Testudo* (= *Psammobates*). Perhaps he was influenced by Duerden's (1907) footnote that considered *H. bergerias* doubtfully referable to the genus *Homopus*. Until the present Siebenrock's decision has been followed in principal by subsequent workers, although as the generic and interspecific relationships of the "*tentorius* group" has evolved, the nomenclatural combinations of this species has increased including *Chersinella verroxii bergeri* (Hewitt 1934), *Testudo verroxii bergeri* (Mertens 1955), *Testudo smithi bergeri* (Mertens and Wermuth 1955), *Psammobates tentorius verroxii* (Loveridge and Williams 1957), and *Testudo tentorius verroxii* (Mertens 1971).

Mertens (1955) was the first to record *Homopus boulengeri* from Namibia on the basis of live specimens supplied to him by Mr. Erni from near Aus. This record was treated with caution by Loveridge and Williams (1957), although subsequent material (Mertens 1971) from Aus (Farms Plateau and Augustfelde) and Udabip-berge (Witpuetz) confirmed the presence of *Homopus* in Namibia. Greig and Burdett (1976) gave a detailed analysis of *H. boulengeri* in the Cape Province, and although considerably extending its range within the Cape, noted the large disjunction between their Cape distribution and Merten's (1971) records from Namibia. Therefore they considered its occurrence in Namibia as "unlikely." New collections of *Homopus* obtained by J.C. Greig in 1981-2 from the vicinity of Aus led to further speculation. Differences in colour pattern and morphology compared to "typical" *H. boulengeri* from the Cape led to speculation that a new species of *Homopus* was

involved, and to the revival, perhaps prematurely, of *H. bergeri* (Newbery and Jacobsen 1986), subsequently followed by Branch (1988) and Branch et al. (1988).

However, the taxonomic problem is not settled as three problems still have to be addressed. Are the Aus *Homopus* conspecific with *H. boulengeri*, and if so, is it a recognizable subspecies? Is the type specimen of *H. bergeri* (Lindholm 1906) referable to the Aus *Homopus*? These problems are now being investigated by Branch et al.

Description

A very small tortoise (female maximum length 109 mm, weight 240 g; males 90 mm, 100 g) with a flattened shell, lacking raised scutes, deep sutures, depressed areolae, or a plastral hinge. There are usually five vertebrals, four costals (the first is often the largest), and 11-12 marginals that are not serrated or upturned. The nuchal is usually small and narrow and the paired gulars wider than long and weakly notched. The undivided supracaudal is neither rounded nor inturned. There are two axillaries, the first being largest, in broad contact with the pectoral, at its greatest extent just abutting the humeral. The single large inguinal is in broad contact with both the abdominal and femoral. The bridge usually has a well defined ridge (in contrast to *H. boulengeri*), except for very old individuals. As in other *Homopus*, there is a high incidence of irregular scutellation, particularly on the carapace. The forelimbs have five toes and are covered anteriorly with large, overlapping scales while the hindlimbs have four toes and lack enlarged buttock tubercles, though some slightly enlarged scales may be present. The tail lacks a terminal spine. The beak is weakly hooked and weakly tricuspid. Males have a shallow plastral concavity, narrower shell, and longer tail.

Coloration is relatively consistent and not sexually dimorphic. Typically the carapace is reddish brown, often with olive tinges in old adults. Each scute usually has a pale areola and a rich red or mahogany border that can be irregularly flecked. The plastron is similarly patterned, although the dark border is often more extensive, particularly on the anterior and lateral margins. The head and limbs are dirty brown. Old individuals

may lose the dark borders on the carapace and plastron. A typical, well-coloured individual is illustrated in colour in Branch (1988).

Distribution

Currently known to be common only from the rugged, granite mountains around Aus, but with scattered records from other isolated mountains in the sand and gravel plains of the Namib Desert. These include the Kowiesberg near Luderitz, as well as the low, granite hills four to five km southwest of Tschaukaib siding, and two to three km southeast of Haalenberg siding (Wendt pers. comm.). The most southerly records are from Witputs on the Huib Plateau near Rosh Pinah in southern Namibia. There is an undocumented record of *Homopus* shell fragments from the eastern rim of the Fish River Canyon opposite Ai-Ais, which may be referable to this species (Griffin pers. comm.).

Status

Homopus bergeri has a very restricted distribution and is poorly known. However, there is no indication that it is being exploited, that its numbers are declining, or its range contracting. The most pressing problem is the resolution of its taxonomic status.

Habitat

Homopus bergeri is restricted to barren, granite mountains, with sparse succulent vegetation in the Namib Desert, and grasslands on the Aus escarpment. Populations on the Kowiesberg, in the Namib Desert near Luderitz, are subject to conditions of extreme aridity, often less than 10 mm rainfall per year. They obtain most of their water from food and fogs from the cold offshore Benguela current. Rainfall at Aus is higher (80-100 mm per year) and occurs mainly from January through June. Maximum temperatures may exceed 40°C in March, while minimum temperatures at Luderitz may drop to freezing in June, and well below freezing at Aus, where winter snowfalls are common.

Ecology

Knowledge of the ecology of *Homopus bergeri* is restricted to habitat data collected during a field trip on 26 through 30 October 1988 and anecdotal comments by local farmers and nature conservation officials familiar with the tortoise. The species is rock-dwelling, although it may forage in sand gullies. It has been reported to shelter under rock slabs and to be particularly active during and after winter rains. It has been observed drinking from rock pools, and tortoises on the Kowiesberg and adjacent mountains may obtain sufficient moisture from the regular fogs that are characteristic of the coastal regions of the Namib Desert. Captive specimens have been noted to climb steep rock faces readily. Possible food plants on the sparsely vegetated Kowiesberg include *Grielum sinuatum*, *Wahlenbergia erophiloides*, *Pellaea frutescens*, *Zygophyllum dregeanum*, *Heliochrysum* sp., and *Limeum* sp. (Muller, pers. comm.). There are no details of reproduction. A broken plastron of a large female was found on the summit of the Kowiesberg in a rock overhang that may have been used by a jackal. Other potential predators include brown hyenas, which could easily crush and consume adult tortoises, and crows which may feed on hatchlings and juveniles.

Threats

There is no evidence that *Homopus bergeri* is threatened, either by habitat destruction or illegal collecting.

Conservation

All tortoises are protected by legislation in Namibia. The western parts of its range is in the "spergebiet" Diamond Area No. 1, an extensive tract of desert from which public access is prohibited.

Current Research

The taxonomic status of this species is currently under investigation (Branch et al. in prep.). The distribution and conservation status is being investigated by the Namibian nature conservation authorities.

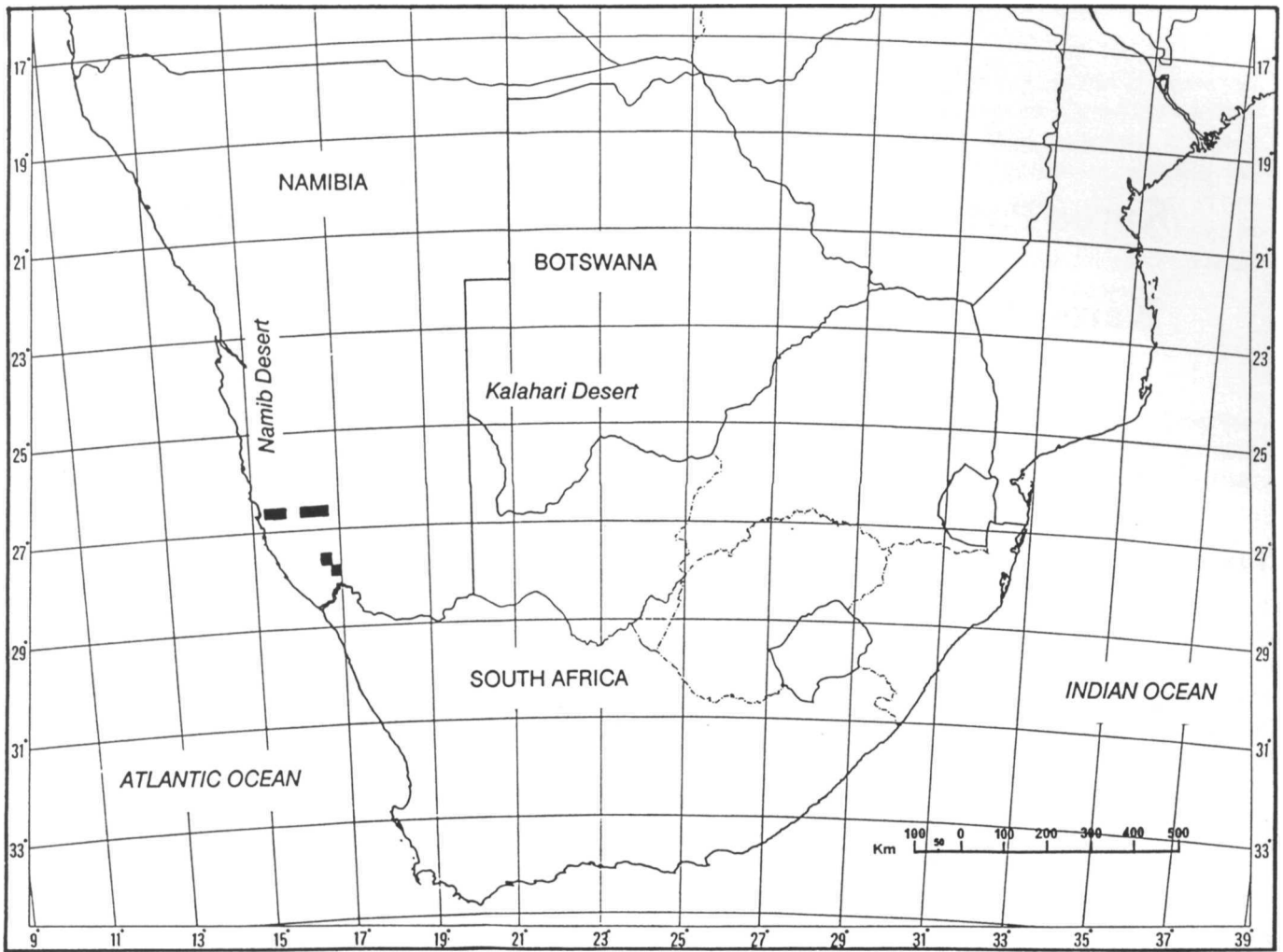


Figure 19. Distribution of *Homopus bergeri*.

Homopus boulengeri
**Karoo Padloper; Boulenger's Padloper; Red Padloper;
Biltong Tortoise (English)**
**Karooskilpadjie; Rooiskilpadjie; Donderweerskilpad;
Biltongskilpad (Afrikaans)**

Richard C. Boycott

Taxonomy

The species was described by J.E. Duerden (1906) from eight specimens. The type locality was not specified, but the specimens originated from Willowmore, Beaufort West, and Aberdeen in the southern parts of the Great Karoo, Cape Province. No subspecies have been described and there is little significant regional variation. The only complication is the relationship of this species to *Homopus bergeri* and the status of the *Homopus* population in the Aus highlands and adjacent mountains (see discussion under *Homopus bergeri*).

Description

A small tortoise, females larger than males, with a maximum carapace length of 110 mm and mass of 150 g. Males measure up to 90 mm and weigh up to 100 g. The shell is dorsally compressed, the carapacial scutes are flat with large areola. The carapace is comprised of five vertebrals, the first usually narrowest and the fifth widest; four, rarely five costals; 12, rarely 11 or 13 unserrated marginals; and a single, undivided supracaudal. The nuchal is small, its shape varying from triangular, square, or rectangular. The plastron is comprised of paired gulars, which together are more than twice as wide than long; numerals which may contact a single axillary, pectorals; abdominals; femorals in broad contact with a single, enlarged inguinal scute; and anals. The bridge is rounded, lacking the sharp ridge typical of *Homopus femoralis*. Five claws are present on the front feet, four on the back. Buttock tubercles are either present or absent. If present they can be large and prominent or small. There is no terminal spine to the tail. The beak is weakly hooked, at most tricuspid, and with a weakly serrated edge. Males are distinguished by their smaller size, longer tails, and well developed plastral concavity.

Coloration is variable. Typically the carapace is a uniformly yellowish-brown, orange-brown, reddish-brown, dark brown, or grey. A narrow black line is often present along the longitudinal seams between the vertebral and costal scutes. Although most striking in juveniles, this may persist throughout life.

Plastral coloration is also variable, from uniformly yellowish brown, orange brown, reddish brown or grey to yellowish brown with a darker central region, to pitch black with the black coloration extending to the outer edges of all the plastral scutes except the axillaries and inguinals. The soft parts are pale yellow, orange, or light brown.

Distribution

Found in the Great Karoo of the Cape Province, from Pearston and Wolvefontein in the east to Sutherland and Carnarvon in the west. Mertens (1955, 1971) records this species from the vicinity of Aus in southern Namibia. The identity of these specimens is problematic (see *Homopus bergeri*).

Status

Homopus boulengeri is often considered rare, but in fact may be locally common, but secretive. The survey of Greig and Burdett (1976) demonstrated that it was widespread within the Great Karoo.

Habitat

Rocky outcrops and dolerite ridges in semiarid karroid veld, including Karoo succulent veld and desert grasslands, are favoured habitats.

Ecology

This is a secretive species, sheltering under rock slabs on rocky plateaus and dolerite ridges. They are very well camouflaged in these habitats. They are active on cool summer days, particularly when thunderstorms threaten, hence their common Afrikaans name "donderweerskilpad". Within the Karoo National Park, Beaufort West, they are absent on the flat karoo plains and the escarpment edge (Branch and Braack in prep.). They are

eaten by crows, which break their shells by dropping them onto rocks. Nothing is known of their diet, which may be specialized, as they fare poorly in captivity. Reproduction is also poorly documented. Nesting has been recorded in December and January (Boycott and Bourquin 1988). A single, elongate egg (32-39 x 22-24 mm, 10-12 g) is deposited.

Threats

There is no evidence that *Homopus boulengeri* is threatened, other than on a minor local level. It is restricted to rocky ridges unsuitable for agricultural development, although it may be affected by habitat degradation following over-grazing by sheep and goats. No evidence of exploitation for the pet trade is known, although this could develop if protective legislation was not enforced.

Conservation

The species has been recorded from a number of conserved areas. A healthy population occurs in the Karoo National Park (Branch and Braack 1989) and adjacent regions. It is well protected by provincial legislation prohibiting collection, export or killing of most indigenous reptiles, including all tortoises. Permits may be obtained by the public to keep tortoises in captivity, but are unlikely to be issued for this species outside its native range, as it rarely survives long in captivity.

Current Research

No specific studies on this species are currently in progress. General aspects of its biology are being noted as part of a general survey of the herpetofauna of the Karoo National Park (Branch and Braack in prep.).

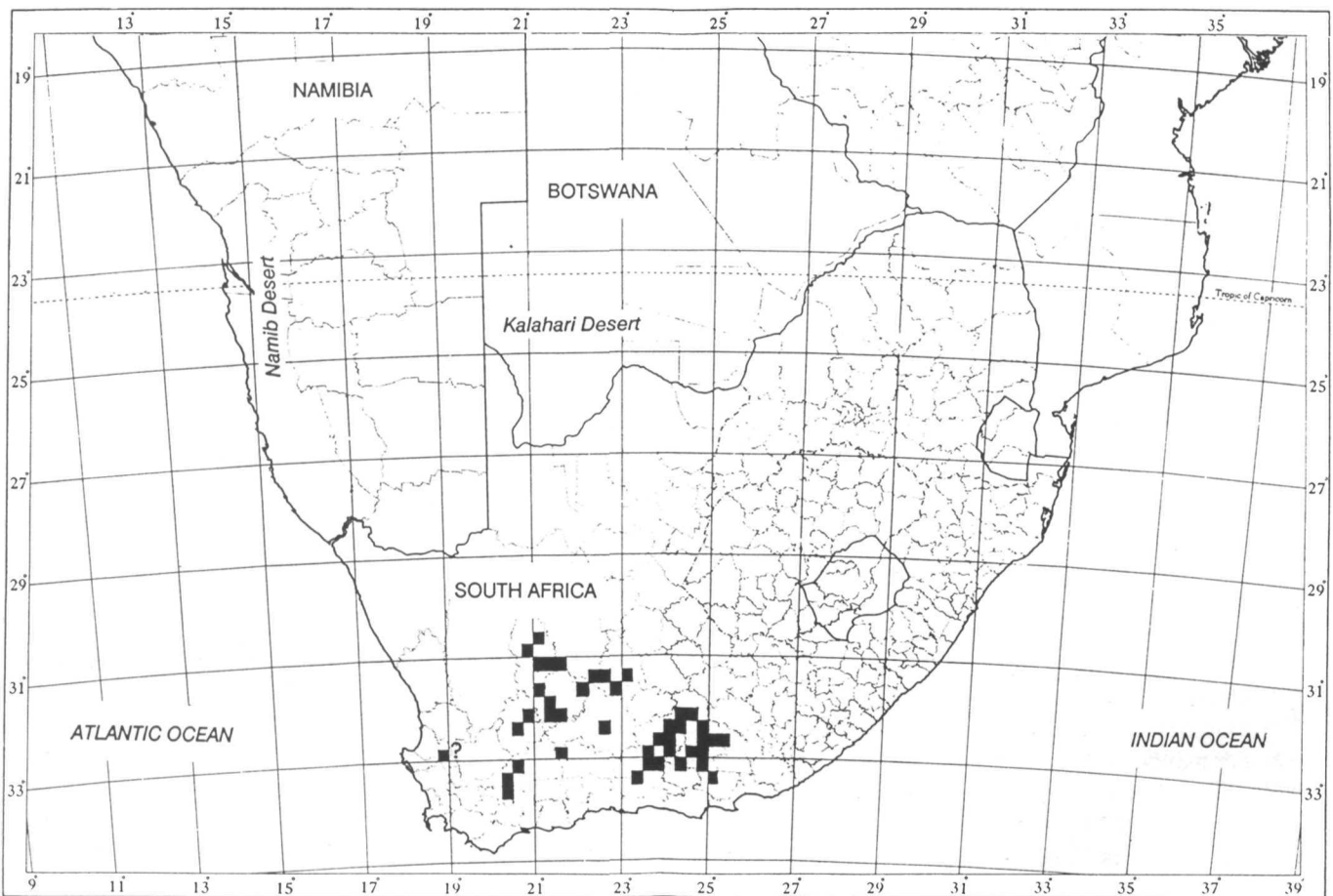


Figure 20. Distribution of *Homopus boulengeri*.

Homopus femoralis

Greater Padloper; Karoo Tortoise (English)

Vlaskilpad; Bergskilpadjie; Groter Padloper (Afrikaans)

William Branch

Taxonomy

No subspecies have been described and there is little significant regional variation. Occasional specimens have five front claws which may lead to confusion with *H. boulengeri*, but these species are easily separated by the sharp ridge on the bridge and rounder shell shape of *H. femoralis*.

Description

A small to medium-sized tortoise, the largest *Homopus*. Females are larger than males (females 160 mm, 600 gm; males 130 mm, 350 g). The carapace is dorsally compressed, covered with flattened scutes without sunken sutures and large areolae. There are five vertebrals, four costals, and 11 (rarely 12) marginals. Marginals may become slightly serrated and up-turned in some individuals. The nuchal varies considerably in size and shape; the supracaudal is single. Supernumerary vertebrals and costals are common. The paired gulars are each broader than long, and the humerals do not contact the paired axillaries. The single inguinal is often fragmented, not contacting the femoral. The forelimbs are covered with large, overlapping scales and have only four toes. Rarely, specimens have five toes on one or both forefeet. The hindfeet have four toes. The tail is longer in males (extending to or beyond the last marginal) and lacks a terminal spine. Buttock tubercles are well developed (reduced or absent in juveniles), and the largest on each side may be surrounded by three or four slightly smaller tubercles. The beak is not hooked, but tricuspid with a serrated edge. The nostrils are below the eye level. Males lack a plastral concavity, but can be distinguished from females by their smaller size and longer tails. Coloration is fairly uniform. Typically the shell is olive to reddish-brown, usually with broad mahogany to black anterior borders on the vertebrals and costals. Often new shell growth is white, so all carapace scutes are separated by thin white lines in the summer. The adult female's shell usually fades to uniform olive or reddish brown. The plastron is usually dirty yellow, often with brown edges along the anterior margins of the scutes as well as a rich orange colour beneath the marginals. The soft skin of the neck and upper legs is uniform dull brown, while the top of the head is often black.

Distribution

It occurs at altitudes of over 900 m in the inland mountains of the eastern and northern Cape, and southern Orange Free State (Greig and Burdett 1976; De Waal 1980). It is now known to extend into extreme southwest Transvaal (Jacobsen et al. 1986). Disjunct, relict populations occur in association with the inland escarpment of the central Cape, as far as the Komsberge, Sutherland District, in the western Karoo.

Status

Homopus femoralis is a common species, not currently endangered, and is well-protected by provincial legislation.

Habitat

It inhabits rocky ridges in mountain and plateau grasslands. Temperatures are very hot in summer, regularly dropping below freezing in winter. Rainfall occurs mainly in summer.

Ecology

Homopus femoralis is a poorly known species despite being common in suitable habitat. It shelters under rock slabs or in abandoned termite nests, hibernating in deep rock crevices from June to September, when winter snows blanket the grasslands. Specimens have been observed active in the early morning. Predators include small carnivores such as mongooses and rock monitors (*Varanus exanthematicus*), which eat juveniles and excavate eggs. One to three eggs (29-35 x 25-27 mm) are laid in summer. The hatchlings measure 25-30 mm and weigh 5-8 gm. Specimens have been observed feeding on sheep faeces.

Threats

There is no evidence that *Homopus femoralis* is threatened, other than on a minor local level. It is possible the species has declined in heavily grazed areas in the northern Cape and Orange Free State, although it favours rocky outcrops rather

than open grassland. Frequent fires may deplete populations, and predation from small carnivores such as mongooses may be increasing.

Conservation

The species has been recorded from numerous conserved areas. Healthy populations occur in the Karoo National Park (Branch and Braack 1989) and Mountain Zebra National Park (Branch unpub. obs.). It is well protected by provincial legislation, prohibiting collection, export, or killing of most indigenous

reptiles, including all tortoises. Permits may be obtained to keep tortoises in captivity but these are unlikely to be issued for this species, as it rarely survives in captivity outside its native habitat.

Current Research

No intensive studies on this species are currently in progress. General aspects of its biology are being noted during a general survey of the Karoo National Park's herpetofauna (Branch and Braack in prep.).

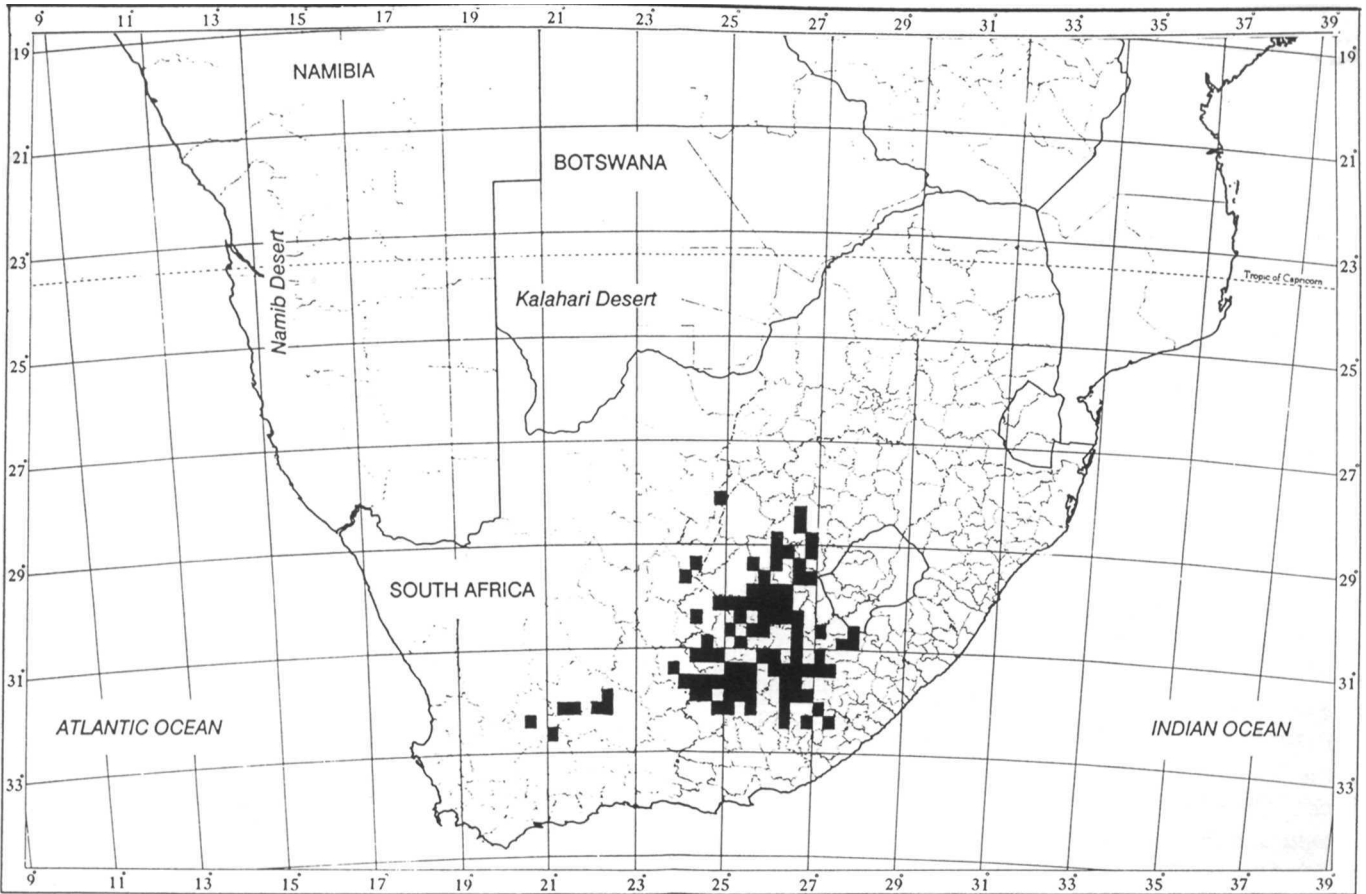


Figure 21. Distribution of *Homopus femoralis*.

Homopus signatus
Namaqualand Speckled Padloper; Peer's Padloper
(for southern race) (English)
Gifskilpadjie; Klipskilpadjie; Namaqualand-
klipskilpadjie (Afrikaans)

Richard C. Boycott

Taxonomy

Two subspecies have been described. Bour (1988) has discussed the nomenclatural history of this species, showing that the nominate form was first described by Gmelin (1789) from two shells without locality. Previous workers (e.g., Loveridge and Williams 1957) have incorrectly attributed authorship to Schoepff, 1792. Hewitt (1935) described a southern subspecies *H. s. peersi* from three specimens originating from Klawer in the western Cape Province. Although recognized by Mertens and Wermuth (1955), the subspecies was overlooked by Loveridge and Williams (1957). Boycott (1986) confirmed the validity of *H. s. peersi* discussing its distribution and characteristics. Subsequently, Bour (1988) demonstrated that Daudin's (1801) description of *Testudo cafra* was the same taxon, and that *cafra* had priority. Nomenclatural stability was not threatened because of the infrequent usage of *peersi*. Daudin's type locality of "Cafrerie" had to be amended, as Kaffraria, an old name for the eastern Cape Province, is out of the species range. Bour (1988) amended the type locality of *Homopus signatus cafer* to "Drainage of the Olifants River, Cape Province, South Africa". The subspecies are distinguished by Boycott (1986). *Homopus s. signatus* has a prominently sulcate carapace, with depressed areolae, patterned with black splashes. The first and second marginals, as well as rear (8-12) marginals are strongly serrated. The nuchal shield is usually wider than long. *Homopus s. cafer* has a carapace which is not prominently sulcate, and its areolae are not depressed. Its carapace pattern consists of fine black stippling on an orange, red, or salmon pink background. Marginals one to two and 8-12 are weakly serrated. The nuchal is usually narrower than long.

Description

This is a small tortoise, and females are larger than males, with a maximum carapace length of 96 mm and mass of 140 gm.

Males measure up to 85 mm and weigh 90 gm, making this the world's smallest testudinid. The carapace is dorsally compressed, the scutes are flat with large, sometimes depressed, areolae. The carapace has five vertebrals, the first usually the narrowest, the third and fifth the widest; four (sometimes five) costals, twelve (rarely eleven or thirteen) marginals. Marginals 1-2 and 8-12 are serrated in the nominate race. The single supracaudal is undivided, the nuchal large. Plastral scutes comprise a pair of broad gulars, which together are between two and four times as wide than long, humerals usually in narrow contact with the single axillary, pectorals, abdominals, femorals in broad contact with single enlarged inguinals, and anals. Five claws are present on the front feet, four on the back. Buttock tubercles are well developed and prominent, the tail lacking a terminal spine. Males can be distinguished by their smaller size, longer tail and prominent plastral concavity.

Coloration varies between subspecies. There are no obvious differences in coloration between sexes. *Homopus s. signatus* has a background carapace coloration of ivory, with a variable number of black splashes radiating outwards from the centres of the scutes. The plastron is mottled ivory or grey with lighter central regions, or entirely grey with lighter patches in the scute centres only. The soft parts are dirty white, grey, or ivory with darker speckles on the head, neck, and limbs. *Homopus signatus cafer* has a background carapace coloration ranging from pale yellow, orange-brown, salmon pink to red, with numerous small, black speckles giving rise to a finely stippled pattern. The plastron is mottled ivory grey, dark brown and black, the tips of the gulars and humerals often tinged with pink or red. The soft parts vary from ivory grey, pale yellow tinged with orange, to pink or red.

Distribution

Endemic to western portions of southern Africa, it occurs from Piketberg, Cape Province in the south, northward to southern

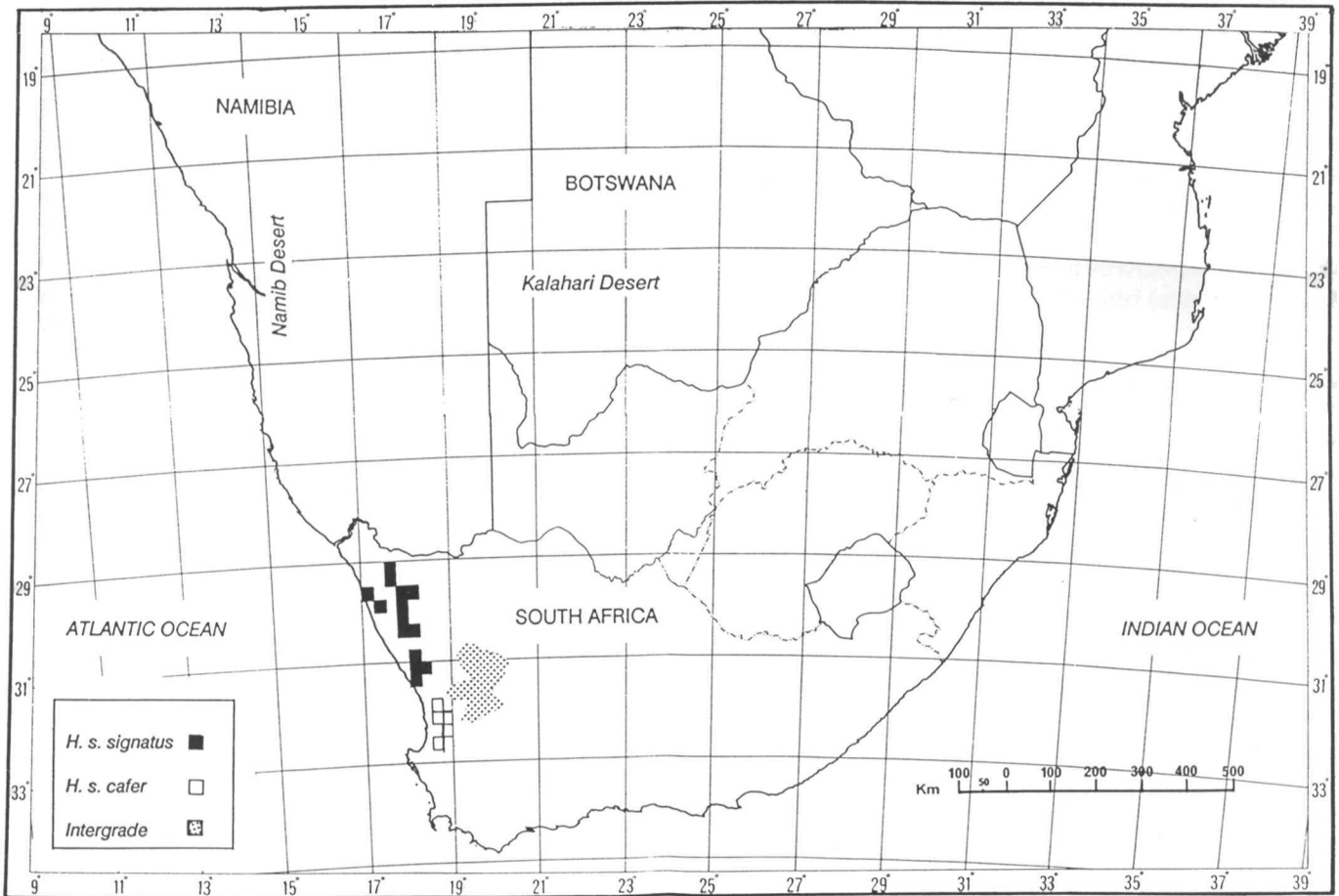


Figure 22. Distribution of *Homopus signatus*.

Namibia. East and north of Clanwilliam, a broad zone of intergradation between the subspecies is evident. The southern subspecies, *Homopus s. cafer*, has a much more restricted range than the nominate race. It is confined to the western Cape.

Status

Homopus signatus is common within its range. Due to the restricted range of the southern race, as well as the general development occurring within the region, it is considered potentially threatened and listed as "Restricted" in the revised South African Red Data Book (Branch 1988).

Habitat

The species shows a strong preference for rocky terrain. It can be found on rock outcrops, along dry, rocky watercourses and in mountains, ranging from sea level to 1,000 m. Veld types inhabited by the nominate species include succulent and bushveld

regions of Namaqualand, the western Great Karoo, and extreme southwestern Namibia. *Homopus s. cafer* occurs in succulent and bushveld regions of the western Great Karoo, and the wetter heathlands and bushveld regions at the northern limit of the fynbos biome in the western Cape.

Ecology

Both races are well camouflaged in their natural habitats. Even when in the open they are difficult to see, as their resemblance to a small rock is remarkable. Their flattened shells enable them to seek shelter in narrow rock crevices and under stones. In the early morning they emerge from beneath large boulders to bask in the sun. Three adult specimens (two females and one male) were found at 07:00h on a low granite koppie, 15 km west of Springbok, Little Namaqualand in November 1988. They were sheltering within individual, small tunnels (up to 30 cm long) in soil accumulated beneath exfoliated granite slabs. As it grew warmer (09:00h) others emerged from crevices beneath much

larger slabs on the same koppie. During the cooler winter months they appear more active and are found wandering among the rocks or sheltering under quite small stones. Nothing is known of their diet in the wild, but they usually do well in captivity. Little is known of their reproduction, but mating behaviour has been observed in captivity in September, November-February, and June-July (*H. s. signatus*) and August (*H. s. cafer*). Boycott and Bourquin (1988) record a single egg laid in summer; McKeown (pers. comm.) reported two eggs (34 x 25, 35 x 26 mm) laid in captivity at Fresno Zoo.

Threats

Neither species is directly threatened at the moment. Habitat degradation due to overgrazing is a potential threat. The attractiveness and small size of this species could lead to exploitation by the pet trade.

Conservation

The Cape Provincial Nature Conservation Ordinance affords general protection to all tortoises. Due to its restricted distribution, *H. s. cafer* is listed as "Restricted" in the revised South African Red Data Book (Branch 1988). The nominate race has been recorded from the Hester Malan Nature Reserve (Greyling and Huntley 1984) and it may be present in the proposed Richtersveld National Park. The southern subspecies has not been reported from any proclaimed reserve, although intergrades between the subspecies may occur in the Cederberg Wilderness Area.

Current Research

No intensive studies on this species are currently in progress, although by occurring in relatively high densities, it readily lends itself to study.

Psammobates geometricus

Geometric Tortoise (English)

Suurpootjie(Afrikaans)

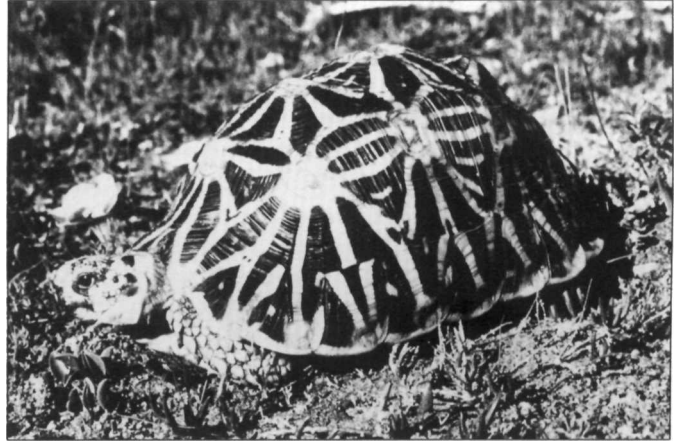
Ernst H.W. Baard

Taxonomy

There is little geographic variation in this species and no subspecies have been recognized. Linnaeus erroneously described *Testudo geometrica* in 1758 from a specimen with the type locality "Asia". The type has now proven to be a *Geochelone elegans* (Wallin 1977). To conserve current usage, Hoogmoed and Crumly (1984) designated a pre-Linnaean figure in Piso (1658) as the lectotype of *P. geometricus*.

Description

This is a small "starred" tortoise with males averaging around 100 mm in length and weighing 200 gm, compared to females averaging 125 mm and 430 gm. The largest recorded specimens are (male) 120 mm, 270 gm; (female) 200 mm, 600 gm. The carapace is highly domed, the sides descending steeply. A nuchal is present. The gulars are paired, and are longer than wide. There are usually five vertebrals, rarely 4-6. These are squatly pyramidal. Costals number four, rarely five. Marginals range between 11-12, those on the bridge being distinctively higher than wide, in contrast to *Psammobates tentorius*. The supracaudal is undivided. The forelimbs have five toes and are covered with scattered large and small scales. The hindlimbs have four toes and buttock tubercles are absent. Sexual dimorphism is marked, males are smaller and have a different carapace profile, sloping gradually to a distinctly rounded supracaudal. They also have a longer tail, and a distinct plastral concavity. Females also appear to be more common (Juvik 1971), but whether this reflects an actual skewed sex ratio (possibly resulting from temperature dependent sex determination), or a sampling bias due to the males' smaller size is unknown. The brilliant pattern makes this one of the most striking and beautiful tortoises. Each carapace scute has a variable number of yellow rays (8-15 on the vertebrals; 9-12 on the costals; 2-4 on the marginals) that radiate from a yellow areola on a shiny dark brown to black background. Occasion-



Female geometric tortoise (*Psammobates geometricus*). (Photo by A. DeVilliers.)

ally all the rays are symmetrically arranged, meeting at the edges of the scutes, resulting in an a perfect geometric pattern (see illustration in De Villiers 1985). A similar radiating pattern is always present on the plastral scutes, except in very old individuals with worn shells. The head, neck, limbs, and tail are yellow with small black patches on the head and tail. There is little variation in colour pattern in adults, although a number of hatchlings with predominantly yellow coloration have been reported.

Distribution

This species is endemic to the region of winter rainfall located in the extreme southwestern Cape Province of South Africa. Formerly, it was found throughout the lowlying, coastal flats between the mountains and the ocean, from Gordon's Bay in the south northwards to the Piketberg. It survives only in a few remnants of its former habitat.

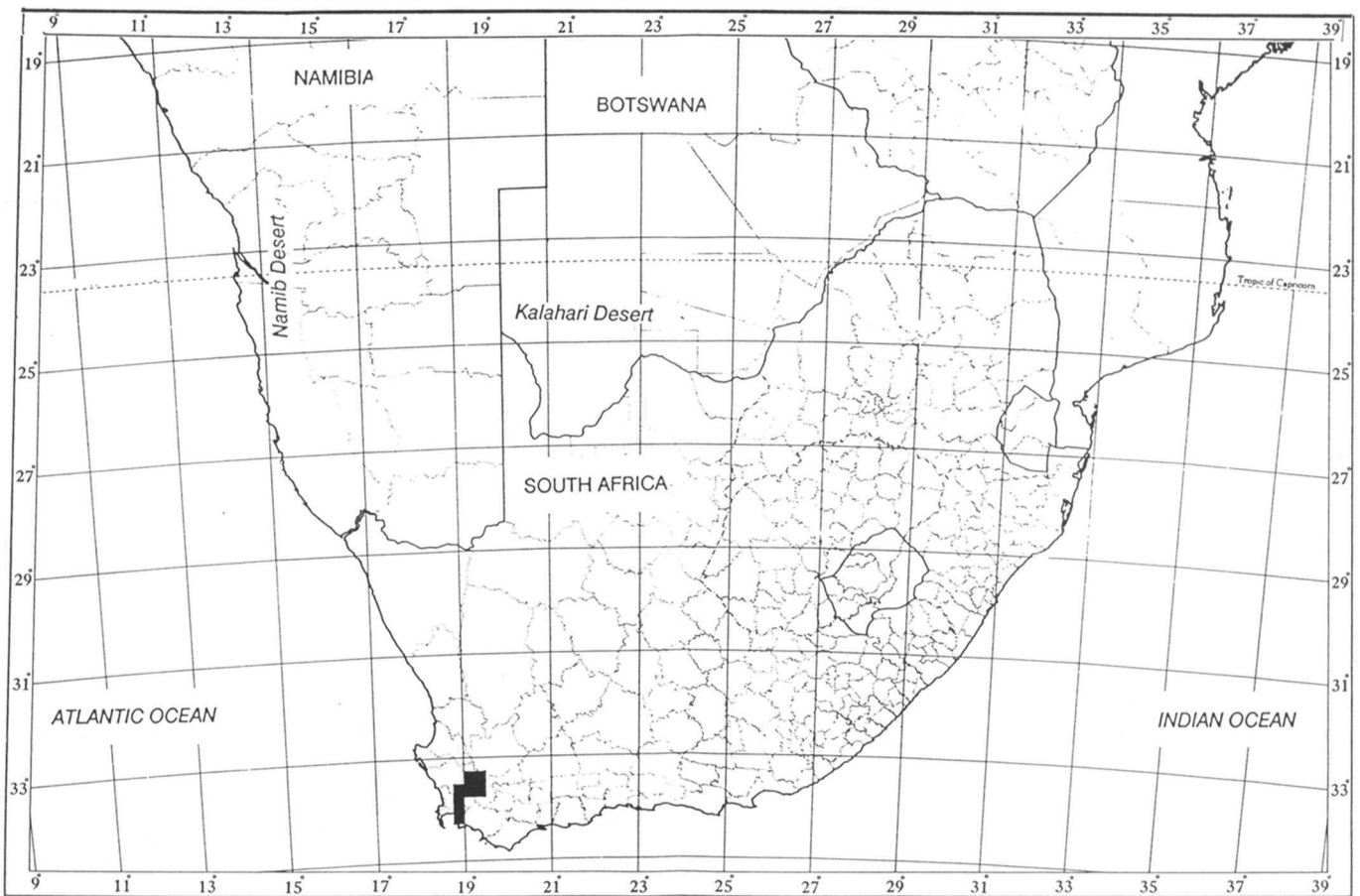


Figure 23. Distribution of *Psammobates geometricus*.

Status

P. geometricus is the only South African chelonian to be listed as "endangered" in the revised South African Red Data Book (Branch 1988). Internationally it is listed in the "vulnerable" category of the IUCN Red Data Book (Groombridge 1982). The conservation status of the species has been reviewed by Baard (1988) and remains critical. Without increased conservation measures, it may become extinct within its natural range.

At present, one private and four provincial nature reserves protect geometric tortoises. These are the Elandsberg Reserve, which is private, encompassing 1,000 hectares, with a population of between 4,000-6,000 tortoises (Baard unpubl. obs.) The four provincial reserves are smaller. Eenzaamheid Reserve (28 hectares, 170 tortoises) (Greig 1984); Romans River Reserve (30 hectares, 41 tortoises); Hartebeest Reserve (30 hectares, 19 tortoises); and Harmony Flats Reserve (9 hectares, 42 tortoises).

Although more than 90% of its natural habitat has been destroyed (Parker 1982), this species is known to occur on at least six other habitat remnants including the area surrounding

Voelvlei Dam, Wellington Dist. ca. 1,000 ha; Krantzkop Dynamite factory, Wellington Dist. ca. 50 ha; Farm Onderplaas, Worcester Dist. ca. 30 ha; Farm Ezelfontein, Ceres Dist. ca. 10 ha; Farm Perdefontein, Ceres Dist. ca. 22 ha; and Farm Glen Etive, Ceres Dist. ca. 10 ha. The Voelvlei Dam, Farm Onderplaas, and Farm Perdefontein are earmarked as future reserves for *Psammobates geometricus*. This species has been reported from two additional sites, Farm Vlakfontein, Malmesbury Dist. and Ellamoer smallholding, Joostenberg, Bellville Dist. Population densities for all eight localities are unknown, but are believed to range from fair to very low (Baard in prep.)

Habitat

P. geometricus is restricted to flat, lowlying renosterveld habitat of the southwestern Cape, including parts of the Worcester and Ceres valleys. The soils are acidic, nutrient-poor and support a low scrub vegetation with *Restio* elements and grasses.

Ecology

Preliminary results from my ongoing ecological studies have shown tortoises preferring relatively open habitats. Activity occurs throughout the year, even in the winter, when tortoises move to higher ground to avoid water logged flats. There are indications that rocky areas may limit tortoise movements to higher ground during these times. Daily activity is bimodal, with peaks at 09:00-10:00h and 15:00-16:00h. They feed on *Crassula ciliata*, *Oxalis* sp., sedges, geophytes, and various grasses (Rau 1969, 1971; Baard unpubl, obs.). Rau (1969) even observed snails and scutes of a *Homopus areolatus* in geometric tortoise faeces, the latter undoubtedly from a scavenged carcass.

Breeding has been observed during spring to early summer (September-November). A single clutch of two to eight eggs (24 x 32 mm) is laid. They hatch six to eight months later (March-May), after the onset of winter rains soften the soil. Hatchlings measure 30-40 mm and weigh 6-8 g. Growth is relatively rapid, with two growth rings being laid down each year. Sexual maturity is reached in seven to eight years, and although longevity has not been established accurately, Greig (1982) states that individuals may exceed 30 years.

Threats

Habitat destruction is the main factor threatening the survival of the geometric tortoise. This species is intolerant of habitat modification (McLachlan 1978), and the irreversible destruction of habitat accounts for population loss. The impact of the pet trade is now considered negligible, due to strict export control (Greig 1982). There is no evidence that it was ever an important factor in the decline of this species. Frequent, uncontrolled fires may threaten the species. The vegetation of the Cape lowlands is fire adapted. Periodic fires are required to maintain species diversity and the veld habitat. Greig (1984) noted that the tortoise reserve at Eenzaamheid was once fenced and protected from grazing. Consequently it became overgrown and tortoises migrated to adjacent heavily grazed veld. Another major threat responsible for habitat alteration is the spread of alien vegetation, especially Australian *Acacia* spp. The importance of increased predation has not yet been established, although Greig (1984) notes the yellow mongoose has increased in the region, and is believed to be a recent invader.

Conservation

Five nature reserves exist where geometric tortoise populations are preserved. The first tortoise reserve was proclaimed during 1972, the result of measures proposed by Rau's preliminary study of the species (Rau 1969, 1971). This reserve (Een-

zaamheid) totals 28 ha. Initially only 8 ha was preserved within a fenced area, but the whole area was managed as reserve in 1987. It has suffered from overgrazing, erosion, bush cutting, and invasion by alien vegetation. Proper management should result in the upgrading of the area. Since 1972, three other provincial reserves have been established. These are Romans River (30 ha), Hartebeest River (30 ha), and Harmony Flats (9 ha). Another very important area is the private Elandsberg Reserve (3,000 ha, of which approximately 1,000 ha is suitable for the geometric tortoise). It supports the biggest population of this species, possibly as many as 4,000-6,000, as well as a large population of *Homopus areolatus* (McLachlan 1978; Greig 1984). Negotiations are currently under way to establish two nature reserves in the Worcester and Ceres valleys.

The geometric tortoise is listed and/or legally protected as follows. It is listed as "vulnerable" in the IUCN Red Data Book (Groombridge 1982) and "endangered" in the revised South African Red Data Book (Branch 1988). It is on Appendix 1 of CITES (Honegger 1981) and listed as an "endangered wild animal" on Schedule 1 of the Cape Province Nature Conservation Ordinance (No. 19) of 1974. Listing on CITES and the Nature Conservation Ordinance implies that none may be collected, transported, imported, exported, or kept in captivity without appropriate permits.

The acquisition of additional natural habitat for conservation of local populations is the main conservation strategy. Equally important is wise management of existing conservation areas, including implementation of management plans for existing reserves. The species is adequately protected by domestic and international conservation legislation. Continued strict enforcement is recommended. A full-scale information campaign should be launched to inform important groups, such as fanners and school children, about the conservation needs of this species and the dangers of extensive habitat destruction. Branch (1988) has recommended the development of techniques for successful captive management and breeding, in case population levels drop critically.

Current Research

Extensive research on the ecology and conservation status of the geometric tortoise is currently underway. When completed, this species' distribution and ecological specializations will be further clarified. The main focus of this project is formulation of a comprehensive conservation strategy, comprising management proposals and conservation measures. Greig (1984), during his tenure as herpetologist at the Jonkershoek Nature Conservation Research Station in Stellenbosch, collected information on the age structure, growth, and movements of the Eenzaamheid reserve population. These latter studies resulted in approximately 200 photographic "identikit" series of individual tortoises, mainly for recapture and growth studies.

Psammobates oculifer
**Serrated Tortoise; Kalahari Tent Tortoise;
Kalahari Geometric Tortoise (English)
Skulprandskilpad; Kalahari-skilpad (Afrikaans)**

Richard C. Boycott and William Branch

Taxonomy

No subspecies have been described and there is little significant regional variation. For the most part the species is allopatric to other *Psammobates*, with the exception of northern populations of *P. tentorius verroxii* in southern Namibia. *P. oculifer* is readily distinguished from *P. tentorius* by the rayed pattern on the plastron and (usually markedly) serrate and upturned marginal scutes. It is distinguished from *P. geometricus* by the prominent buttock tubercles.

Description

P. oculifer is a small tortoise in which females grow larger than males (female maximum size 147 mm total length, mass 450 g; males 110 mm, 200 g) (Branch and Baard 1989). The shell is convex, not flattened, with steep sides and without a hinge. The scutes are flattened, or only slightly raised, and usually have well-defined growth rings, lacking depressed areolae or deep sutures. There are five vertebrals, four costals, and 11 (rarely 10 or 12) marginals. The anterior and posterior marginals are markedly serrate. The nuchal is large, usually twice as long as broad, occasionally curved to one side. The single supracaudal is not markedly recurved. The plastron has paired gulars which are wider than long. The humerals are in contact with the single axillaries. Rarely, the humerals and axillaries are fused. The femorals contact the single inguinals. The beak is hooked and tricuspid. The forelimbs, which have five claws, are covered with large, overlapping scales. The hindlimbs have four claws and large buttock tubercles that are often surrounded by two or

three smaller tubercles. The tail lacks a terminal spine. Males can be distinguished by the longer tail, smaller size, and plastral concavity. In some males this concavity may be minimal or even absent. Coloration varies little. Typically the carapace is light yellow-brown, with each scute having five to eight wide brown to black rays. The pattern is never as vivid as that of *Psammobates geometricus* or the southern or western populations of *P. tentorius*. The plastron is also yellowish-brown with prominent, roughly symmetrical radiating black rays. The head and neck may occasionally have small black patches. In some old specimens the dark rays may fade, but they are never absent.

Distribution

Endemic to southern Africa, it is found throughout the Kalahari region from the northern Cape, throughout Botswana (except the northeast), and into adjacent regions of the southern Orange Free State, eastern Namibia and northern Transvaal. It has not been recorded south of the Orange River or north of the Kunene-Zambezi boundary.

Status

It is a widespread and relatively common species, although usually found in low population densities. Auerbach (1988) notes that it is fairly common throughout Botswana. It does not appear to be threatened by either exploitation or habitat destruction. Little is known of its biology.

Habitat

P. oculifer inhabits arid grassland and open acacia savannah covering deep Kalahari sands in the centre of the sub-continent. None of this region receives less than 100 mm of rainfall per year. In the south it is dry and cold in winter. The northern parts are warmer with moderately high summer rainfall that gives rise to open *Brachystegia* woodland. In the Orange Free State they "occur on sweet grassveld, bushveld and karoo veld types" (Bates 1988).

Ecology

Milstein (1968) found two specimens hibernating in mid-May. They were almost half-buried in soft red sand under the "scant shelter of fallen *Acacia tortilis* branches". With a minor move by one individual, both stayed in these shelters until late September. It is also possible that one of the tortoises returned to its winter retreat several months later. Broadley (1966) noted that a captive specimen caught and devoured grasshoppers. The diet in the wild is poorly known and is currently under investigation (M. Rall pers. comm.). Initial findings indicate that the species utilizes plants of the Liliaceae, Fabaceae, Portulacaceae, and Mesembryanthemaceae families. They have also been noted to eat the droppings of sheep and game. Bates (1988) observes that in the Kalahari they supplement their normally vegetarian diet with hyaena droppings "in order to obtain calcium". Other recorded predators include hyaenas (Bates 1988), jackals, honey badgers, mongooses, secretary birds, and eagles (Boycott and Bourquin 1988). They are often tracked in loose sand to their burrows or place of refuge (Auerbach 1988). They fare poorly in captivity, although on the Transvaal highveld they have been kept with more success than other *Psammobates*.

Little is known of their reproduction. Auerbach (1988) notes that a "few individuals have successfully bred them" and that "2-4 eggs measuring about 30 x 23 mm are laid". However, Boycott and Bourquin (1988) state that the species is known to produce only one oval-shaped egg at a time during the summer months, measuring 40 x 30 mm. They also record captive mating in July, September, and December (on the Transvaal highveld), and in November in the wild. During courtship the

male butts the female and produces occasional soft, grunting sounds. Bates (1988) records hatchlings appearing in March and April onwards.

Threats

There is no evidence that *Psammobates oculifer* is threatened, other than on a minor local level. It may have declined in areas subject to heavy collecting pressure for the tourist trade. The shells of tortoises have always been utilized by bushmen to make "buchu" pouches that are used for storing snuff and other treasures. The ornate and decorative shells of the Kalahari tent tortoise are obviously favoured for making these pouches. There is a ready tourist market for such bushmen "artifacts", and there is a danger that these may be collected in large numbers for the commercial market. Although tortoises are protected in Botswana, bushmen are permitted to collect indigenous fauna and flora for their use.

Conservation

This species has been recorded from numerous conserved areas including Kalahari Gemsbok National Park (Haacke 1984), Bloemhof Dam Nature Reserve, Barberspan Nature Reserve, and Wolwespruit Nature Reserve in the southwest Transvaal (Greyling and Huntley 1984), and Doorndraai Dam Nature Reserve, S.A. Lombard Nature Reserve, and Nylsvley Nature Reserve in the northern Transvaal (Greyling and Huntley 1984). Vast tracts of the Kalahari in Botswana are preserved as reserves and moreover, are very inhospitable, with very low human densities. It is well protected by provincial legislation, prohibiting the collection, export, or killing of most indigenous reptiles, including all tortoises. Although the public may apply to provincial authorities for permits to keep tortoises in captivity, these are rarely granted for any *Psammobates* due to their poor survival in captivity.

Current Research

The only specific study in progress on this species is an investigation on feeding behaviour and diet (Rall pers. comm.).

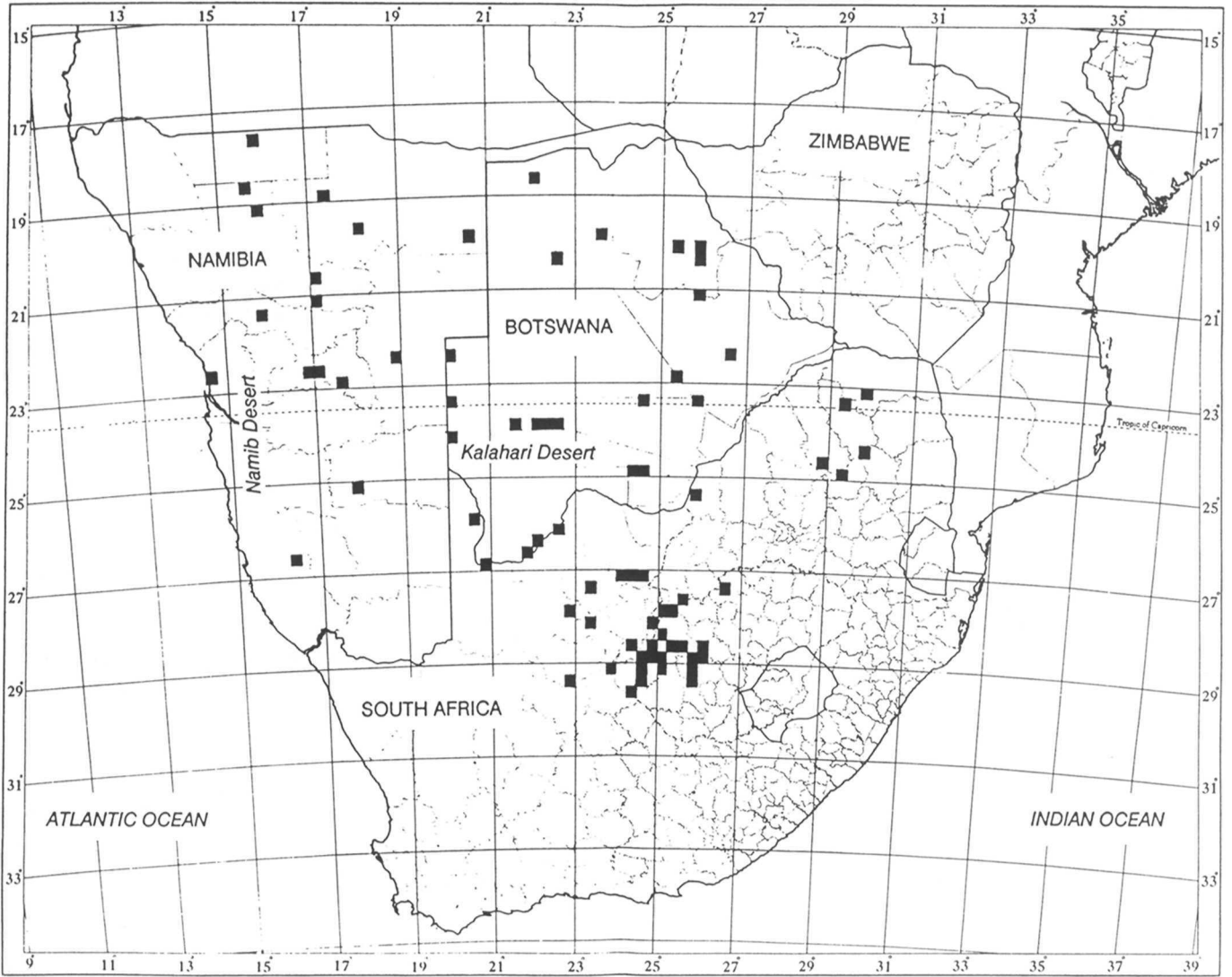


Figure 24. Distribution of *Psammobates oculifer*.

Psammobates tentorius

Tent Tortoise; Starred Tortoise; Union Jack Tortoise (English) Knoppiesdopskilpad; Tentskilpad; Sterretjieskilpad; Skuwedop; Vlaskilpad; Veldskilpad (Afrikaans)

William Branch

Taxonomy

Numerous species and subspecies have been described. The degree of significant regional variation is disputed and needs further analysis. Following the revision of Loveridge and Williams (1957) only three subspecies are currently recognized. However, as Greig and Burdett (1976) noted following their extensive survey of tortoises of the Cape Province, "the taxonomic situation appears to be further complicated rather than simplified." This is indicated in the extent of their intergrade zones, which in some cases overlap by a third of the species' range. A modern review may result in the resurrection of some of Hewitt's numerous taxa. The recognized subspecies are defined mainly by their plastral pattern, although the degree of "knoppie" (pyramid) development and carapace coloration are also useful. Given the qualifications previously noted, the following descriptions should be accepted as generalizations based on contemporary data. Many intergrades may occur.

P. tentorius tentorius (Bell 1828) has a plastron with a solid, sharply defined dark brown or black central blotch, which has only very reduced areas of lighter pigmentary intrusion. The domed carapace has a geometric pattern of thin yellow rays on a black background with well-developed "knoppies." It attains a maximum length of 125 mm. *P. tentorius trimeni* (Boulenger 1886) has a bright yellow or light brown plastron with the central figure sharply defined, but fragmented by lighter rays or broad pigmentary intrusions. The carapace is beautifully coloured with a geometric pattern of wide yellow to orange rays on a black background. These rays merge at the base of each scute turning blood red. The domed carapace has well developed "knoppies" and reaches a maximum length 145 mm. *P. tentorius verroxii* (Smith 1839) often has a uniformly pale yellow or light brown plastron, occasionally with an indistinct dark central blotch. The carapace is often uniform russet or dark brown, but usually faintly patterned with darker brown rays. "Knoppies" are rarely developed, the shell often low, smooth and rounded. The maximum length is 145 mm.

Description

This is a small tortoise that comes in a bewildering range of shapes and colours. Females grow much larger than males (maximum length: female 145 mm, maximum weight 400 g; males 100 mm, 170 g). Dependent upon subspecies, the carapace is domed or flat, with or without raised scutes ("knoppies"), and is unhinged. A nuchal is present, typically broader than it is long. The nuchal is often reduced, but rarely absent. There are five vertebrae, four costals, 11 marginals (sometimes 12), with those on the bridge being almost square in contrast to *P. geometricus*, and a single supracaudal. The paired gulars are longer than broad, the humerals are separated from or in narrow contact with the axillaries (2-3, rarely 1), and the single inguinal is usually in contact with the femorals. The forelimbs are covered in large, abutting scales and have five claws. Buttock tubercles are typically present but may be reduced in western races, the tail lacks a terminal spine. The beak is usually hooked and either bicuspid or tricuspid. Males are much smaller than females (usually less than 100 mm), with narrower and lower shells, longer tails, and a well-developed plastral concavity.

Coloration is varied (see previous subspecies descriptions for the most typical patterns). In most populations, a well-developed rayed pattern occurs on the carapace scutes, but never on the plastron, in contrast to other *Psammobates*.

Distribution

This species is found throughout the central karroid regions of the Cape, from Grahamstown in the east and Matjiesfontein in the west. In the north their range skirts the sandveld of the Kalahari and extends into southern Namibia. There are large intergrade zones between the recognized subspecies, whose main ranges are as follows. *P. t. tentorius* occurs in the southern and eastern Karoo, from Grahamstown to Matjiesfontein, including the Little Karoo, intergrading with *P. t. verroxii* in the

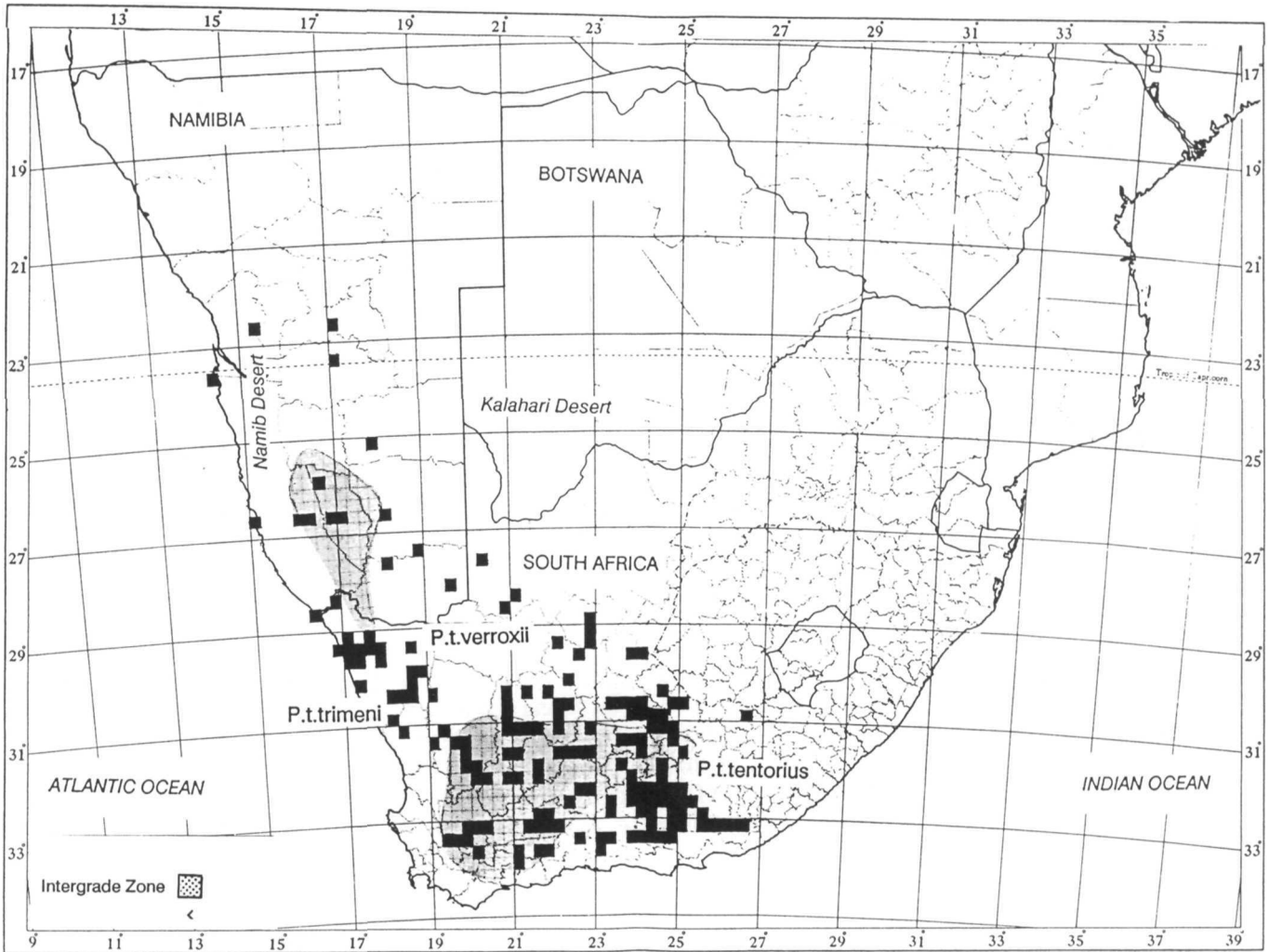


Figure 25. Distribution of *Psammobates tentorius*.

central Karoo. *P. t. verroxii* occurs in the northern Karoo, Bushmanland and north of the Orange River into the escarpment grasslands of southern Namibia, intergrading with *P. t. trimeni* in Bushmanland, and along the escarpment edge of southern Namibia. *P. t. trimeni* occurs in Little Namaqualand along the northern Cape coastal region, from Lambert's Bay in the south, extending across the Orange River into the lowlands of southern Namibia.

Status

This is a widespread species usually found in low population densities, although no population estimates have been published. Due to cryptic coloration, they are easily overlooked. There is no evidence of exploitation or range contraction.

Habitat

Their habitat is varied, usually arid karroid semidesert, with low scrub, shallow, rocky soils, and an annual rainfall of less than 100 mm with hot summers and cold winters. The western race, *P. t. trimeni*, inhabits succulent karoo, characterized by sandy soils, numerous small succulent plants (particularly Crassulaceae and Mesembryanthemaceae), and low winter rainfall. The northern race (*P. t. verroxii*) inhabits a transitional region between semidesert and rocky grassland and sandveld, with slightly higher rainfall.

Ecology

Despite their wide distribution, these species remain among the most poorly known of the subcontinent's tortoises. This is

attributable to their low population densities, cryptic coloration and presence in relatively unpopulated areas. They are poor captives, rarely surviving a year in captivity (maximum seven to eight years). During droughts they burrow into sandy soil at the base of low scrub, emerging after rains. They are active in the cooler parts of the day (early morning and evening), when they feed on small succulents and annuals. They drink by raising the rear of the shell during rainshowers, sipping the water that runs down the shell and forelimbs. Enemies include small carnivores, rock monitors, eagles, crows, and even ostriches. In the Little Karoo, the pale chanting goshawk (*Melierax canorus*) appears to be a major predator on juvenile *Psammobates*. In February and March these tortoises may constitute up to 15% of these birds' diet (Malan pers. comm.).

Few details concerning reproduction are known. Copulation occurs in spring (October-November) and nesting has been reported from September through January. Clutch size is very small; 1-2 eggs (24 x 35 mm) in the western race, and 1-3 eggs in the typical race (21-24 x 27-31 mm). They hatch after about 220 days, and hatchlings have been recorded in May, measuring 25-30 mm in length.

Threats

There is no evidence that *Psammobates tentorius* is threatened, other than on a minor local level. It may have declined in areas

subject to heavy grazing, particularly throughout much of the Great Karoo. There is no evidence of any range contraction and it is still relatively common, albeit rarely seen.

Conservation

The species has been recorded from numerous conserved areas, including Karoo National Park (Branch 1985; Rowlands 1988); Tankwa Karoo National Park; Akkerendam Nature Reserve, Calvinia District (Greyling and Huntley 1984); Karoo Nature Reserve, Graff Reinet District; and Hester Malan Nature Reserve, Springbok District. It is well protected by provincial legislation prohibiting the collection, export, or killing of most indigenous reptiles, including all tortoises. Permits may be obtained to keep tortoises in captivity from the Chief Directorate of Nature and Environmental Conservation, Cape Province, but these are rarely granted, as *Psammobates* do poorly in captivity.

Current Research

No specific studies on the species are currently in progress. General aspects of its biology are being noted during a herpetofaunal survey of the Karoo National Park (Branch and Braack in prep.).

Acinixys planicauda Madagascar Flat-tailed Tortoise, Kapidolo

Lee Durrell, Brian Groombridge, Simon Tonge, and Quentin Bloxam

Introduction

Madagascar lies in the Afrotropical biogeographic realm, although it is considered a separate faunal region due to a marked biotic endemism and heterogeneity (Darlington 1957). *Acinixys planicauda* is confined to 150 sq km in Madagascar's Western Domain, which is characterized by a 6-8 month dry season and a climax forest of dense, deciduous vegetation (Koechlin 1972). Its former range and current numbers are unknown.

As the representative of its genus, *A. planicauda* is extremely important in terms of global biodiversity. It is likely to suffer from continued environmental deterioration unless long-term measures are taken soon to protect its habitat.

Description and Taxonomy

This is a small species, reaching 137 mm carapace length (Kuchling and Bloxam 1988). Some adults have a uniform grey carapace when adult (Bloxam and Durrell 1985) while others retain the juvenile coloration (Klemens pers. comm.). Juveniles are brightly coloured chestnut and black with a broad yellow band running across each scute (Bloxam and Durrell 1985).

A. planicauda has been widely treated as forming a monotypic genus (Loveridge and Williams 1957). Recent reassessments (Obst 1980; Bour 1981) support treating *A. planicauda* as the northern representative of the genus *Pyxis*. (*Pyxis arachnoides* occurs along the western and southern coast regions of Madagascar).

Status and Distribution

A. planicauda is listed as "Indeterminate" in the 1988 IUCN Red List of Threatened Animals (IUCN 1988). A Madagascar endemic, *A. planicauda* has been recorded only from the Andranomena and Amborompotsy forests, situated 20 km and 50 km respectively northeast of Morondava on the west-central coast, although it may occur as far north as Maintirano. The total area of habitat remaining in the two forests in the Morondava region is about 15,000 ha (Kuchling and Bloxam 1988). No precise estimates of the population are available.

Habitat and Ecology

A. planicauda occurs in dry lowland deciduous forest and bush, relatively less arid than bush zones further south in the range of the related *P. arachnoides*. Mean temperature in the coolest month (July) is 21°C and in the hottest month (January) is 27.7°C. Annual rainfall, restricted to a 4-5 month period, is 780 mm. The hot, rainy season lasts 3-5 months (November/December to March/April), and the cool, dry season lasts 7-8 months (Kuchling and Bloxam 1988). Ponds are present in the Andranomena (Bour 1981) and Amborompotsy (Kuchling and Bloxam 1988) forest areas.

Virtually nothing is known of the biology of the species. In their 1985 study, Kuchling and Bloxam (1988) found that these tortoises were active during the daytime, mainly during and

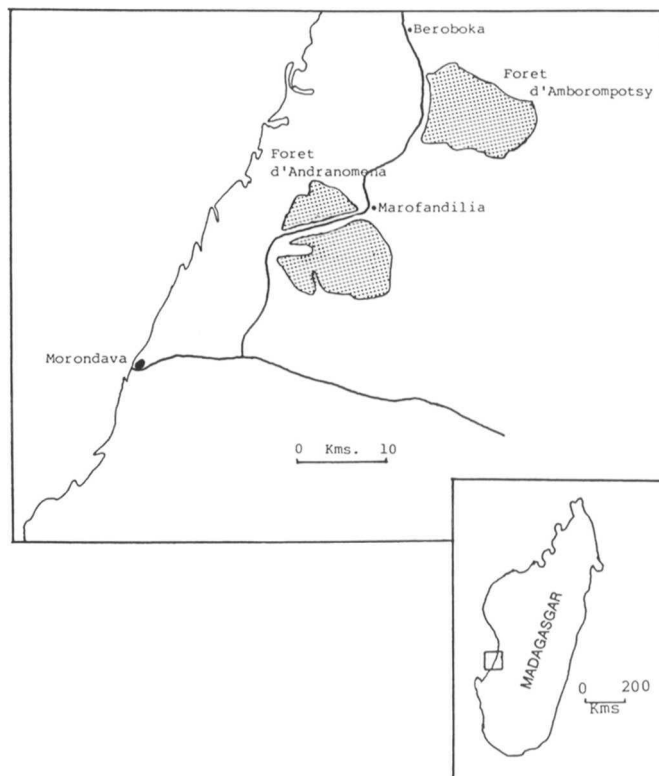


Figure 26. Distribution of *Acinixys planicauda*.

after rains. At night, as well as in dry periods, they were buried in the forest litter. Tortoises were never found in water or on the shores of rivers and pools, but most frequently in parts of the forest far away from open water. The single egg is relatively large, 25-30 x 33-35 mm (Bour 1981), weighing 15-20 g (Pritchard 1979). The number of clutches per year is unknown. The species is thought to aestivate underground during the long dry period, and probably breeds during the wet season (Bloxam and Durrell 1985).

Threats to Survival

Habitat destruction is cited as the cause of population decline (Bloxam and Durrell 1985). The Andranomena forest is largely surrounded by modified habitat and agricultural development, a vast area of cleared forest being devoted to a maize growing scheme (Bour 1981). In the region where this species is found, timber is exploited commercially and for fuel. The burning of native vegetation for agricultural and pastoral purposes is extensive, and exploration for oil has already led to forest clearance (Bloxam and Durrell 1985). *A. planicauda* does not occur in forest areas other than Andranomena and Amborompotsy, although apparently suitable habitat exists (Domergue 1981 in Bour 1981). Bush pig populations are increasing throughout Madagascar, and are considered a threat to tortoise eggs and young.

Conservation

The Andranomena area is privately owned, and at least part of it comprises the Analabe private reserve (Albignac pers. comm.). The Amborompotsy area is leased by the Malagasy government to the Swiss, who operate Le Centre de Formation Professionnelle Forestiere de Morandava and are attempting to manage the forest on a sustainable yield basis using native species.

This species is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and

Flora (1977). Appendix II listing implies that commercial trade is allowed, given that a permit from the country of export is obtained. These permits can provide a method of monitoring trade levels.

Protection of remaining *A. planicauda* habitat should be strengthened. Further field study on the status and biology of *A. planicauda* is urgently required (Bour 1981).

A pair maintained at Knoxville Zoo from 1975 onwards produced no eggs. Only the male was surviving in 1987 (Slavens 1987).

Five specimens were collected from the Amborompotsy forest in April 1988 and taken to the Ampijoroa Forestry Station, where it is intended to establish a breeding group. Until the season's first rains in November 1988 the specimens remained dormant, except during a rare July rain when two individuals were seen "basking" in the shower. After the November rains, they became active, primarily attempting to mate, but also feeding. No successful union had been observed by the end of December. The animals are timid and spend most of their time hiding under dry leaves (Reid pers. comm.).

Current Research

Research within the last ten years on wild *A. planicauda* consists of only two brief surveys conducted in 1985 and 1988 (Kuchling and Bloxam 1988). There has been no research on the species in captivity, other than routine observations on the specimens at Ampijoroa (Reid pers. comm.)

Conclusions

A. planicauda is considered to be "threatened," but there is too little information to assign the degree of threat in IUCN terminology (IUCN 1988). Long-term measures are needed to secure habitat in its very restricted range. Unless this is done soon, it is likely to decline in the wild. Attempts at captive breeding have only just begun but should be pursued.

Geochelone radiata

Radiated Tortoise, Sokake

Lee Durrell, Brian Groombridge, Simon Tonge, and Quentin Bloxam

Introduction

Madagascar lies in the Afrotropical biogeographic realm, although it is considered a separate faunal region due to a marked biotic endemism and heterogeneity (Darlington 1957). *Geochelone radiata* is confined to Madagascar's Southern Domain, which is characterized by low, irregular rainfall and a xerophytic, often spiny vegetation, dominated especially by members of the endemic Didieraceae and of the genus *Euphorbia* (Koechlin 1972). Although the species is protected by local custom, its range has been contracting at its eastern and western extremities due to collecting for food and curios by non-indigenous peoples.

As one of eleven extant species in a pan-tropical genus, *G. radiata* has a smaller distribution than some other tortoises, but as part of the unique, generally threatened fauna of Madagascar, its importance should not be understated.

Wild populations of *G. radiata* are apparently still flourishing in some areas, but this owes more to low human densities and relatively intact habitat than to protective legislation, which is rarely enforced. The species is well-represented in captivity, where it has recently reproduced successfully.

Description and Taxonomy

This is a large terrestrial species reaching around 38 cm carapace length and 13 kg (Pritchard 1979). Its carapace is black with an attractive pattern of yellow lines radiating from the centre of each scute.

G. radiata is probably the nearest relative of the endangered *G. yniphora* of northwest Madagascar. Their hypothesized common ancestor inhabited xeric regions. Its range may have split into southern and northwestern enclaves as more mesic conditions spread after an arid Pleistocene phase (Juvik et al. 1981).

Until quite recently (Loveridge and Williams 1957; Pritchard 1979), this species was assigned to the genus *Testudo*, a usage still maintained by some authorities (Wermuth and Mertens 1977). Recently (Bour 1979) assigned this species to the genus *Astrochelys*, but this usage is not widely accepted.



Radiated tortoise (*Geochelone radiata*). (Photo courtesy of the Jersey Wildlife Preservation Trust.)

Status and Distribution

G. radiata is listed as "Vulnerable" in the 1988 IUCN Red List of Threatened Animals (IUCN 1988). Juvik (1975) summarized its distribution as a species endemic to Madagascar, restricted to the Didieraceae formations occurring in a narrow arc across the south, recorded from near Amboasary in the southeast to near Morombe in the southwest.

The species was relatively common in 1974 in the more inaccessible areas of the Mahafaly and Karimbola Plateaus (which form the present core of the range), but has been severely depleted in or eliminated from the extremes of its range in the vicinity of Taolanaro (= Fort Dauphin) in the east, and Toliara (= Tulear) and Morombe in the west (Juvik 1975). A relatively high density has been recorded along National Route 10 where it penetrates into prime *G. radiata* habitat. After heavy rain (when tortoise activity is most apparent) one tortoise may be encountered per kilometre of road. The species has been subjected to heavy collection in this area for several years, suggesting that population densities may be satisfactory in

more inaccessible areas (Juvik 1975). It still appears to maintain good numbers south of the Onilahy River in the territory of the Mahafaly and Antandroy (Bour 1981). In the small (80 ha) Beza-Mahafaly Special Reserve density has been estimated at 1.33 tortoises per ha (Andriamampandry 1987).

Although populations are reported to be declining at least locally (Honegger 1979), the short-term prospects for the survival of *G. radiata* may be adequate insofar as significant portions of the present range remain relatively free of heavy exploitation or habitat destruction (Juvik 1975).

Habitat and Ecology

G. radiata is restricted to xerophytic forests of the cactus-like *Didieraceae* in the arid southern and southwestern extremity of Madagascar, where the erratic annual rainfall is less than 400 mm. Within this forest type, the species apparently prefers areas with low thornbush and grass cover, rather than dense thickets of *Didierea* itself (the former perhaps offering better food resources) (Juvik 1975). It has also been observed in riverine forests dominated by *Tamarindus indica* in the southwest.

Most aspects of the biology of *G. radiata* remain largely unstudied in the wild. Tortoises at Beza-Mahafaly have been observed to feed on the soft parts (mostly leaves) of eighteen plant species, and occasionally on dried leaves dampened in the rain, as well as the droppings of the bush pig *Potamochoerus larvatus* (Andriamampandry 1987). In captivity, a variety of leaves, grasses, vegetables, and fruits (including *Opuntia* pads and fruit) are eaten (Burchfield et al. 1980). It has been reported that in the wild, a clutch of about twelve eggs is laid in September (Paulian 1955), but clutches of three, four, and six are known in captivity. Eggs are almost spherical (36 to 42 mm in greatest diameter) and laid in a flask-shaped nest 15 to 20 cm deep dug by the hind feet. At the New York Zoological Society's Wildlife Survival Centre, where one hundred offspring have been produced, mean clutch size for seven laying females is 5.1 (ranging from two to nine eggs per clutch), and incubation length appears to be temperature dependent, ranging from 71 to 197 days (Behler pers. comm.).

Threats to Survival

Depletion or extinction of *G. radiata* around the port towns of Toliara, Morombe, and Taolanaro is largely attributed to heavy commercial exploitation during the 18th and 19th centuries, when large numbers were shipped to the nearby Mascarene Islands, notably Reunion, for food (Honegger 1979).

Present exploitation is for food or pets (occasionally kept with the village chickens in the belief that their presence will ward off poultry diseases), or commercial collecting (with

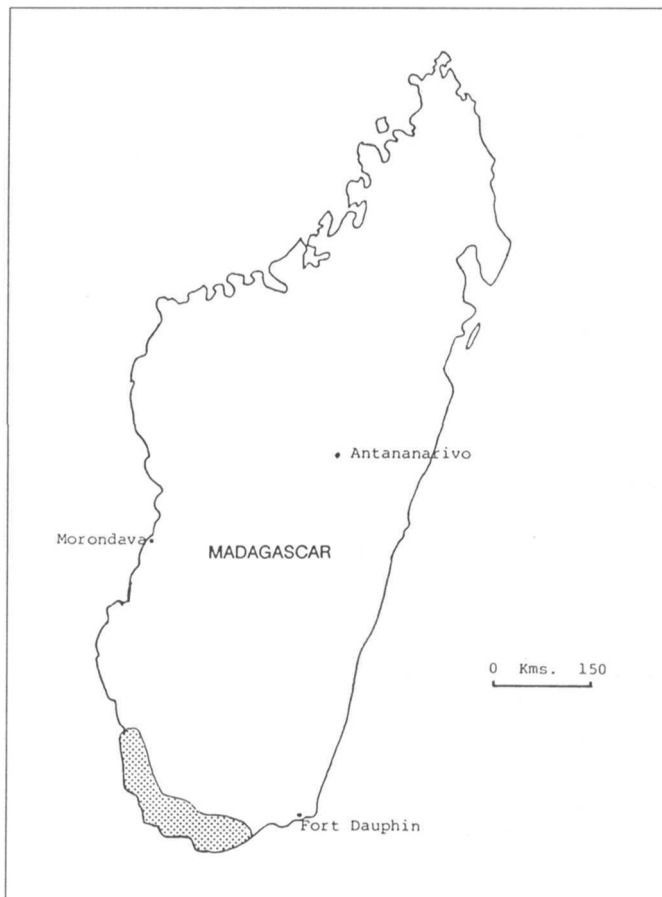


Figure 27. Distribution of *Geochelone radiata*.

resale as food, varnished shell curios, or for the live animal trade) (Juvik 1975). Although the two indigenous peoples in the range of *G. radiata*, the Antandroy and Mahafaly, do not eat tortoises (Bour 1981), they are a favoured food item for people from other parts of Madagascar, generally coming into the area as government workers. People travel by boat southward across the mouth of the Onilahy in order to collect *G. radiata* for food (Bour 1981). Although it is widely known that *G. radiata* is protected, present protective legislation is only weakly enforced, and the animal can still be ordered secretly in many restaurants in the south.

Prepared tortoise shells can be seen everywhere in Toliara and there has been a lively trade in tortoise carapaces at Antananarivo market (Kitchener 1973, in Honegger 1979); polished carapaces are still on sale there (Bloxam pers. comm.). At Toliara in 1976, an adult specimen could be bought for 100 FMG, or less than the price of a chicken (Bour 1981). Vehicles often stop along the National Route 10, connecting Taolanaro and Toliara, allowing passengers to collect tortoises seen on the road (Juvik 1975; Waugh pers. comm.). There seems to be no

regular large-scale collection (Juvik 1975), although heaps of carapaces from tortoises used for food may be seen from time to time (Bour 1981).

The species has also suffered from habitat destruction (Blanc 1968-69, in Honneger 1979), which in the xerophytic forests of the south and southwest is caused by burning, livestock grazing, and cutting for building materials and fuel (O'Connor et al. 1987).

Conservation

The aridity and harshness of the habitat and the sparsity of human population have afforded *G. radiata* a significant degree of protection. Furthermore, the indigenous Antandroy and Mahafaly people consider the species sacred and are inhibited from eating it by a traditional taboo (Juvik 1975).

In the west, the species is present in the Lake Tsimanampetsotsa Natural Reserve in the Mahafaly Plateau, and in the Beza Mahafaly Special Reserve. In the south it is present in the Cap Ste. Marie Special Reserve, and in the southeast in the Andohahela Natural Reserve. It is protected under Decree No. 60-126 of 3 October, 1960 with infringements punishable by fine or imprisonment (Andriamampandry 1987). Export of live or preserved *G. radiata* is restricted, and an export tax of 20,000 FMG is levied on each specimen (Bour 1981).

The species is listed under Category "A" of the 1968 African Conservation Convention (Honegger 1979) and on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (1975). Appendix I listing requires that trade in the taxon and its products is subject to strict regulation by ratifying states and international trade for primarily commercial purposes is prohibited.

Trade controls appear to have resulted in a substantial decline in numbers of *G. radiata* leaving Madagascar (Juvik 1975), and there is apparently no traffic through the capital Antananarivo (Bour 1981). However, in 1982, about 70 specimens of *G. radiata* were confiscated by customs officials in Hong Kong from a ship whose recent port of call had been Toamasina on the east coast of Madagascar. Six specimens remained at the Hong Kong Zoo and 61 were flown to the Jersey Zoo, from where they were dispersed to other collections with the approval of the Malagasy government, which retains ownership. Current information about the rate of confiscation by government authorities of animals being smuggled out of Madagascar indicates that illegal trade is on the increase.

Although there have been two recent studies on the biology of the Beza-Mahafaly population of *G. radiata* (Andriamampandry 1987; Bloxam pers. comm.), further research on the biology and population status of the species is necessary. The impact of present exploitation requires evaluation, and existing conservation laws should be more rigidly enforced.

Captive breeding could play a role in slowing the overall decline of *G. radiata*. 307 specimens are registered in the U.S. Species Survival Plan (AAZPA 1988). Most breeding has

occurred in zoos in the U.S., notably Gladys Porter Zoo (Burchfield et al. 1980) and the New York Zoological Society's Wildlife Survival Centre, where 100 have hatched (Behlerpers. comm.). Zoos in Cairo, Mauritius, Sydney, Zurich (Honegger 1975), and Jersey have also bred the species. There is a group held at the forestry station at Ivohina on the east coast of Madagascar that is said to breed regularly (Andriamampandry 1987), and a group at Parc Tsimbazaza in Antananarivo, both of which consist mainly of animals confiscated by the authorities as they were being smuggled out of the country. A group is also held on a private estate at Berenty in the south. There are several groups comprising many adult specimens introduced on Reunion, where breeding occurs with some regularity, the young are sold as pets (150 FF), and adults are very occasionally eaten (Bour 1981). As mentioned above, specimens held in the U.S. are registered, but an international register or studbook for all captive specimens of *G. radiata* should be established as soon as possible (Durrell 1987).

Current Research

Research within the last ten years on wild *G. radiata* consists of work on the Beza-Mahafaly population by a student at the University of Madagascar on demography, morphometrics, seasonal activity, and diet (Andriamampandry 1987), and by Bloxam on activity rhythms and reproductive behaviour as related to temperature.

In captivity, Burchfield et al. (1980) have investigated management techniques, and Bloxam, Tonge, and Bell initiated a three year study in 1988 on temperature, reproductive behaviour, and fertility on the 15 specimens held at the Jersey Zoo.

Conclusions

G. radiata is considered a "Vulnerable species," i.e. likely to become endangered if threats causing its decline continue unchecked (IUCN 1988). The rate of habitat deterioration and opportunistic collecting, coupled with an extensive range and locally high population densities relative to other threatened Malagasy fauna, indicate that its decline will not be precipitous. However, although commercial exploitation of the species has been suggested (Andriamampandry 1987), particularly of animals confiscated by the authorities, it would be likely to encourage illegal trade and should not be considered. Enforcement of trade controls would be highly problematic given current economic and social conditions in Madagascar. A more practical approach would be to release animals recently taken from the wild into suitable habitat, in conjunction with local education programmes to stimulate conservation awareness. Existing legislation concerning trade and protected areas should be enforced. Local customs, which protect *G. radiata*, should be respected, and breeding of captive populations should be internationally coordinated.

Geochelone yniphora

Ploughshare Tortoise, Plowshare Tortoise, Angulated Tortoise, Angonoka

Lee Durrell, Brian Groombridge, Simon Tonge, and Quentin Bloxam

Introduction

Madagascar lies in the Afrotropical biogeographic realm, although it is considered a separate faunal region due to marked biotic endemism and heterogeneity (Darlington 1957). *Geochelone yniphora* is restricted to small patches (totalling < 100 sq km) of suitable habitat in the northwest of Madagascar's Western Domain, which is characterized by a 6-8 month dry season and a climax forest of dense, deciduous vegetation (Koechlin 1972). Historically, it is known only from an area of 1,500 sq km, where it is still protected by local custom, but was subject to commercial trade in the past.

As one of eleven extant species in a pan-tropical genus, *G. yniphora* is less significant in terms of global biodiversity than some other tortoises, although some of its anatomical features are highly distinctive. However, as part of the unique, generally threatened fauna of Madagascar, as well as being a species on the verge of extinction, its importance cannot be overestimated. There are thought to be no more than 400 specimens left in the wild in areas receiving no legal protection. Existing legislation curtailing capture and trade is not enforced and there are no breeding groups in captivity outside Madagascar.

Description and Taxonomy

A large terrestrial species reaching around 45 cm carapace length or 70 cm if measured over the dome (Juvik et al. 1981), with a light brown carapace with darker wedges on the costal scutes. The species is noteworthy as it has a median anterior horn-like projection of the plastron, formed by extension of the two epiplastrals and fused gular plates (seen to a lesser extent in the South African bowsprit tortoise, *Chersina angulata* (Juvik and Blanc 1974)).

G. yniphora is probably the nearest relative of the vulnerable *G. radiata* of southern Madagascar. Their hypothesized common ancestor inhabited xeric regions. Its range may have split into northwestern and southern enclaves as more mesic conditions spread after an arid Pleistocene phase (Juvik et al. 1981).

Until quite recently (Loveridge and Williams 1957; Pritchard 1979), this species was assigned to the genus *Testudo*, a usage still maintained by some authorities (Wermuth and Mertens 1977). Recently (Bour 1979) assigned this species to the genus *Astrochelys*, but this usage is not widely accepted.

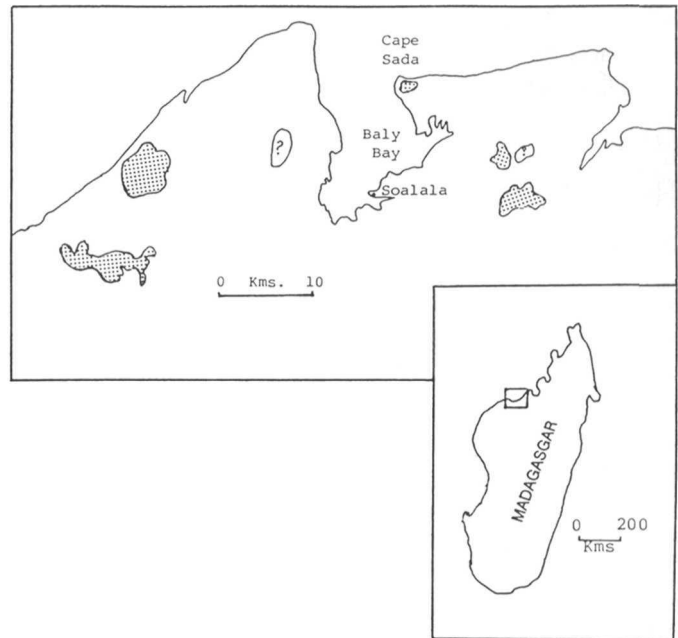


Figure 28. Distribution of *Geochelone yniphora*.

Status and Distribution

G. yniphora is one of only two tortoise species listed as "Endangered" in the 1988 IUCN Red List of Threatened Animals (IUCN 1988). A Madagascar endemic, it is largely restricted to three "islands" of forest within an area of about 60 by 25 km in the vicinity of Baly Bay (including Cap Sada) in the northwest (Andrianarivo 1977; Bour 1979, 1981; Juvik et al. 1981; Curl et al. 1985).

G. yniphora is exceedingly rare and considered to be in imminent danger of extinction (Juvik et al. 1981). During approximately 375 hours spent in searching for *G. yniphora* between 1971 and 1976, only five specimens were encountered in the wild. Four were found at Cap Sada in the wet season, and one near Ankoro on the opposite (west) side of Baly Bay. In addition, fresh tortoise droppings were found at two other localities east of Cap Sada (Juvik et al. 1981). These findings represent one tortoise sighting per 75 hours in the field. In a recent but much briefer study at one locality, encounters occurred at one tortoise per 22 hours in the field (Reid pers.

comm.). For another Madagascar endemic, *G. radiata*, one sighting per eight hours is reported (Baudy 1970). It is estimated that the density of *G. yniphora* is unlikely to exceed five individuals per square kilometre, even in optimum scrub forest habitats. With less than 100 sq km of suitable habitat remaining within the species' known range, a total population of possibly only a few hundred individuals is suggested (Juvik et al. 1981). One recent estimate is that only 10-20 individuals remain, but specimens are extremely well camouflaged despite their size, suggesting that some individuals may be overlooked (Bour 1981). A 1983 expedition considered the wild population was likely to consist of between 100 and 400 individuals, along with an additional 50 captives in villages within the area (Curl et al. 1985). A brief 1986 study revealed a few populations additional to those reported in the 1971-76 work (Curl 1986). Some recruitment is still occurring in the wild, since specimens of all sizes have been found between 1971 and 1983 (Juvik et al. 1981; Curl et al. 1985).

Habitat and Ecology

The species prefers xeric mixed scrub/bamboo secondary growth, which is found particularly in porous, rocky, and exposed coastal areas, forming "islands" within a mosaic of tropical deciduous forest and palm savanna/grassland. The natural climax vegetation in much of the region is tropical deciduous forest, including such species as *Erythrophleum couminga*, *Terminalia bovinii*, and *Acridocarpus excelsus*, frequently with an understory of bamboo *Nastus* spp. (Juvik et al. 1981). In the Baly Bay area this formation is frequently degraded to scrub forest or grassland by annual burning by local inhabitants intended to promote herbaceous growth for grazing of cattle (Juvik et al. 1981). Curl et al. (1985) discuss additional factors responsible for grassland in the region.

Both the natural closed canopy deciduous forest, with scarcity of herbaceous tortoise food plants, and the grasslands, with the danger of fires, are avoided by *G. yniphora*. They favour mixed habitats with open herbaceous zones for foraging and dense thickets for protection and concealment. Such mixed habitats comprise only a small proportion of the vegetation of the Baly Bay area (Juvik et al. 1981; Curl et al. 1985).

Precipitation at Soalala, on the southeast of Baly Bay, is strongly seasonal, with more than 90% of the mean annual rainfall of 1,231 mm occurring from December to March. The soil appears to have a low moisture storage capacity. Much of the year's rainfall is lost as runoff, and there is a moisture deficit during most of the dry season (May-October) (Juvik et al. 1981).

The species seems to be primarily herbivorous in the wild. In a 1971-76 study (Juvik et al. 1981), droppings collected from two adult tortoises at Cap Sada contained 90% (volume) leaves of the leguminous shrub *Bauhinia* cf. *pervillei*, generally swallowed whole, with the remainder consisting of the grass *Heteropogon contortus* (bitten off in 2 cm lengths). A sample from another individual contained 95% leaves of *Foetidia retusa* and *Erythrophleum couminga*, with 5% sedges and grasses. One immature female at Cap Sada was observed feeding on newly

emerged shoots of *Pycneus mundtii* in open rocky terrain, and droppings from this individual contained equal amounts of *Pycneus* and *H. contortus*. In 1983, wild tortoises were observed eating the droppings of bush pigs, and pet tortoises in local households feed on green leaves, fruit, young sugar cane and bamboo shoots, chicken and dog droppings, and cooked rice (Curl et al. 1983). At the Ampijoroa Forestry Station, *G. yniphora* has eaten approximately a dozen species of grass and native herbaceous plants, banana, other fruits and vegetables seasonally available (mango, melon, papaya, pumpkin, cabbage, Chinese cabbage, Malagasy "greens," tomato), as well as raw chicken eggs, dead chick embryos, hardboiled chicken eggs, raw duck eggs, lean raw meat (fed infrequently due to the adverse calcium-phosphorous ratio), cattle dung, crumbled and powdered chicken and duck eggshells, cuttlebone, and a vitamin/mineral supplement (Curl pers. comm.; Reid pers. comm.).

The species shelters amid surface litter in *Terminalia-Nastus* thickets and remains largely inactive during the dry season (May-October), which is also the season of lowest temperatures. The mean low in June-July is 24°C, whereas the mean high in the hottest month, December, is 33°C. Seasonal growth differences are apparently reflected in the well marked growth rings on the carapace scutes (Juvik et al. 1981). Curl et al. (1983), however, found some evidence of activity in both wild and captive tortoises during the dry season, supported by observations of variation in growth rings. He suggested that this phenomena was related to local food abundance. Specimens have been encountered actively foraging only during the morning (08:00-10:00h) and late afternoon (after 16:00h) when surface temperatures are below 45°C. Shelter is sought in *Terminalia-Nastus* thickets during the night and midday (Juvik et al. 1981).

No data are available on the reproductive biology of wild populations, but the species has bred in captivity at the Honolulu Zoo (by artificial insemination) and at the Ampijoroa Forestry Station.

At Ampijoroa, from September through early December, males engage in combat (Curl 1986; Reid pers. comm.) similar to fighting behaviour in *Chersina angulata* (Curl 1986). They use the gular scute to ram, push, and occasionally overturn one another, apparently in tests of strength. "Losers" retreat and show little interest in the females (Reid pers. comm.). Courtship and mating begins in October, continuing into January and early February, with maximum activity in November and December. Courtship behaviour is similar to that of the closely related *G. radiata* (see Auffenberg 1978). One distinctive element is the repeated insertion of the male's enlarged epiplastral projection beneath the female's rear marginals. He pushes and lifts her, frequently turning her onto her back, but she is subsequently righted by the male's continued attentions (Curl 1986; Reid pers. comm.).

Since 1979, one female has laid several clutches at the Honolulu Zoo. All eggs have been artificially incubated but were infertile, except for one produced by artificial insemination. Clutch size ranged from three to six eggs. Eggs were white, nearly spherical with a mean maximum diameter of 42-47 mm and weighed between 40.5 and 50 gm. Flask-shaped nest holes were excavated in moist soil, to an average depth of

11.1 cm, with an average basal width of 11.6 cm. Nesting typically took place in early morning, and sometimes several "test holes" were started before the final nest was constructed (McKeown et al. 1982).

The remainder of the information contained in the "Habitat and Ecology" section of this account comes from Reid (pers. comm.) unless otherwise noted. Observations similar to McKeown et al. (1982) have been recorded from two females at the Ampijoroa Forestry Station during 1987 (one nest) and 1988 (10 nests). A third female laid only five eggs in 1988, but all were soft except one. She was diagnosed as having a calcium deficiency and put on a high calcium diet. She was not allowed to mate during the 1988 season. Because nesting behaviour and incubation are allowed to proceed uninterrupted, morphometric data were obtained only on a single nest deposited in April 1987. The nest was 12-15 cm deep and contained three eggs, each about 35 mm in diameter. In 1988, clutch size ranged from two to five eggs. Subsurface ground temperatures at a depth of 13 cm near all nests were recorded three times daily for the duration of incubation. Egg laying begins in late January or February and continues well into May. Each female deposits four or five clutches approximately a month apart.

One hatchling emerged in December from the 1987 nest. The mother of this hatchling produced 16 fertile eggs distributed among four nests in 1988 which were deposited from mid-February through early May. Of these 16 fertile eggs, six hatched successfully in December. The other female produced 20 eggs in 1988 of which 12 were known to be fertile. These were distributed among five nests deposited from late January through late May. Four young hatched successfully from these eggs in December. Incubation periods ranged from 191 to approximately 267 days.

In 1988, success of hatching seemed to be negatively correlated with incubation time—most "older" clutches contained dead hatchlings unable to emerge from the nest. This phenomenon is thought to be related to the onset of seasonal rains. In other *Geochelone* species, emergence from the ground is timed to coincide with climatic conditions suitable for plant growth (Reid pers. comm.). In Madagascar, the 1988 summer rains were unusually late, bringing subsurface ground (nest) temperatures to above 38°C in late November. In other *Geochelone* species, embryos are endangered at temperatures above 37.5°C. The rains began on 30 November, and within four days, six hatchlings from the last two clutches (deposited in May) successfully emerged. The other nests were then excavated, yielding four live hatchlings from nests deposited late in the nesting season. One had head deformities and died within 48 hours. Reid hypothesizes that multiple, staggered clutching in *G. yniphora* is a strategy to ensure some successful hatchings, given the unpredictability of the onset of seasonal rains.

Threats to Survival

The endangered status of *G. yniphora* is attributable to commercial and subsistence exploitation, habitat modification, and predation by wild pigs (Andrianarivo 1977; Bour 1981; Juvik et al. 1981; Curl et al. 1985; Curl 1986). The species is further

at risk by virtue of its extremely restricted range and reduced chances of contact between remaining isolated individuals.

From at least the 17th century onward, Arab traders collected large numbers of the species at Soalala for export to the nearby Comoro Islands as a food source. The first specimens known to science were obtained in the Comoros. This trade extended into the late 19th century. At this time, around Soalala, this species could still be readily collected using trained dogs (Juvik et al. 1981). Historical commercial exploitation of *G. yniphora* may have contributed to its range contraction (Juvik et al. 1981), but current commercial usage for food or collection for the live animal trade does not appear to be a major factor in the species' decline (Juvik et al. 1981; Curl 1986). A specimen was offered for sale in Soalala in 1974 for 20,000 FMG (Bour 1981).

The indigenous people of the Baly Bay area regard *G. yniphora* as taboo and do not eat it, although other ethnic groups sometimes do so. Locally, this species is occasionally kept as a pet, often with the village chickens, in the belief that it will ward off a cholera-like poultry disease. Opportunistic collecting is likely to have a major effect on an already depleted population (Curl et al. 1985).

Citation of predation by bush pigs (*Potamochoerus larvatus*) as a threat rests on circumstantial evidence. Feral pigs are known to have a substantial impact on Galapagos giant tortoises *G. elephantopus*. In *G. yniphora* habitat around Baly Bay, pig trails and rooting activities are evident everywhere (Juvik et al. 1981; Curl 1986), and the number of pigs seems to be increasing (Reid pers. comm.).

The expansion of savanna/grassland at the expense of dry tropical forest, produced by deliberate annual burning to promote fresh herbage for cattle grazing, may have contributed to past range contraction (Juvik et al. 1981). Annual burning has been observed to destroy scrub/bamboo secondary growth, the species' currently preferred habitat (Curl et al. 1985). Fire is the major long term threat to remaining *G. yniphora*, although large scale habitat changes within the species' current range over the period 1983-1986 were not apparent (Curl 1986).

A recent decision to develop major iron ore reserves in the Soalala area can be expected to have significant impacts on the environmental and economic structure of the region (Juvik et al. 1981). The possible development of the beach at Cap Sada and extension of agricultural usage north of Cap d'Amparafaka are potential threats (Bour 1981).

Conservation

G. yniphora is protected by Malagasy law (Decree 61-095, 16/2/61) and from local use as food by a taboo maintained by the indigenous people (Curl et al. 1985).

The species is listed under Category "A" of the 1968 African Conservation Convention (Honegger 1979) and on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (1975). Appendix I listing requires that trade in the taxon and its products are subject to strict regulation by ratifying states, and international trade for primarily commercial purposes is prohibited.

Survival of *G. yniphora* in the wild is critically dependent on preservation of suitable natural habitat in the Baly Bay area (Juvik et al. 1981). The Cap Sada peninsula has been proposed as the optimum site (Blanc 1973; Curl et al. 1985; Reid pers. comm.) as it combines the presence of tortoises, absence of people, lack of agricultural or pastoral activity, as well as providing suitable habitat, including fire-resistant vegetation, the feasibility of controlling numbers of feral pigs, and ease of protection. Tortoises bred at the Ampijoroa Forestry Station and those held by local inhabitants could be moved to such a reserve. However, because of the expense of creating a new reserve here with no potential for tourist support due to inaccessibility, it may be prudent to investigate the possibility of introducing tortoises to a nearby existing reserve (Reid pers. comm.). In any case, existing laws protecting *G. yniphora* should be enforced. International support and local interest (see Andrianarivo 1977 and Curl et al. 1985) are essential in the realization of these goals (Juvik et al. 1981).

There have been only a few, scattered specimens of *G. yniphora* in captivity outside Madagascar (IUCNAJNEPAVWF 1987). Four specimens reported from South Africa and Japan (Olney 1986) were misidentified specimens of *G. radiata*. At present, there are three specimens at the New York Zoological Society's Wildlife Survival Centre and two at the Honolulu Zoo (Behler pers. comm.).

In 1986, the IUCN/SSC Tortoise Specialist Group in collaboration with WWF—International and the Jersey Wildlife Preservation Trust initiated a major programme for the recovery of *G. yniphora*. The first stage was the relocation of a captive colony of seven specimens (held by the Malagasy Directorate of Waters and Forests on the east coast in an area considered too humid for the species) to the Ampijoroa Forestry Station. This site is adjacent to the Ankarafantsika Natural Reserve, which is relatively near Baly Bay and has very similar climatic conditions. An additional specimen, kept as a pet in a household on the west coast, was obtained for the programme, bringing the total to eight. Since 1986, twelve tortoises have hatched, with ten surviving. Local educational projects and research on the status, ecology, and behaviour of wild *G.*

yniphora with a view to making specific recommendations on the establishment and management of a reserve, are also part of this programme, which is operated in collaboration with the Malagasy Directorate of Waters and Forests.

Current Research

Research within the last ten years on wild *G. yniphora* consists mainly of brief field trips to determine its distribution, status, and habitat condition (Juvik et al. 1981; Curl et al. 1985; Curl 1986; Reid pers. comm.). In-depth work on ecology and behaviour has yet to be done, although studies have been proposed (e.g., Durrell and Swingland 1989).

Recent research on captive *G. yniphora* outside Madagascar includes an investigation of male fertility (McKeown et al. 1982). Ongoing work at the breeding colony at Ampijoroa includes investigations into food preferences, incubation temperature variations within egg clutches relative to temperature-dependent sex determination, as well as routine husbandry methods, medical conditions, and treatment. Biometric data are being gathered and observation of various behavioural patterns are being recorded (Reid, pers. comm.).

Conclusions

G. yniphora is considered in danger of extinction (IUCN 1988), but some natural recruitment in the wild is still occurring. Principal threats are habitat modification, opportunistic collecting, and predation by wild pigs. Although the first two threats may be operating at modest levels relative to threats to other highly endangered species in the world, all three spell imminent disaster for *G. yniphora* because of its small population.

The only optimistic note is the presence of a vigorous captive breeding population in Madagascar and the willingness of the Malagasy government to attempt to rectify the situation if funds are available.

Pyxis arachnoides

Madagascar Spider Tortoise; Tsakafy; Kapila

Lee Durrell, Brian Groombridge, Simon Tonge, and Quentin Bloxam

Introduction

Madagascar lies in the Afrotropical biogeographic realm, although it is considered a separate faunal region due to a marked biotic endemism and heterogeneity (Darlington 1957). *Pyxis arachnoides* is confined to Madagascar's Southern Domain, which is characterized by low, irregular rainfall and a xerophytic, often spiny, vegetation. Members of the endemic Didieraceae and of the genus *Euphorbia* are common (Koechlin 1972). Its former range and current numbers are unknown, but it is reported to be declining in the wild due to habitat deterioration and over-collecting.

As the sole representative of its genus, *P. arachnoides* is extremely important in terms of global biodiversity. It is likely to suffer from continued environmental deterioration and over-collection unless effective measures are taken to protect it and its habitat.

Description and Taxonomy

A small species, attaining 150 mm carapace length (Pritchard 1979), with an intricate webbed carapace pattern of yellow lines. There is clinal variation in plastral kinesis. In the southern subspecies *P. a. matzi*, the anterior plastral lobe is highly mobile, but is less so (especially in adults) in the southwestern subspecies *P. a. arachnoides*, and is rigid in the western form *P. a. brygooi* (Bour 1979).

Until quite recently (Loveridge and Williams 1957) this species had been assigned to the genus *Testudo*, a usage still maintained by a few authorities (Wermuth and Mertens 1977). Subspecies of *P. arachnoides* have recently been discussed by Bour (1979, 1981).

Status and Distribution

P. arachnoides is listed as "Indeterminate" in the 1988 IUCN Red List of Threatened Animals (IUCN 1988). A Madagascar endemic, *P. arachnoides* is restricted to southern and southwestern coastal regions, extending 10-50 km inland. It ranges

from Morombe in the north to Amboasary (near Taolanaro = Fort Dauphin) in the south (Bour 1981).

No precise population estimates are available, but it is reported to be declining (Blanc 1979, in Honneger 1979), perhaps rapidly. It is localized, but not rare north of the Onilahy River (Bour 1981). Although the potential distribution area is relatively large, populations are often disjunct from one another, containing variable numbers of individuals.

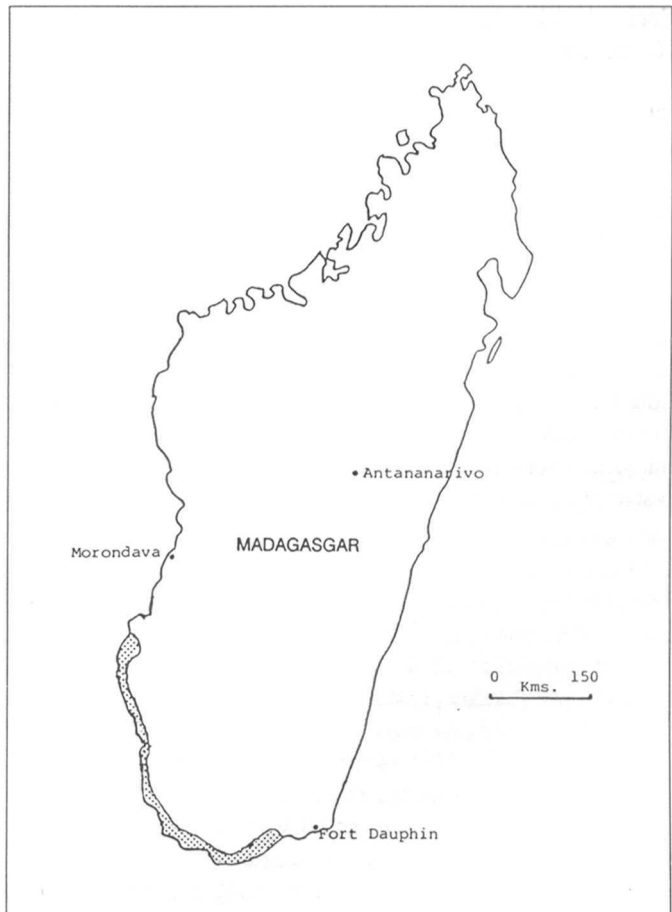


Figure 29. Distribution of *Pyxis arachnoides*.

Habitat and Ecology

P. arachnoides is found in arid or semiarid thorn-bush scrub dominated by members of the Didieraceae. Mean temperature of the coldest month is 19°C, and the sparse annual rainfall of less than 500 mm falls within a two to four month period. The tortoises aestivate underground during the long dry season. They deposit a single large egg, measuring 25-30 x 33-35 mm (Bour 1981). The number of clutches per year is unknown. Very little is known of the biology of *P. arachnoides*.

Threats to Survival

Habitat destruction (by man and by bush fires) and over-collection for the pet trade and other purposes, are cited as the main threats (Blanc 1979, in Honneger 1979). The species is sometimes used in barter, at the port of Toliara (= Tulear) for example (Bour 1981), but is rarely used for food.

Conservation

P. arachnoides is protected to some extent by the aridity and harshness of its habitat (partly shared with *Geochelone radiata*) and low human population densities. It probably exists within the Lake Tsimanampetsotsa Natural Reserve.

The species is listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (1977). Appendix II listing implies that commercial trade

is allowed provided a permit is obtained from the country of export. This can provide a method of monitoring trade levels. Each specimen exported is subject to a tax of 5,000 FMG (Blanc 1979, in Honneger 1979).

Field research on biology, distribution, and status is required. Suitable segments of habitat should be protected.

In 1986, there were reported to be 13 individuals in seven zoos, with only Leipzig (West Germany) having both males and females (Olney 1988). In the late 1970s, egg laying occurred repeatedly among the colony of four kept at the Knoxville Zoo (U.S.A.), but all eggs laid were infertile. By 1984, the Knoxville collection had only two males surviving (Olney 1986). In Madagascar, a few individuals are held on a private reserve at Berenty near Taolanaro.

Current Research

Within the last ten years the only research on this species has been concerned with its systematics (Bour 1979; Bour 1981).

Conclusions

P. arachnoides is considered to be threatened, but there is too little information to assign the degree of threat in IUCN terminology (IUCN 1988). Unless current protective legislation is enforced, it is likely to decline in the wild. There are few specimens in captivity, and these have not reproduced.

Geochelone gigantea Aldabran Giant Tortoise

Ian R. Swingland

Summary

Giant tortoises were formerly common on the islands of the western Indian Ocean, but over the last two centuries, all endemic species have been exterminated with the exception of that on Aldabra Atoll. Present world population is approximately 150,000 on Aldabra with several introduced or captive populations (ca. 5,000) from Aldabran stock on other islands, notably Curieuse and Mauritius. Captive groups, some of which are breeding, are to be found worldwide. There is no evidence of decline but the population is at risk being concentrated on one island vulnerable to development, catastrophe, or natural disaster. There has been a considerable rise in trade of live animals over the last ten years which has only exacerbated the market. This species is now under threat from this activity. Aldabra is a World Heritage Site and the species is listed on CITES Appendix II.

Distribution

Confusion is rife among the Indian Ocean tortoise species since there are too few characters for adequate analysis (Arnold 1979), and waif dispersal was probably common, giving rise to multiple colonizations and extinctions. An excellent example is that of Aldabra, which has submerged and re-emerged several times in the last 125,000+ years, and on each occasion has supported a tortoise population (Taylor et al. 1979). Human transportation of domestic animals (e.g., goats) and tortoises between islands, and introductions for the future food requirements of travellers, was a common practice then as today, and would have further served to confuse the taxonomic picture. Arnold (1979) and Bour (1984) believe that giant *Geochelone* can be divided into two groups: *Aldabrachelys* (Madagascar, Aldabra, and Seychelles) and *Cylindraspis* (Mascarenes, now extinct). These groups shared derived characters which distance them from other *Geochelone* as possible ancestors (Crumly 1984).

Today wild populations of the only living species of Indian Ocean giant tortoise (*Geochelone gigantea*) are confined to Aldabra Atoll with introduced populations on the Seychelles islands of Fregate, Cousin, Mahe, and Curieuse. Breeding groups established on the Seychelles are from Aldabran stock. There are now introduced colonies, for example, on Reunion, Mauritius, Pemba, Nossi Be, and in an increasing number of



Shipping Aldabran giant tortoises (*Geochelone gigantea*) from Aldabra to Curieuse for introduction. (Photo by I.R. Swingland.)

zoological collections worldwide. The colony on Cousin Island in the Seychelles is *gigantea*, although it was long considered to be the remnant population of the granitic Seychelles species which was wiped out during the last century.

Before the early 1800s, giant tortoises were to be found in very large numbers on oceanic islands. Their demise was precipitated by man's exploitation for food and the depredations of introduced and feral mammals. Remains of giant tortoises (*Geochelone grandidieri* and *G. abrupta*) have been found on Madagascar which date from 2290-2060 B.P. and 2850-1910 B.P. respectively (Mahe and Sourdat 1973). This indicates that the two species and human colonization probably overlapped (temporally and spatially) and extinction was brought about by the first settlers (Mahe and Sourdat 1973). On one of the Amirantes, a fossilized egg was found buried four feet below coralline sandcrust by Bruce (Gunther 1898), and on Denis Island in the Indian Ocean a giant tortoise egg dated about 1310 B.P. has been found (Burleigh in Stoddart and Peake 1979).

Rothschild (1915) listed the islands of the western Indian Ocean where he considered tortoises to have been extant: Madagascar, Aldabra, Farquhar, Astove, Chagos, Providence, Iles Africaines, Alphonse, the Amirante, Agalega, Cosmoledo, Iles Glorieuses, Assumption, the Comores, Mauritius, Reunion, Rodrigues, Mahe, St. Anne, Moyenne, Ile aux Cerfs, Con-

ception, Silhouette, Ile du Nord, Ile aux Recifs, Ile aux Fregates, Praslin, Aride, Felicite, Marianne, La Digue, Les Soeurs, and Ile aux Vaches (also listed by Gunther 1877, 1898; Sauzier 1895; Stoddart 1971; Stoddart and Peake 1979).

Some of Rothschild's locations for tortoises must be incorrect; for example African Banks (=Iles Africaines) may be inundated regularly (Swingland pers.obs.) as they are very low, sandy cays. No substantive evidence of tortoises has been found on them. Stoddart and Peake (1979) reviewed the evidence (Table 1), and Bour (1984) mapped the distribution in the granitic Seychelles.

Table 1. Past distribution of tortoises on Western Indian Ocean islands (from data in Stoddart and Peake 1979).

Island	Fossil	Status	Authority
African Banks	-	-	Froberville 1848
Agalega-	-	intro	Froberville 1848
Alphonse-	-	?	Froberville 1848
Chagos-	-	intro	Rothschild 1897
Farquhar-	-	?	Grossin 1742
Amirantes	e	extinct	Gunther 1898
Assumption	e/b	extinct	Fryer 1908
		3m BP?	Honegger 1966
Cosmoledo	e	extinct	Fryer 1911
Denis	e	extinct	Homell 1927
		[1310B.P.Burleigh 1979]	
Gloriosa	b	extinct	Battistini and Cremers 1972
Bird-	-	-	Froberville 1848
Cargados-	-	-	Rothschild 1915
Carajas	-	-	
Coetivy-	-	-	Froberville 1848
Europa-	-	-	Rothschild 1915
Platte-	-	intro	Rothschild 1915
Providence-	-	intro	Froberville 1848
			Coppinger 1883
St. Pierre	e?	?	Fryer 1911
Tromelin-	-	-	Rothschild 1915

N.B. e=egg, b=bone, intro=introduced

Arnold has provided us with one of the most authoritative accounts of the systematics of these species (Arnold 1979). He defines three subgenera: *Asterochelys* (Gray 1873), confined to Madagascar encompassing the small tortoises such as *Geochelone radiata* and *Geochelone yniphora*; *Cylindraspis* (Fitzinger 1835) containing the Mascarene forms; and *Aldabrachelys* (Loveridge and Williams 1957) on Madagascar and the islands to the north.

Cylindraspis and *Aldabrachelys* are distinguishable in the morphology of their skulls, nasal passages, shell thickness, ankylosis, size of the shell opening, and plastron structure. The development of a posteriorly directed diverticulum arising from the ventral wall of the nasal passages in *Geochelone* (*Aldabrachelys*) *gigantea* is of particular interest (Arnold 1979).

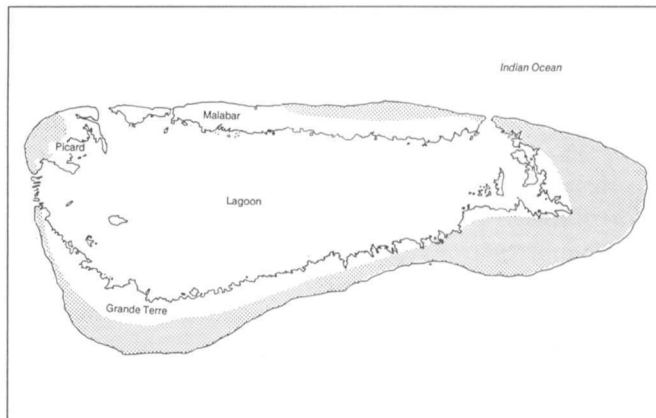


Figure 30. Distribution of *Geochelone gigantea*.

It may have evolved in the short space of time that Aldabra has been above the sea surface and in response to the arid habitat of the coralline surface of the atoll, which is highly permeable to water. Rainfall quickly evaporates or drains away, apart from the few semi-permanent pools on parts of Grande Terre, leaving small puddles of water no bigger than a teaspoon. The giant tortoise's pointed snout and the flap-like ridge preventing flooding of the olfactory area allows them to use such small, shallow, and temporary sources of water and drink through their nose.

Cylindraspis has a thicker carapace, it shows frequent ankylosis, the height/width ratio of the front opening to the shell is greater, and the plastron is smaller than in *Aldabrachelys*. Where *Aldabrachelys* came from is unknown, but marine migration seems most likely (Arnold 1979) since Aldabra has submerged twice in recent geological time (Braithwaite et al. 1973). The Mascarene forms *Cylindraspis* were extinguished fairly early, and few specimens exist. However, two species are generally recognized: *Geochelone peltastes* and *Geochelone vosmaeri*, which have different shell shapes. In the case of *peltastes*, all the shell bones are fused. Shell shape may be functionally correlated with food availability and competition reduction (assuming synchrony, which is probable, Arnold 1979) as they are in the Galapagos tortoises (Fritts 1983). Their other skeletal material is very similar, suggesting close-relatedness; a situation paralleled in other sympatric species such as European *Testudo* and *Geochelone denticulata* and *G. carbonaria*.

On Mauritius itself two synchronous species appeared: *Geochelone inepta* (Gunther 1873) and *G. triserrata* (Gunther 1873), the former having a dome-shaped shell, while the latter is more saddle-backed (Arnold 1979). *G. inepta* may have floated from Mauritius after *triserrata* was already established. Arnold argued that *inepta* might have obtained a foothold against *triserrata* during a dry period common in the Quaternary, since it is more dry-adapted than *triserrata*. However, since *inepta* is more dome-shaped than *triserrata*, it is probably less well adapted to dry conditions.

Tortoise remains from Reunion confirm that a species with a similar degree of ankylosis to other Mascarene species was definitely present, although the only carapace known, the type

of *Testudo indica* (Schneider 1783), is almost certainly *triser-rata* with some minor differences, and comes from Mauritius, not Reunion (Petit 1737; Arnold 1979; Bour pers. comm.). Without doubt, tortoises existed on Reunion, and they were probably similar to the Mauritian forms.

Aldabrachelys consists of seven species, all of which are probably referable to *Geochelone gigantea* with less variation found amongst them than exists among *G. elephantopus* (Arnold 1979: 138). The presence and absence of the nuchal scute has been emphasized in the literature as the critical difference in classifying these species. On Aldabra, of 16,000 individuals examined, the nuchal was absent in 83 animals. Nuchal absence was more prevalent on Grande Terre than Malabar. While enormous variation exists within and between populations of tortoises (giant tortoises in particular), both inter- and intra-specifically, it is obvious that the granitic Seychelles had a distinct form, varying in shape from dome-shaped to slightly saddle-backed. Although the latter material was collected after exportation from Aldabra to Mahe had begun, the shell shapes are quite distinct from any found on the atoll (letter from Gadow 1916 (BMNH archives) on the Percy Sladen Trust Expedition, in Arnold 1979).

Nine specimens from Madagascar are attributed to *Geochelone grandidieri* (Vaillant 1885) and have flattened and robust carapaces; two from Madagascar are attributed to *G. abrupta* (Vaillant 1885) (similar to *gigantea*) with less flattened and narrower carapaces. Neither species is conspecific (Arnold 1979), but both occurred on the western side of the island (Mahe and Sourdat 1973) and were sympatric in areas, probably occurring synchronously (Arnold 1979). The population of *abrupta* in north west Madagascar may have been the seed stock for giant tortoises on Aldabra and the Seychelles. The oceanic current flows from Madagascar toward these islands, and the morphology of *abrupta* is similar to *gigantea*.

Geochelone gigantea is now restricted to Aldabra Atoll (46°0'E long., 9°24'S lat.) in the Indian Ocean, 400 km north of Madagascar, and part of the Republic of the Seychelles since 1976. Aldabra is 29 km long and the large central mangrove-fringed lagoon is surrounded by a coral limestone surface covered in dense scrub (*Pemphis*) alternating with open areas of grass and herbs. The atoll is divided into four major islands, of which Grande Terre, the southernmost, is the largest.

Population Status

One hundred and twenty seven years after Mauritius was discovered, Herbert (1634) reported the existence of tortoises on the island (four years after his visit), and others confirmed his observations (Morisot 1651; Flacourt 1658; Mandelslo 1669). Within 37 years they were rare, and only found in abundance on nearby islands such as Ile aux Cerfs (Pitot 1905). Pitot (1905) also reported in 1673 that animals were being taken for salted meat and rendering into fat (400-500 tortoises=100 liters of oil), and that eggs and young were being destroyed by pigs. Although numbers had almost disappeared, one year later over 300 animals were taken from Ile Plate (a nearby islet), but by 1778 they were rare on Mauritius itself (Sauzier 1895).

To the southwest of Mauritius lies Reunion (discovered 1512), also with substantial giant tortoise populations. These were reported in 1650 (Leguat 1708) and 1665, although by the later date pigs had begun molesting eggs and young (Grant 1801). In 1671, tortoises were still very abundant, and by 1688 they were the common food of the indigenes (Froidevaux 1899). By 1732, they were nearly completely extinguished, and by 1754 they were rare (Vaillant 1899).

Rodrigues (discovered 127 years after Mauritius) had herds 2,000-3,000 strong in 1691 (Leguat 1708), which were dense enough for a person to walk on their backs without touching the ground for a hundred metres or so. The largest animal was about 45 kg. Today such a feat can only be attempted on the coastal grasslands of Grande Terre (Aldabra) during the migration. Milne-Edwards (1875) reports them being abundant in 1725 and reaching 90-110 cm long. A settlement was established to collect tortoises for export to Mauritius before 1750 (Herbert and Nicholson 1780), and it was still going strong in 1761. Thirty thousand tortoises were exported in four vessels in 1759 alone (Gunther 1898), and 21,000 animals were removed in six voyages during 1759-61 with a probable survival rate of just over 50% (Milne-Edwards 1875). This trade continued for at least twenty years (1750-70), with an annual export of around 4,000-5,000 animals averaging 9 kg (Froberville 1848). By 1775, rats, feral cats, and the trade had their effects, and by 1800, tortoises were probably extinct on Rodriguez (Dupon 1969).

Little is recorded of the Madagascan giant tortoises and their eventual demise. It is almost certain that they were over-utilized from the time of the first colonization onwards, for today only four relatively small species remain: *Geochelone radiata*, *G. yniphora*, *Pxyis arachnoides*, and *Acinixys planicauda*.

In the Seychelles, tortoises were common. Settlement in 1768, 159 years after the islands were first discovered (Silhouette), heralded the beginning of the massive exploitation that was to follow. Even as early as 1787, Malavois became concerned that some control over the tortoise trade had to be exerted if they were to be prevented from extinction. He estimated the remaining population as being 6,000-8,000 with 13,000 having been exported between 1783-1787. Stoddart and Peake (1979) estimated the trade as being about 300 animals per year, suggesting an original Seychelles population of over 20,000. With the threat of rats, cats, local consumption, and export to Mauritius, Malavois (1786) proposed splitting the remaining population between reserves on St. Anne and Ile aux Cerfs (Fuavel 1909). Sometime around the turn of the century, granitic Seychelles tortoises became extinct, because by 1839, tortoises were being imported to Mahe from Aldabra Atoll (Harrison 1839).

Stoddart and Peake (1979) mention that the later history of the tortoises was one of domestic existence in small, privately-owned herds (e.g., Gordon in Stoddart and Peake 1979; Coppinger 1883; Davidson 1911). A colony of 42 animals was established on Curieuse, only a few miles from Mahe, in 1895 (Gunther 1898), but the effort was unsuccessful. Another attempt was made recently (Stoddart et al. 1982) starting with exports from the atoll in 1976, when several hundred were

transported from Aldabra to enable tourists to see this species in semi-natural habitat. Other small populations still exist on Cousin and Fregate.

Since 1744, Aldabra has been reported as having large concentrations of tortoises (Dalrymple 1784; Horsburgh 1809; Moresby 1842), and Owen mentions large numbers on Ile Malabarin 1824 (Stoddart and Peake 1979). By 1822, tortoises were being exported to Mauritius and Mahe, and whalers were operating by 1823. Stone enclosures were built in the early 1800s to pen animals prior to export (Sauzier 1895; Voeltzkow 1896; Stoddart 1971; McKenzie 1971), and it can be estimated from the various reports that conservatively 50,000-100,000 animals were removed between 1800 and 1880 when numbers were very low (e.g., Kersten 1871). Stone enclosures were noted on Aldabra at the settlement on Picard (Baty, 1896) and at Takamaka on Grande Terre (Voeltzkow 1896).

From reports, Aldabran animals were bigger than Rodrigues tortoises (ca. 45 kg, Dalrymple 1784), and Kersten (1871) reports that the largest animals in an 1842 export weighed 360-410 kg (today the largest animals weigh <130 kg). Tortoises from Silhouette in the granitic Seychelles were bigger and more numerous than those in Mahe (Froberville 1848). Large body size in island tortoises is characteristic of those from more mesic environments, particularly on elevated oceanic islands. In the higher Galapagos islands and the granitic Seychelles, the rain shadow (or at least higher rainfall) and its effects on body size are in stark contrast to the xeric, flatter islands where tortoises are small by comparison.

In 1874, a group of prominent British biologists led by Hooker wrote to the Governor of Mauritius expressing the need for conservation since the atoll's lessee intended to cut wood. Wharton and a party of able seamen took three days to find a single animal in 1878 (Wharton 1879). Rivers found none in December 1878, but he reported large concentrations at Cinq Cases (southeast Grande Terre) when it rained. Leguat (1708) also reported that they were so dense one could walk 100 yards on their backs, and I can confirm that the situation is the same today. Leguat also remarked on the damaging effect of feral pigs that had already died out by his visit and the absence of the bleached carapaces of dead animals (Stoddart and Peake 1979) which he must have seen in some abundance elsewhere.

By 1879, officialdom had become concerned about the plight of the tortoises and their possible extinction, and thought a guardian should be stationed on the atoll "...to strictly preserve the forest" (Chief Commissioner to Governor of Seychelles 21.1.1879). In 1890, a visitor was told by 15 Seychellois living on Picard since 1889 that in two months they had only seen one tortoise, but that Malabar was said to have a few. James Spurs arrived as the new lessee in 1891, and introduced 11 tortoises onto Picard from other parts of the atoll, since there were few on Picard itself. Spurs was instructed to tell his labourers not to kill tortoises, and plans were afoot to export a number of animals to Curieuse near Mahe "at the first opportunity" (Administrator to Lt. Governor 1893). During the 1890s, conflicting reports of estimated numbers filtered in from Aldabra. Spurs' estimate (Griffiths to Administrator 13.6.1892) was >1,000, although Griffiths thought this was an overestimate. Rats were thought to be limiting numbers (Griffiths to Lt.

Governor, Mauritius 4.4.1893). "Traces" were found on Picard (Baty 1896). Abbott found "few" over a four-month visit (Abbott 1893), the population probably having been reduced by whalers. Nine animals and no skeletons were found by Voeltzkow (1896). None were found in 1900 (Bergne 1900) nor in 1906 (at Picard and Takamaka, Nicoll 1908).

Reports from 1900 onwards indicate a gradual recovery of the population (Seychelles Governor to Secretary of State for the Colonies 29.7.1900; Dupont 1907).

In 1909, de Charney, the lessee of Aldabra, reported that tortoises were in danger of disappearing because of "cranes" (sacred ibis) preying on the young and that although there was no danger of extinction as Government House had a herd, numbers could be placed on Astove, Curieuse, Felicite, and Long Island with the "advice of Mr. Standley Gardiner of Gaius College, Cambridge and Mr. Fryer" (Governor to Secretary of State for the Colonies 26.7.1909). A further letter (20.8.1909) states that the Governor reached various conclusions in conversation with local experts: "The Aldabran population was safe from depredation because of their wild (remote?) state even though damage to the young by rats was considerable but not that by florentins (grey herons). Even though adult tortoises fall into pits and perish they are limited by their food supply. Ultimately the race will die out in a wild state at Aldabra, as they have died out in other islands where remains of them have been discovered in a wild state." The Governor did not think it worth transferring Aldabra animals to other islands since it would be ineffectual in protecting them "since they are as safe there (on the atoll) as anywhere." "The race will not die out as apart from Government House (where a herd is recorded in a stud book, subsequently lost), several other large herds are in private hands which will be well looked after as long as they have a market value for sale to zoos. I shall place on record that, in the event of any revision in the lease of the Aldabra Group of islands, the lessee shall be bound to present yearly to the Governor of the Seychelles an adult pair of land tortoises for preservation at Government House. There are specimens of *Testudo daudinii* (Gunther) in the herd at Government House that correspond to the drawings and descriptions in Dr. Gunther's Monograph (1877) and these may be the only survivors of the Mahe breed."

Fryer saw some tortoises on Malabar, Picard, and eastern Grande Terre (17 in a day) and thought that after years of living on Aldabra it would be quite possible not to see any tortoises (Fryer 1910, 1911). In 1911, Davidson included wild cats apart from rats and grey herons as threats to the young, and thought that nothing would prevent the tortoises' extinction on Aldabra. By 1916, thousands were seen at Cinq Cases and in 1927 they were ubiquitous (Dupont 1929). From 1890 onwards, a trickle of Aldabran animals were exported from Mahe, averaging about 30-50 a year (Stoddart and Peake 1979).

In 1881, Gordon listed 13 families on Mahe, Praslin, La Digue, Ile Cerf, and Deux Soeurs with herds (the largest animals 170 cm 230 kg), and in 1883 Coppinger saw a male of 181 kg and a female 227 kg at Government House. In 1904, there were 42 tortoises at Government House. Most of them came from a private herd at Val des Pres which was transferred to Curieuse before returning to Mahe in 1902 (Governor to Secretary of State for the Colonies 1.6.1910).

The herd included "Gordon" presented by General Gordon in 1881 (carapace length (CL) 4 feet, 9 1/2 inches, plastron length (PL) 3 feet, 9 inches) and "Spurs" (*Testudo elephantina*, CL 4 feet, 5 inches, PL 3 feet, 7 inches) presented by Mr. Spurs (Europa Island lessee). Seventeen young hatched between 1902-1903. The largest female (CL 3 feet, 8 inches, PL 2 feet, 8 inches) has not grown since 1907. The breeding season is January to April, and females carry eggs for ten weeks. Clutch sizes vary from 9-25 eggs. Females deposit two clutches per year. The incubation period is 120-130 days, but half the eggs at Government House are infertile. In dry periods, few young emerge, not being able to work their way upwards through the top of the nest. At four years, they vary between 18-22 inches CL and are sexually mature at 25 years. Number of young 1904-1909 was 168. Losses to rat predation are high until the shell hardens. On Aldabra, young are killed by cranes (sacred ibis), rats, and wild cats. Some specimens have been sent by Sir John Durnford to Groot Schuur (Pretoria, South Africa) and London Zoo. Four adult males, 18 adult females and 27 young have been sent to Long Island, Seychelles (Governor to Secretary of State for the Colonies 1.6.1910).

The last intensive survey estimated there were $150,466 \pm 16,441$ giant tortoises on Aldabra (Morgan and Bourn 1981). Numbers have built up considerably since the turn of the century when visitors were unable to find any tortoises after hours of walking (Wharton 1879). The Grande Terre population is a large (approx. 145,000) and very dense population (ca. 27 per ha) of relatively small individuals. Those populations on the northerly island Malabar (12 per ha), and Picard (5 per ha) to the west, are very accessible to man, small (<4,000) and are composed of large individuals.

On Aldabra, the inhabited island of Picard has the lowest tortoise population density (5 per ha) and is an open, vegetated habitat; Malabar has a more dense and shady vegetation with a low population density (7 per ha); and Grande Terre has the highest density (27 per ha) and a very open, drier habitat. Rain falls throughout the hot, wet season from December to April, and the dry, cool season is from May to November. All the islands are affected similarly, none being over 10 m above sea level. All three islands have similar temperature characteristics. Rainfall is as irregular and unpredictable as on the Galapagos, but not as severe as an El Niño event. Other than the migration on southeast Grande Terre, no nesting migrations occur.

The global population outside Aldabra, either in captivity or introduced, is about 5,000 animals.

Habitat and Ecology

Depending on population density, *Geochelone gigantea* males can reach 105 cm straight carapace length and over 250 kg, and females 87 cm and 167 kg respectively. At higher densities, individuals stop growing at smaller body sizes, and their sexual maturity is delayed. Translocation from higher to lower-density populations results in an increase in growth and annual fecundity, even in adult individuals. Large herds frequent open grassy swards punctuated by trees and shrubs, but individuals also live in scrubland and mangrove swamps. Heavy grazing on

Grande Terre, the densest population, has resulted in a genetically dwarfed sward of grasses, sedges, and herbs dubbed "tortoise turf". Little browsing occurs, although fallen leaves and some living leaves (such as *Guettarda*) are eaten, particularly during the dry season.

Mating occurs from February to May, and nesting takes place from June to September. Eggs laid early take longer to develop than eggs laid later. This is the result of the higher ambient temperatures later in the season and the effect of temperature on incubation rate. Clutch size and egg size vary inversely to population density, although annual variations are due to fluctuations in rainfall, mediated through the effect on primary production, and are most marked in the high-density population. On Grande Terre, the clutch size is 4-5, on Malabar ca. 14, and on Picard intermediate between these two figures. Adults from the low-density population of the same age and sex are twice the size of those from the high-density population. Low-density females can lay multiple clutches, while those in the high-density population may lay only every two or three years. This species has environmental sex determination and lacks heteromorphic chromosomes.

Recruitment has effectively ceased in the high-density population and it is likely that this population on Grande Terre has reached the carrying capacity. Recent work has identified groups of sub-population blood isozymes found in particular locations, suggesting little mixing of individuals over long distances. In general, animals spend many years in the same locality, becoming increasingly sedentary with age. A migration occurs in southeast Grande Terre, where animals move from inland areas onto the coastal grasslands in large numbers immediately prior to and during the rainy season, from October to April. The advantage in migrating is the availability of more food than inland, but there is little shade, which is vital for surviving the midday sun. More animals die on the coast than inland, but the larger supply of food insures larger clutches and more frequent laying by migrants. There is strong evidence indicating that the same individuals migrate each year, and that differences in migratory behaviour cannot be ascribed to sex or age. The system is frequency dependant, and migratory animals are longer and narrower than non-migratory individuals.

Threats to Survival

The atoll has effectively protected the population as a result of its inhospitable terrain and lack of fresh water. However, population structure in the various islands and sites indicates an under-representation of successive age cohorts at those sites which are accessible (e.g., sites on Malabar, west Grande Terre, and Picard). This is particularly noticeable as during the Second World War, no animals could be taken, resulting in relatively larger cohorts from 1939-1946. This further suggests that the main trade was in hatchlings or young, rather than adults.

The atoll's strategic position in the Indian Ocean and the extremely limited range of the species make *Geochelone gigantea* at risk from military development, resource usage (mangrove, fish), epidemic, natural catastrophe (hurricane), and possibly tourism (if the difficulties of water supply and transport could be economically overcome). The presence of the

necessary workforce for various types of development may be ultimately destructive to the wildlife as it has been on Diego Garcia, which was bought by the British Government to provide the USAF with an Indian Ocean base. In 1964, the British Labour Government announced plans to build an airbase for the American Air Force on the atoll, involving a controlled atomic explosion to create a harbour for fuel tankers, but these plans were shelved after devaluation of the pound and an orchestrated outcry by scientists. Until the beginning of the 1980s a number of temporary or permanent scientific expeditions were mounted by the Royal Society which built a research station on Picard in 1970 using a Parliamentary Grant-in-Aid.

Conservation Measures Taken

In 1980, the Seychelles Islands Foundation was established to conserve the atoll in collaboration with the Government of the Republic of the Seychelles. The atoll has since been designated as a World Heritage Site. However, since 1980 there has been a reduced level of scientific activity, which by its very presence acted as a monitoring service. The species is on Appendix II of CITES, allowing commercial trade providing a permit is issued from the country of export. This can provide a means of monitoring the trade levels but large numbers of adults, and even marked animals from the atoll, have been appearing in trade in the U.S.A., Germany, U.K., North Africa, South Africa, Canada, and even India and Hong Kong.

Consignments of tortoises have been taken since 1976 from the atoll to Mahe, the capital, and Curieuse, where some animals are being released to establish a captive colony to enable tourists to see giant tortoises in semi-natural circumstances. A research project has been mounted by the Zoological Society of London to monitor this introduction, where there is already evidence of poaching.

With the increased trade in this species, the very high prices paid for adults (U.S. \$6,000), the lack of effective monitoring or control, and the vulnerability of the Aldabra population to exploitation, there is now an established case for placing this species on Appendix I of CITES. Unlike mammals, many reptile populations are not capable of gross exploitation. Regardless of the large population of Aldabran tortoises presently extant, removal of large numbers will precipitate a population crash such as has occurred in the Galapagos.

Current Research

Between 1965-1980, intensive work on the species resulted in numerous papers on the ecology and behaviour of *Geochelone gigantea*. Since then, little work has been done on Aldabra and the research efforts have switched to Curieuse and captive individuals in collections. Future research in scientific conservation should focus on establishing a life table, investigating reproduction, particularly environmental sex determination and sperm storage, and preparing a soundly-based plan to integrate species conservation and local interests.

Tortoises of Tropical Asia: Regional Introduction

Edward O. Moll

The Indomalayan Realm comprises tropical and subtropical Asia, and lands south and southeast of the Himalayas. Included are Pakistan, India, Nepal, Bhutan, Bangladesh, Burma, Thailand, Laos, Cambodia, Vietnam, southern China, Malaysia, Indonesia, and the Philippines. This is chiefly a land of monsoon and tropical rain forests. Much of India is an exception, being much drier than the rest of the region, including the great Thar Desert in northwestern India, and the central and peninsular portions, which are dominated by thorn scrub, dry deciduous forest, and savanna. Another substantial area of dry deciduous forest and savanna habitat surrounds the Mekong River in Indochina.

Six tortoises of three genera are definitely known from this region. Four species are forest dwellers, *Manouria emys*, *M. impressa*, *Indotestudo elongata*, and *I. forstenii*. Another, *Geochelone elegans*, occupies a wide range of xeric habitats including thorn scrub, dry deciduous forest, savanna, and various man-made or altered situations. The habitat of *G. platynota* is unreported. Although the tortoise fauna of this region is not diverse, it is of some zoogeographic interest as *Manouria* appears to be the most primitive of the extant tortoise genera. *Indotestudo* shows affinities with *Testudo* and certain African species. These species also have some economic importance. They are eaten and used in various folk medicines and remedies throughout the region. The shells are utilized as pots, bowls, scoops, decorations, and even musical instruments. Four species (*G. elegans*, *I. elongata*, *M. emys*, and *M. impressa*) are regularly sold in the international pet trade.

There are few areas in the Indomalayan Realm where tortoises are presently common. Presumably their sparsity is due in part to longstanding exploitation and habitat loss. However, as there have been few status surveys on Oriental tortoises and no baseline data available for comparisons, such conclusions are largely speculative.

Today, exploitation has both local and international components. For the most part the utilization of tortoises as food is localized. Being slow and unaggressive, they are particularly vulnerable to human predation. But since they are seldom obtained in large numbers, it is not economical to ship them long distances for sale as food. Most are eaten by the collector or sold in local markets. The pet trade is different. Foreign buyers pay extravagant prices for tortoises, making interna-

tional trade profitable. The drug trade is also international. Demand for tortoises by Chinese apothecaries has led to the importation of Thai species (Shibata 1975) but the extent of this trade is unknown.

Habitat destruction must also be a key limiting factor, but again, without baseline data, it is impossible to ascertain the magnitude of its effect. Nevertheless, it is known that the available habitat for forest-dwelling species has long been declining in tropical Asia. The advent of colonialism which encouraged growing more crops for trade, modern medicine which reduced mortality and created a rapidly growing human population, and increasing demands for lumber have all promoted deforestation.

India was once largely covered with forests. Present estimates of forested area range from 8 to 19.5 percent of the country depending on the definition of forest used (Vohra 1988; MacKinnon and MacKinnon 1974). Malaysia's forests have declined by over half since the turn of the century (Nor 1988). Thailand is losing its forests at a rate of 3 to 6 percent per year (Brown and Lugo 1988). With habitat decreasing rapidly, we must assume that, at the very least, tortoises are declining at a similar rate.

To date, the most important conservation actions taken involve laws and treaties limiting trade in tortoises. All Oriental region species are classified as threatened (i.e., Appendix II of CITES). This means a permit is required to trade these tortoises internationally. Within the region, India and Thailand have passed similar laws (Indian Wildlife Protection Act of 1972 and Wild Animal Reservation and Protection Act of 1960) which provide national protection to their tortoises. I am aware of no other conservation measures for tortoises in tropical Asia.

While protective laws and treaties, if enforced, help to slow the trade of tortoises, they do not protect the animals from habitat destruction. The most important long-term conservation action may be to establish refuges which protect both habitat and animals. The refuge or sanctuary concept can assure the survival of a species without eliminating exploitation and trade. Refuges for tortoises serve somewhat the same purpose as banks do for money, protecting the principal, or in this case a breeding nucleus of a species. Like an investment, the principal generates interest and grows. In this situation "interest" is new tortoises providing recruitment and population

growth. Subsequently, population pressure forces individuals outside the refuge where they can be harvested. As long as the "principal" = breeding nucleus is protected, "interest" continues to accrue and may be utilized by the people.

Before other actions can be taken, additional status surveys of the tortoises throughout the region are needed. Objectives of these surveys should include:

1. Obtaining baseline data on the size of populations.
2. Determining what limiting factors are most significant in each part of the range.
3. Identifying potential sanctuary areas (i.e., areas of optimum habitat harboring viable populations).

In addition to numerous authors cited from the literature, I am indebted to the following for supplying unpublished information and other assistance. Dr. Charles Crumly graciously shared his extensive knowledge of the taxonomy of Asian

tortoises and provided an outline map used to plot distributions. Mr. Indraneil Das provided a report of his 1988 survey of tortoises in northeastern India. Dr. Jack Frazier contributed unpublished manuscripts and findings resulting from a nine-month status survey of Indian tortoises in 1986-87. Information was gleaned from these five manuscripts:

- a. *Have you seen the star of India?*
- b. *Report on the star tortoises in the Sakkarbagh Zoo, Junagarh.*
- c. *Report on chelonians of the Gir Wildlife Sanctuary.*
- d. *A biologist's visit to Rangoon.*
- e. *The land tortoise in Nepal: A review.*

Mr. Anson Wong provided information about the pet trade in Malaysia. Dr. John Iverson allowed me to consult his thorough compilation of turtle distributions in preparing the maps included herein.

The following accounts provide the most recent information on the habits and status of these six species.

Geochelone elegans Indian Star Tortoise

Edward O. Moll

Description and Taxonomy

This medium (35 cm shell length) species may be distinguished from other tortoises of the region by the combined carapacial pattern of lightradiating lines on a dark background and plastral pattern of dark radiating lines on a light background. Additional characters distinguishing *G. elegans* from certain other tortoises of the region include a divided supracaudal scute, absence of a cervical scute, an entoplastron not crossed by the humeropectoral seam, and a relatively long trachea. The head, limbs, and tail are yellow to tan.

G. platynota of Burma is the closest relative of *G. elegans*. Both have a star pattern on the carapace, but *elegans* differs by having more rays on the costals (eight or more). The Indian star tortoise also differs by lacking distinct shields on top of the head and by having radiating lines on the plastral scutes (juveniles have dark blotches).

Distribution and Status

Indian star tortoises are a CITES Appendix II species. They range from Pakistan across India to Sri Lanka. Jayakar and Spurway (1966) cite a secondhand record for Bangladesh.

Pakistan

Records from here are few, the most recent being three specimens obtained by Anderson and Minton (1963) from the Thar Pakar Desert in the extreme southeastern Sind.

India

Geochelone elegans occurs throughout peninsular India reaching its known northern limits in Rajasthan to the west and Orissa to the east. Jack Frazier (pers. comm.) concluded that the star tortoise is the most common and widespread of the Indian testudinids. He found the largest populations in the Arvali Hills of Rajasthan, the Chittoor District of Andhra Pradesh, and the Little Rann of Kutch in Gujarat. Their current success seems due chiefly to their ability to thrive in habitats altered by man. Although eaten locally, the species is unimportant in the commercial trade. *G. elegans* is listed on Schedule IV of the Indian Wildlife (Protection) Act of 1972.

Sri Lanka

Deraniyagala (1939) reported that star tortoises, though widespread in Sri Lanka and particularly abundant in Udappuva and the island of Karaduva, were absent on the west coast from

Negombo to Weligama. Dattatri and Vijaya (1983) and Dattatri (1984) found that the tortoise was common in Yala and Wilpattu National Parks and could be "obtained in sackfuls on the western coast between Negombo and Matare." A belief that the tortoise is poisonous gives the species some protection, but large numbers are now being sold to tourists and exported.

Habitat and Ecology

Star tortoises are highly generalized in habitat preference. Deraniyagala (1939) reported that they inhabit sand dunes, brush wood, scrub forests, and park jungle in Sri Lanka. In India, they are chiefly found in human altered habitats including waste areas, deserts, scrub lands, and plantations. In Gujarat, Frazier (1987c unpubl.) found the tortoise living in fence rows of *Euphorbia* surrounding cultivated fields in the Kutch and in teak forests at the Gir Wildlife Sanctuary. Hutton (1837 in Smith 1931) reported the habitat as high grassy jungles skirting the base of the hills in Udaipur. In 1982 found two in a grove of planted *Eucalyptus* trees near Madras.

Females are larger than males, and attain maturity in about 10 years (Frazier 1987). Frazier (1987b unpubl.) measured 23 adults in the Sakkarbagh Zoo, Junagarh. Carapace lengths of females (n=14) ranged from 26.8 to 32.2 mm (mean 28.9) and of males (n=9) from 16.5 to 25.7 mm (mean 22.7).

Hutton (1837) has one of the most complete accounts of the tortoise's habits, which is partially reprinted in Smith (1931). In brief, tortoises are most active during the monsoon rains when they forage and copulate throughout the day. Later in the hot season, they only venture out in early morning and late afternoon and hide under bushes or tufts of grass throughout the rest of the day. Eggs vary from 38-51 x 30-39 mm in length and width and weigh 22 to 38 g (Smith 1931; Deraniyagala 1939; Jayakar and Spurway 1966). Deraniyagala (1939) reported that clutches comprised three to six eggs and that two or three clutches were laid per year. Whelan and Coakley (1982) recorded a captive female of unknown origin laying nine clutches over 40 months, averaging six eggs per clutch (range 5-10). Four clutches were the maximum laid in any 12-month period.

Data on the nesting season vary and come chiefly from captives. Nesting has been recorded in Gujarat during October and November (Frazier 1987), in Bombay on February 24 (Kehimkar 1981), in Sri Lanka during June and October (Dera-

niyagala 1939), and in Orissa during January, March, April, October, and December (Biswas and Acharjyo 1984; Jayakar and Spurway 1966). Reported incubation periods include 111, 113, and 127 days (Whelan and Coakley 1982) and 47 to 147 days (Jayakar and Spurway 1966).

Star tortoises are chiefly herbivorous but will occasionally take animal food. Deraniyagala (1939) reported tortoises feeding on young snails. Jayakar and Spurway (1966) observed captives nibbling at cuttlefish "bone" and goat bones.

Threats to Survival

Star tortoises are eaten by tribal peoples throughout their range, including the Jogi in western Rajasthan, the Vagris in Saurashtra, and the Irula in Tamil Nadu (Frazier 1987). Prior to the passage of the Indian Wildlife (Protection) Act of 1972, star tortoises were heavily exploited for both domestic and interna-

tional pet trade. Sri Lanka still supplies this trade. The CITES Parties recorded 62 specimens in international trade in 1978 and 92 specimens were imported by Switzerland from 1975 to 1979 (Honneger 1980).

Due to a generalized habitat preference, *G. elegans* has been less affected by habitat loss than other tortoises. Still, some habitats such as cultivated fields and extreme deserts are unsuitable even for these hardy tortoises.

Conservation Action

Present laws adequately control exploitation in India if properly enforced. Effects of habitat loss can be reduced by establishing sanctuaries in areas supporting viable populations. The tortoise trade in Sri Lanka and its effects on present populations require evaluation and monitoring. The status and distribution require study in Pakistan and Bangladesh.

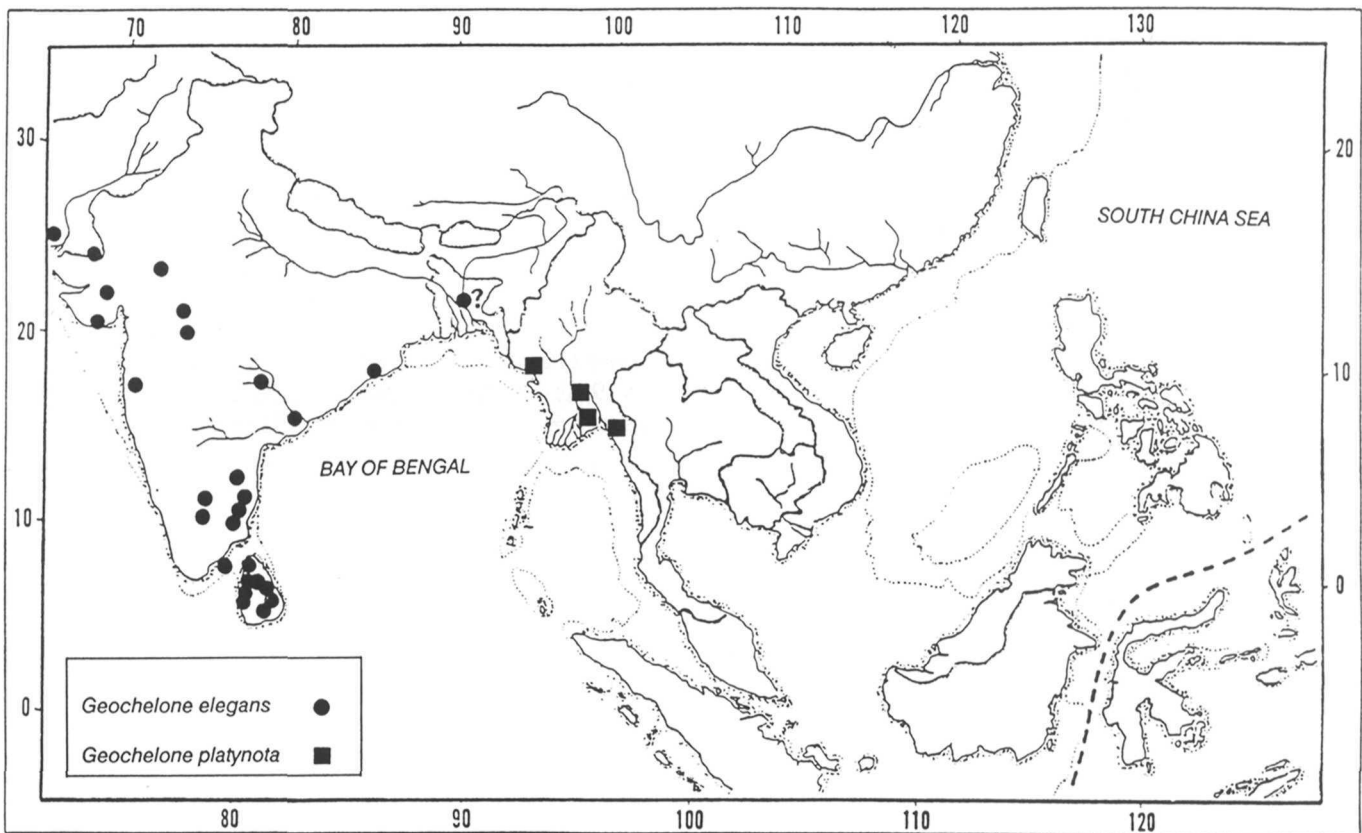


Figure 31. Distribution of *Geochelone elegans* and *Geochelone platynota*.

Geochelone platynota

Burmese Star Tortoise

Edward O. Moll

Description and Taxonomy

A poorly-known, medium-sized (28 cm shell length) tortoise endemic to Burma. With its close relative, the Indian star tortoise, *G. platynota* shares a star pattern on the carapace, an undivided supracaudal scute, and the absence of a cervical scute. The Burmese star tortoise differs from its relative by having distinct frontal and prefrontal shields on the head, a flatter shell, fewer rays on the costals (seven or less), and either no plastral pattern or a pattern of dark blotches (like *G. elegans* juveniles) rather than rays. Some authors have used the lack of distinct humps on the vertebrals and costals to separate *platynota* from *elegans* but this character is highly variable.

Anderson (1878-9) also reported variation in coloration. The carapace may be dark with yellow radiating lines or of yellow ground colour with brown radiating lines. The plastron is yellowish, usually with some brown blotches. The head and limbs are dull yellow-brown. Claws and scales on the limbs are bright yellow.

Status and Distribution

The Burmese star tortoise is generally distributed over upper Burma occurring as far south as Moulmein (Anderson 1878-9; Smith 1931). Although there is no current information on the status, Blyth (1863 in Gunther, 1864) reported that the species was difficult to obtain alive because the Burmese were so fond of eating them. Theobald (1868) mentioned that large numbers

of the tortoise were taken during the hot season when the habitat was burned and at other times they were hunted with dogs.

The Burmese star tortoise is listed as Appendix II on CITES, as "Insufficiently Known" in the IUCN Red Data Book (Groombridge 1982) and as APR 2 in the Tortoise and Freshwater Turtle Group Action Plan (1989).

Habitat and Ecology

Anderson (1878-9) reported the species is found in the hilly region about Akyab, Burma. Theobald (1868) indicated that the *G. platynota* and *Indotestudo elongata* were obtained by burning "grass jungles and forest." It was not clear if each species occurred in both habitats or one in grass and the other in forest. Anderson (1878-9) observed that nesting occurs in February and the eggs measure ca. 55 x 38 mm.

Threats to Survival

Based on the aforementioned 19th century accounts, the species is probably heavily exploited for food.

Conservation

A status survey is needed since there is no recent information on this species, and its conservation requirements are completely unknown.

Indotestudo elongata

Elongated Tortoise

Edward O. Moll

Description and Taxonomy

The elongated tortoise is a medium-sized (32 cm shell length, 3.5 kg) woodland species of tropical Asia. Males exceed females in size (Anderson 1878-9). *I. elongata* is distinguished by a long, narrow central scute (occasionally absent), an undivided supracaudal scute, an interpectoral seam as long or longer than the interhumeral, a humeropectoral seam which crosses the entoplastron, and a short trachea. The head is light, coloured cream, yellow, or yellowish green. Limbs are dark brown, studded with enlarged yellow to yellow brown scales. The carapace is typically yellow to light brown with central, dark blotches on most scutes. The plastron is yellowish, either plain or patterned with central and/or scattered, dark blotches.

The elongated tortoise and its close relative the Travancore tortoise are the only extant species in the genus *Indotestudo*. Their short tracheas suggests a closer relationship to *Testudo* and African tortoises than to those inhabiting tropical Asia (Crumly 1982).

Status and Distribution

I. elongata is the most widespread, and probably the most common of the Indo-Malayan tortoises. It ranges through Nepal, India (Uttar Pradesh, Bihar, West Bengal and Meghalaya), Burma, Thailand, Peninsular Malaysia, Laos, Cambodia, Vietnam, and southern China. The status is listed as "Insufficiently Known" in the Red Data Book (Groombridge 1982), Appendix II in CITES, and APR 1 by the IUCN Tortoise and Freshwater Turtle Specialist Group Action Plan (Stubbs 1989). The known status in specific countries is summarized below:

India

Smith (1931) reported the elongated tortoise as rare in the northern part of its range. Biswas et. al. (1978) noted that the species was becoming rare due to the reduction in the sal forest. Anderson (1878-9) first recorded the species in the vicinity of Chaibassa in Bihar, but *I. elongata* may never have been common in the region. Annandale (1913) was able to obtain only one specimen from the area in several years of trying. In March 1983, I spent two days in a sal forest approximately 115

km southwest of Chaibassa interviewing inhabitants about this species. They reported that the tortoise was rare but was eaten whenever found. A shell was obtained from each of two villages at 1,500 to 1,600 feet altitude (EOM 2711 and 2712 which are in the Bombay Natural History Society collection). Other recent records come from Uttar Pradesh (Ross and Crumly 1982) and Orissa (Biswas et al. 1978).

Old records of the tortoise include West Bengal circa 1916 (Zoological Survey of India 17992, 18016, 18125) and the Garo Hills of Meghalaya (Baylis and Daubny 1922). However, a survey of northeastern India (Das 1988) found no definite evidence of the species. The elongated tortoise is listed on Schedule IV of the Indian Wildlife (Protection) Act. Therefore, a permit must be obtained to collect them.

Nepal

Smith (1931) recorded *I. elongata* from Nepal based on a drawing made by Hodgson. Although Swan and Leviton (1962) questioned Smith's identification, Frazier (1987e unpubl.) has examined the drawing and concurs with Smith. A 1985 collection of a portion of an *elongata* shell by J. C. Mitchell (United States National Museum 267020) at Sauraha, Chitwan Narayani District, Nepal confirms its continued existence in Nepal. In fact Mitchell and Zug (in press) report that they are "apparently common in the sal forest of Nepal."

Bangladesh

The species is known from the Chittagong Hill Tracts (Biswas et. al. 1978) where it is reportedly "not rare" in forested areas (Khan 1982).

Burma

Most records were collected in the 19th and early 20th century. Dr. Jack Frazier visited Rangoon (1987d unpubl.) collecting information on chelonians. He found four *elongata* in the Rangoon Zoo and stated that it is "the most common" tortoise in Burma.

Thailand

Wirot (1979) stated that this is the most common tortoise in Thailand occurring in every part of the country except for Bangkok. It is listed as threatened in the Wild Animal Reservation and Protection Act (1960).

Malaysia

In a 1987 survey of animal dealers in northwestern Malaysia, two dealers of five visited had *I. elongata*. One of the largest exporters in the country reported that this is the most common tortoise collected and that he receives 25 to 30 per month.

Indochina

Bourret (1941) indicated that the tortoise was common throughout the region. There are no recent status reports for Cambodia, Laos, or Vietnam.

China

Fang (1930) purchased several living *elongata* from Nanning in Kwangsi. There are no recent status reports.

Habitat and Ecology

I. elongata inhabits forested areas in hilly to mountainous regions. In Nepal and India it is typically associated with sal forests (dominated by *Shorea robusta*). Wirot (1979) reported that it prefers cool, humid areas, but Swindells and Brown (1964) found that the tortoise can stand temperatures up to 48°C.

During the breeding season, the skin around the eyes and nostrils turns pink (Smith 1931; Pritchard 1979). One to five oblong eggs (50 x 40 mm) are laid per clutch (Bourret 1941). An egg from a captive kept by Paull (1985) measured 38 x 27 mm and hatched after 137 days at 29.4°C. Spencer (1987) reported that captives in the Minnesota Zoo lay eggs throughout the year with a peak from October through January. Incubation times of

nine eggs kept in the low 80s°F ranged from 96 to 146 days (mean 116). Hatchlings averaged 26 gm.

The species is chiefly herbivorous but eats some animal food. Wirot (1979) reported slugs in the diet.

Threats to Survival

Loss of habitat and exploitation for food, drugs, and the pet trade are the most obvious threats. Effects of deforestation have not been studied for this species. Consumption is chiefly local. The great demand for tortoises in the pet trade makes exportation far more profitable than sales for food. Thailand is the main exporting state and the FRG, Switzerland, U.K., and U.S.A. are the major importers (Honneger 1980). Some statistics are available. Honneger (1980) reported 2,774 specimens recorded in international trade by CITES parties in 1978; FRG imported 260 specimens from Thailand in 1979; Switzerland imported 150 from 1975 to 1979. Shibata (1975) reported that this species is exported from Thailand to Hong Kong for the manufacture of "gui ban," a popular Chinese medicine.

Conservation

Establishing reserves encompassing extensive tracts of upland forest would provide the best long-term protection. Although *I. elongata* is the most common tortoise in Thailand and Malaysia, export controls should be introduced before the species becomes depleted. Trade and population studies are needed to determine the extent of the measures needed.

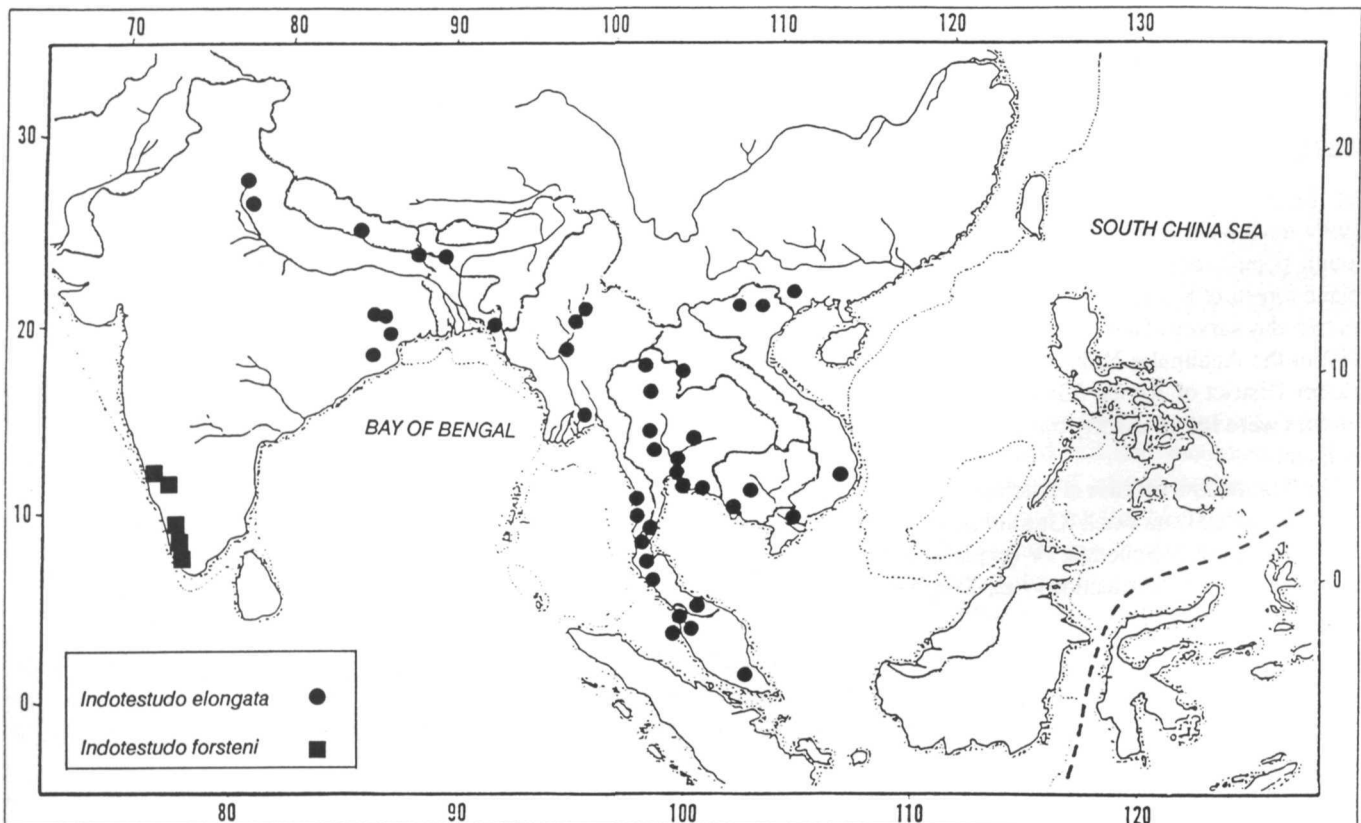


Figure 32. Distribution of *Indotestudo elongata* and *Indotestudo forsteni*.

Indotestudo forstenii

Travancore Tortoise

Edward O. Moll

Description and Taxonomy

This is a medium-sized tortoise (31 cm shell length) inhabiting southwestern India. The Travancore tortoise differs from its closest relative, the elongated tortoise, by usually lacking the cervical scute and by the length of the interhumeral seam exceeding the interpectoral seam. Characters separating it from other Oriental tortoises include a single supracaudal scute, the humeropectoral seam crossing the entoplastron, and a relatively short trachea. Coloration resembles *I. elongata* with a yellow head and a yellow-brown to brown carapace with dark central blotches. The yellowish plastron may be plain but is more commonly marked with dark blotches (at least in the areolar portion of some scutes). Large yellow scales deck the brown ground color of the limbs.

The species has long been known as *travancorica*. Hoogmoed and Crumly (1984) presented evidence that the population of *I. forstenii* of Sulawesi probably originated from Travancore tortoises introduced from India. The name *forstenii* (Schlegel and Muller 1844) has priority over *travancorica* (Boulenger 1907) and will now be used for both populations.

Status and Distribution

The Travancore tortoise occurs from the Western Ghats of Kerala northward into the Coorg District of Karnataka. Although populations are not dense, the tortoise is not rare in upland forests of Kerala which have not been heavily lumbered. In a two-day survey of terrestrial turtles made during November 1982 in the Anaimalai Hills (some 25 km east of Chalakudi, Trichur District of Kerala (Groombridge et al. 1983)), seven tortoises were found in forty man hours of searching (or 0.175 per hour).

The Travancore tortoise is listed as "Insufficiently Known" in the IUCN Red Data Book (Groombridge 1982), as Appendix II on CITES, and as Schedule IV (exploitation with permit) on the Indian Wildlife (Protection) Act. Das (1985) classified the species as "Vulnerable."

Habitat and Ecology

The tortoise occurs in mesic, semi-evergreen to evergreen forest of the Western Ghats up to at least 450 m altitude. Vijaya (1983) reported that *I. forstenii* basks in patches of sunlight penetrating the forest canopy. During times of inactivity, they tunnel into piles of fallen debris leaving characteristic tracks which are used by tribes to locate individuals. The tortoises are chiefly herbivorous, foraging in early morning and evening on fungi, bamboo shoots, fallen fruits, and flowers. Captives will take pieces of beef.

As in the elongate tortoise, the skin around the eyes and nostrils becomes pink during breeding season (Auffenberg 1964). Courtship behaviour has been described by Auffenberg (1964) and Vijaya (1983). Three phases are recognized, including: recognition of females by olfaction during which males use species-specific head movements; immobilization of the female by shell ramming; mounting and copulation (often accompanied by vocalizations).

The breeding season has been reported as November through January (Auffenberg 1964). However, a specimen collected October 12 by a hunter near Sholayar, Kerala contained two eggs (58 x 42 and 58 x 44 mm) when it was eaten on October 31. Another female kept in captivity at the Madras Snake Park laid an egg (54 x 40.5 mm, 58.5 gm) on March 4 (Vijaya 1983).

Threats to Survival

Habitat loss may be the most serious threat to the species. The tropical evergreen forests of Kerala have suffered large-scale destruction to establish plantations and hydroelectric projects (Saharia 1982). Human exploitation may also be important. The tortoise is an important protein source for tribes such as the Kadars of the Anaimalai Hills (Groombridge et al. 1983) and the Hill Pandaram of the Pandalam Hills (Morris 1982).

Conservation

Establishing extensive sanctuaries in the uncleared forests of Kerala will protect tortoise populations along with other unique forest species such as the vulnerable cane turtle, *Geoemyda silvatica*.

Manouria emys

Asian Brown Tortoise

Edward O. Moll

Description and Taxonomy

The Asian brown tortoise, attaining some 60 cm in shell length, is the largest tortoise inhabiting tropical Asia. One of two species in the primitive genus *Manouria*, it is distinguished from other Indo-Malayan tortoises (except its congener *M. impressa*) by having a short, wide cervical and divided supra-caudal scutes. It differs from *M. impressa* by its larger size, a domed (as opposed to flattened) carapace, slightly (versus strongly) serrate posterior marginals, and several (rather than one) prominently enlarged spurs (pointed scales) on the posterior thighs. *M. emys* tends to be uniformly dull brown to almost black, but centres of the carapacial scutes may be somewhat lighter than the periphery. Two subspecies are recognized, *Manouria e. emys* (Schlegel and Muller 1844), the brown tortoise, and *Manouria e. phayrei* (Blyth 1853), the Burmese brown tortoise (which includes *Testudo nutapundi* (Wirot 1979)). The brown tortoise is the smaller (to 50 cm shell length and 20 kg) and has widely separated pectoral scutes. Burmese brown tortoises attain 60 cm shell length and 37 kg (Wirot 1979), have the pectoral scutes in contact, and are darker, approaching black in older individuals.

Status and Distribution

Manouria emys ranges from Assam and Meghalaya, India eastward to Burma and western Thailand and southward through Peninsular Thailand and Malaysia to the Sunda Islands. Specimens have been reported from Vietnam (Tirant 1855) and China (Mell 1922; Siebenrock 1906), but Smith (1931) suggested that these may have been imported. *Manouria e. phayrei* occurs from Assam to Western Thailand. *M. e. emys* ranges from peninsular Thailand through Malaysia, Sumatra, and Borneo.

Brown tortoises have been heavily exploited and are presently rare throughout their range. They are listed on Appendix II of CITES and as "Insufficiently Known" in the IUCN Amphibia-Reptilia Red Data Book (Groombridge 1982).

India

Presently listed on Schedule IV of the Wildlife (Protection) Act of 1972. Species on this Schedule cannot be taken without a

permit. There appears to be no international trade in this species. A recent survey of tortoises by Das (1988) in northeastern India including sites in Arunachal Pradesh, Assam, Meghalaya, and West Bengal found no living specimens. Persons interviewed indicated that the tortoise, though very rare, still occurs in the Tirap Frontier Division of Arunachal Pradesh and the Cachar Hills, Goalpara, Gauhati, Mikir Hills, and Naogaon Districts of Assam. It appears most common at the Nongkhyllam Wildlife Sanctuary in the East Khasi Hills District of Meghalaya where forest guards may encounter a half dozen tortoises annually without searching for them.

Bangladesh

The tortoise is known from the Chittagong Hill Tracts (Khan 1982). It is eaten both by the tribal Chakmas and Bengali Hindus, who use dogs to locate them. Older tribals related that 30 years ago 1-3 could be caught per year by a single individual, but now they are seldom seen (Das 1988).

Burma

Reported in the 19th century from Tennasserim and Arakan (Blyth 1853 and Gunther 1864). Dr. Jack Frazier observed a large specimen in the Rangoon Zoo (Frazier 1987d unpubl.).

Thailand

The tortoise is eaten throughout Thailand and is becoming rare "except in the more uninhabited hilly and mountainous districts" (Taylor 1970). The species is listed as "threatened" by the Wild Animal Reservation and Protection Act and by Bain and Humphrey (1980).

Malaysia

Today, due to human exploitation and development, it is most common in sparsely-populated hill and mountainous areas (Moll 1976). A 1987 survey of animal dealers (n=5) and markets (n=2) conducted in northwestern Malaysia found no *M. emys*. However, one dealer interviewed claimed to handle 10-15 per month. Five individuals were seen in two turtle temples and twelve at the Zoo Negara.

Sunda Islands

No recent information. De Rooij (1915) summarized early collections in Sumatra, Java, and Borneo.

Habitat and Ecology

M. emys inhabits broadleaf evergreen forests of tropical Asia, particularly in uplands. They need moisture and frequently burrow into damp soil. Captives do not survive well in dry surroundings (Wirot 1979). Although chiefly herbivorous, some animal food is eaten (Bain and Humphrey 1980). The diet of *M. e. phayrei* includes aquatic plants (Wirot 1979).

McKeown et. al. (1982), described the following unusual reproductive behaviour. A female *M. e. phayrei* at the Honolulu Zoo built a mound nest of forest litter and defended the site for two or three days following oviposition. Clutch size averaged 39 eggs (maximum 51) with a mean maximum diameter and weight of 52.5 mm and 73.4 g respectively. Hatchlings averaged 63.1 mm shell length and weighed 49.9 g. A Malaysian *M. e. emys* (44 cm shell length) laid 30 eggs averaging 51 x 47 mm.

Threats to Survival

The chief threats appear to be exploitation and habitat destruction. Tortoises are sought for food and medicine (Bain and Humphrey 1980; Moll 1976; Das 1988) and for the pet trade. Large *M. emys* sell for over U.S. \$200 in the United States and

for over U.S. \$500 in Japan, making this a lucrative trade animal. Thailand and Malaysia are the main exporting countries, while the United States and the Federal Republic of Germany are the chief importers. The effects of deforestation on the tortoise are presumably considerable but have not been documented.

Conservation

Recommendations include:

1. Upgrading CITES listing to Appendix I.
2. Establishing reserves throughout the range to protect tortoises and habitat.
3. Legislating or listing as necessary to provide protection in countries where it is native.

Current Research

Obst (1983) reviewed knowledge concerning the species. Bour (1980), Crumly (1984), and Hoogmoed and Crumly (1984) revised the taxonomy.

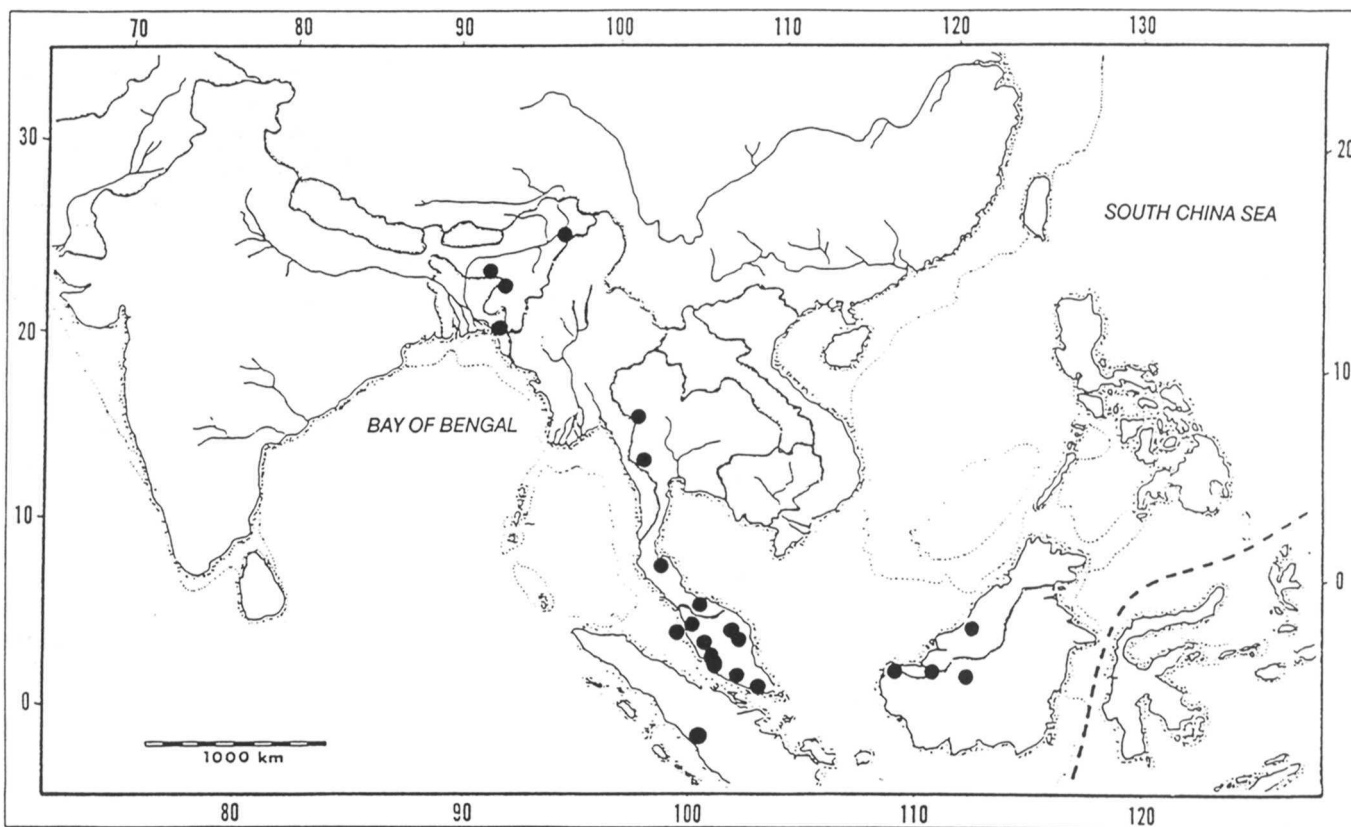


Figure 33. Distribution of *Manouria emys*.

Manouria impressa

Impressed Tortoise

Edward O. Moll

Description and Taxonomy

A medium-sized tortoise (up to 31 cm) distinguished by a dorsally- flattened carapace with a strongly serrate margin, a short, wide cervical scute, and a divided supracaudal scute. Carapacial scutes have brown to yellow-brown centres often encircled by bands of darker pigment and with yellow (or lighter) borders around the seams. A dark blotch is typically present at the anterior of each marginal. The plastron is brown to yellow-brown with dark pigmented seams or dark rays present in some. The head is yellow to yellow-brown, and the forelimbs are brown to black. The hindlimbs and tail are brown. The impressed tortoise is the nearest relative of *M. emys* and the only other extant member of this primitive genus.

Status and Distribution

The impressed tortoise ranges from eastern Burma (Karrenni Hills) and Thailand southward into Peninsular Malaysia and eastward to Vietnam. It is generally regarded as rare throughout its range (Groombridge 1982; Pritchard 1979). It is currently listed on Appendix II of CITES, as "Insufficiently Known" in the IUCN Red Data Book (Groombridge 1982) and as APR I in the IUCN/SSC Tortoise and Freshwater Turtle Group Action Plan (1989). The only recent information on status comes from Thailand and Malaysia.

Thailand

Wirot (1979) reported *M. impressa* to be rare, occurring at high elevations (700 to 2,000 feet) only in the northwestern portion of the country. Thailand exports this species to China for the drug trade (Shibata 1975) and to the West for the pet trade (Honneger 1980). It is listed as threatened on the Thai Wild Animal Reservation and Protection Act.

Malaysia

The rarest of the three tortoises native to Peninsular Malaysia, *M. impressa* is restricted to highlands (e.g., Gunung Jerai, Frazier's Hill, Maxwell's Hill) in the northern half of the country. It is eaten locally and exported to Europe and the United States for the pet trade.

Habitat and Behaviour

Due to its rarity, little is known about the biology of this species. It inhabits forested upland areas, where it forages chiefly on vegetation. Wirot (1979) reports grass and bamboo shoots in the diet. A female (30.8 cm carapace length and 3.3 kg) from Frazier's Hill, Malaysia laid a clutch of 20 eggs averaging 44 x 40 mm and 39 g in March.

Threats to Survival

The tortoise is threatened directly by exploitation for food, medicine, and the pet trade and indirectly by loss of habitat. As exploitation for food is generally on a non-commercial basis, there are no records of volume. In Malaysia, the Orang Asli (aborigines) are very fond of tortoise, and regularly seek them as food. Shibata (1975) listed *M. impressa* as one of five species being exported from Thailand to China for preparation of the drug "gui ban."

In regard to the pet trade, Honneger (1980) lists Thailand and Malaysia as the main exporters, and the U.S. and FRG as the main importers of the species. A major reptile dealer in Malaysia stated that he obtains around five individuals per month and that large specimens can sell for \$300 or more.

Encroachment on the forests by the region's growing population for living space, plantations and lumber is steadily reducing the habitat available for the impressed tortoise.

Conservation

As this tortoise inhabits inaccessible areas, its status is poorly known. Status surveys are needed before conservation action can be considered.

Current Research

Obst (1983) has reviewed current knowledge of the species. Bour (1980) and Crumly (1984) have revised the taxonomy.

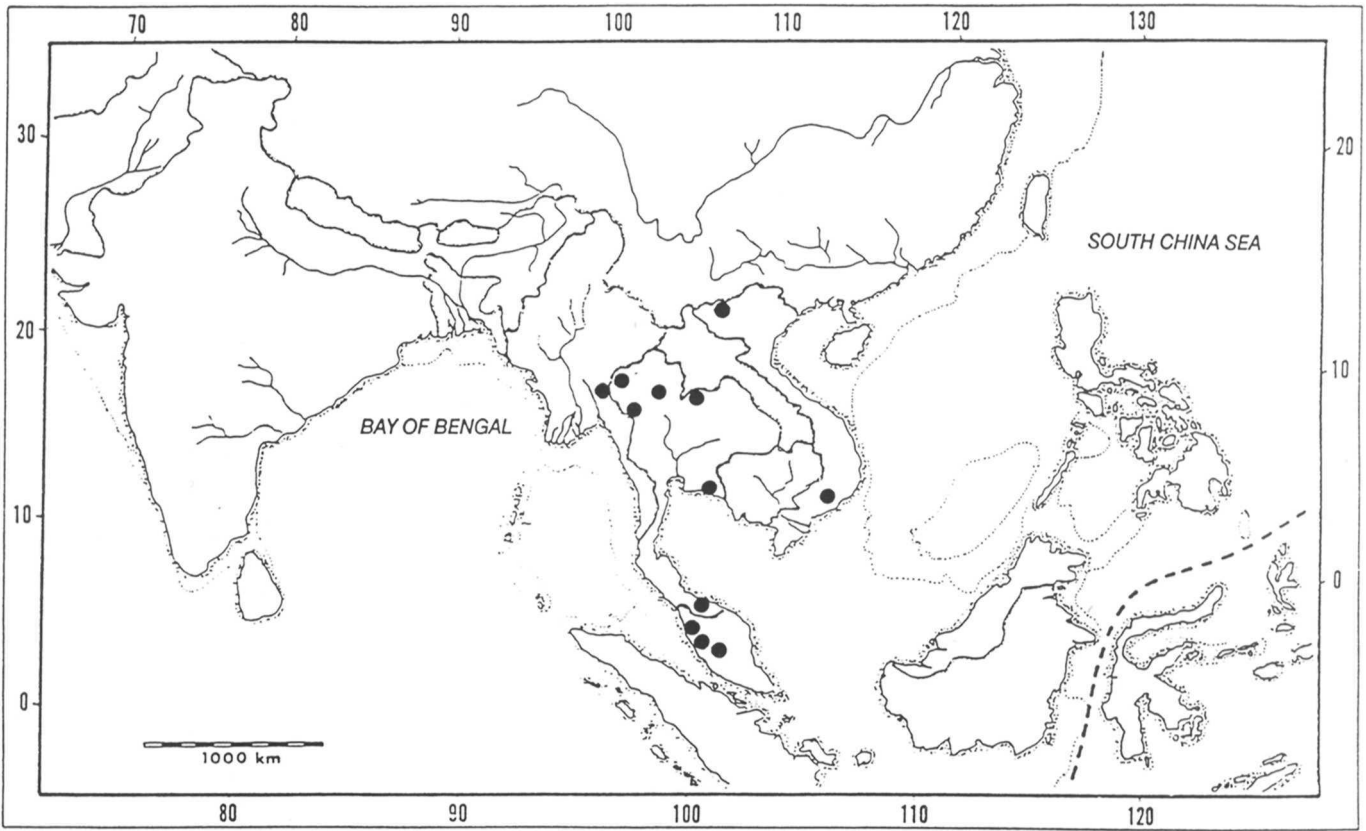


Figure 34. Distribution of *Manouria impressa*.

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Appendix 2. Classification of the Testudinidae

A classification of the Testudinidae primarily based on lower jaw structure and the length of the trachea. (From Swingland (in prep.), modified and adapted from Crumly 1984)

Family Testudinidae

Forty living species and 200 fossil forms (Auffenberg 1974).

Subfamily Gopherinae

Arose in Eocene (55m BP), northern hemisphere.

Tribe Manourinii

Once over Laurasia, now only found in southeast Asia.

Genus *Manouria* Gray 1852

Ten extinct species, two living species.

Manouria emys

Asian brown tortoise, southeast Asia

Manouria impressa

Impressed tortoise, southeast Asia

Tribe Gopherinii

Restricted to North America.

Genus *Gopherus* Rafinesque 1832

Fifteen extinct species, four living species.

Gopherus agassizi

Desert tortoise, Mexico, U.S.A.

Gopherus polyphemus

Gopher tortoise, U.S.A.

Gopherus berlandieri

Texas tortoise, Mexico, U.S.A.

Gopherus flavomarginatus

Bolson tortoise, Mexico

Subfamily Geocheloninae

Thirty three living species, largely restricted to the southern hemisphere.

Tribe Geochelonini

South America, Africa, Madagascar, India, and Burma.

Genus *Geochelone* Fitzinger 1835

Fifty extinct species, eleven living species¹.

Geochelone gigantea

[or *Aldabrachelys* Loveridge and Williams 1957 *elephantina* (Dumeril and Bibron 1835)]

Aldabran giant tortoise, Aldabra

Geochelone elephantopus

[or *Geochelone nigra*, (Quoy and Dumeril 1824)]

Galapagos giant tortoise, Galapagos

Geochelone radiata

Sokake, Radiated tortoise, Madagascar

Geochelone yniphora

Angonoka, Madagascar

Geochelone elegans

Indian starred tortoise, Indian Subcontinent

Geochelone pardalis

Leopard or Mountain tortoise, Africa

Geochelone denticulata

Forest tortoise, South America

Geochelone carbonaria

Red-footed tortoise, South America

Geochelone chilensis

Chaco tortoise, South America

Geochelone sulcata

Spurred tortoise, Africa

Geochelone platynota

Burmese starred tortoise, Burma

Tribe Testudinini

Africa, Madagascar, southern Europe, southwest Asia and India.

Genus *Acinixys* Siebenrock 1902

No known fossils, one living species in western coastal Madagascar.

Acinixys planicauda

Flat-shelled tortoise, Madagascar

Genus *Chersina* Gray 1831

One fossil species, one living species in southern Africa.

Chersina angulata

Bowsprit or Angulate tortoise, South Africa and Namibia

Genus *Homopus* Dumeril and Bibron 1835

No known fossils, five living species in southern Africa.

Homopus areolatus

Parrot-beaked tortoise, South Africa

*Homopus bergeri*²

(to be re-instated), Namibia

Homopus boulengeri

Boulenger's tortoise, South Africa

Homopus femoralis

Karoo tortoise, South Africa

Homopus signalus

Speckled tortoise, Southern Africa

Genus *Indotestudo* Lindholm 1929

One fossil species, two living species in southeastern Asia, India, and Indonesia.

Indotestudo elongata

Yellow tortoise, Asia

Indotestudo forsteni (including *Indotestudo travancorica*)

Travancore tortoise, Southwest India and Sulawesi

Genus *Malacochersus* Lindholm 1929

No known fossils, one living species in eastern Africa.

Malacochersus tornieri

Pancake tortoise, East Africa

Genus *Psammohates* Fitzinger 1835

No known fossils, three living species in southern Africa.

Psammobates geometricus

Geometric tortoise, South Africa

Psammobates oculifer

Serrated tortoise, Southern Africa

Psammobates tentorius

Tent tortoise, South Africa

Genus *Pyxis* Bell 1827

No known fossils, one living species in southwestern coastal Madagascar.

Pyxis arachnoides

Spider tortoise, Madagascar

Genus *Testudo* Linnaeus 1758

At least forty fossils, five living species, found over southern Europe, northern Africa and southwest Asia.

Testudo marginata

Marginated tortoise, Greece, Sardinia

Testudo graeca

Spur-thighed tortoise, Mediterranean basin

Testudo hermanni

Hermann's tortoise, Mediterranean basin

Testudo horsfieldi

Horsfield's tortoise, Asia

Testudo kleinmanni

Egyptian tortoise, southeastern Mediterranean basin

Genus *Kinixys* Bell 1827

No known fossils, four living species in sub-Saharan Africa.

Kinixys belliana

Bell's hinged tortoise, Africa

Kinixys erosa

Forest hinged tortoise, Central Africa

Kinixys homeana

Home's hinged tortoise, Central Africa

Kinixys natalensis

Natal hinged tortoise, Southern Africa

¹Crumly (1984) mentions only 8 species in *Geochelone*. This is a typographical error.

²Crumly (1984) counts only four living species in *Homopus*. *Homopus bergeri* (Lindholm 1906) was erroneously synonymized with *Homopus boulengeri* by Siebenrock 1909. A population was only very recently rediscovered (Greig pers. comm.).

Bibliography of Tortoise Literature

Kent R. Beaman, Russell L. Burke, and Pamela K. Harpel-Burke

Introduction

We assembled this bibliography with information from a variety of sources, relying most heavily on Zoological Record and a computer search of the BIOSIS and Dissertation Abstracts databases through December 1988. The bibliography itself is divided into six sections:

1. North America
2. South America
3. Galapagos
4. Africa, Mediterranean, and Indian Ocean
5. Asia
6. Fossil

We attempted to locate every technical and popular article dealing with tortoises in which new information or syntheses were presented. We are aware that we probably missed a number of important papers, and we hope that these will be brought to our attention for a future addendum. We did not duplicate the bibliographies or extensive literature reviews of previous authors.

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