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Chersina angulata (Schweigger 1812) – Angulate Tortoise, South African Bowsprit Tortoise

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Summary. – The angulate or bowsprit tortoise, *Chersina angulata* (Family Testudinidae), is endemic to southern Africa and is the type species of the monotypic genus. No subspecies are distinguished, but mtDNA markers indicate the presence of two distinct evolutionary lineages associated with the southern and western regions of South Africa, respectively. The species is medium-sized (carapace length to ca. 350 mm), sexually dimorphic with males larger than females, characterized by a large, protruding, undivided gular scute, and displays substantial color and size variation. The species is active throughout the year but temperature and rainfall modify its activity patterns. Males appear to establish dominance hierarchies in spring when they use their large gular scute to overturn rival conspecific males. Females produce single-egg clutches from late summer to late spring and can lay up to six clutches annually. Egg retention time varies substantially and correlates with temperature and rainfall. The diet includes a wide range of angiosperms as well as mosses, mushrooms, insects, snails, and animal feces. They are selective feeders and their diet changes with season and site. *Chersina angulata* is not threatened and is adequately protected.

Distribution. – Namibia, South Africa. The range extends along the southern and western regions of South Africa into southwestern Namibia.

Synonymy. – *Testudo angulata* Schweigger 1812, *Testudo* (*Chersina*) *angulata, Chersina angulata*, *Goniochersus angulata, Neotestudo angulata, Chersine angulata*, *Testudo bellii* Gray 1828, *Chersina angulata pallida* Gray 1831.

Subspecies. – No subspecies currently recognized.

Status. – IUCN 2008 Red List: Not Listed (= Least Concern, LR/lc) (assessed 1996, needs updating); CITES: Appendix II (as Testudinidae spp.); South African Red Data Book: Not Listed.

Taxonomy. — Constant Duméril named the angulate or bowsprit tortoise *Testudo angulata* but Schweigger (1812) was the first to officially describe the species (Bour 2008). Subsequently, Gray (1828) named the angulate tortoise *Testudo bellii*, but synonymized it with *Testudo* (*Chersina*) *angulata* after he saw the specimens labeled by Duméril in the Paris Museum (Bour 2008). Gray (1831) attributed authorship of *Chersina* to Merrem (1820), but used the name in error

Figure 1. Subadult female *Chersina angulata* from the West Coast National Park, South Africa. Photo by M.D. Hofmeyr.

Figure 2. Young adult male *Chersina angulata* from Clanwilliam, South Africa, with red plastron. Photos by M.D. Hofmeyr.

because Merrem used the name *Chersine* as a subgeneric substitute name for *Testudo* (Bour 2008). Lindholm (1929) and Hewitt (1931), respectively, used the names *Goniochersus* and *Neotestudo* for *Testudo angulata* but Loveridge and Williams (1957) reinstated the name *Chersina angulata* (Bour 2008). Bour and Ohler (2008) recently argued for the retention of *Chersina* Gray 1831 (distinct from *Chersine* Merrem 1820) to maintain nomenclatural stability.

Chersina is a monotypic genus and a sister taxon of *Homopus* (Le et al. 2006; M.D. Hofmeyr and S.R. Daniels, unpubl. data). *Chersina angulata* has no described subspecies, but mitochondrial DNA markers indicate the presence of two genetically distinct clades associated with the western and southern regions of South Africa, respectively. The western clade is comprised of two subclades (northwestern and southwestern), which overlap in the Citrusdal region (Daniels et al. 2007). Genetic material from *C. angulata* in Namibia fits with the northwestern clade (S.R. Daniels and M.D. Hofmeyr, unpubl. data). Further research is required to determine whether the clades of *C. angulata* may represent independent taxonomic units.

In the past, fossil material from the Miocene (Arrisdrift) and early Pliocene (Langebaanweg) has been assigned to *Chersina* (Meylan and Auffenberg 1986), but Lapparent de Broin (2003) has shown that the Miocene material belongs to *Mesochersus* and not to *Chersina*. The validity of assigning the Langebaanweg material to *Chersina* is currently being investigated.

Description. — The shell of adult angulate tortoises is elongated and domed with no hinges. The carapace typically has five vertebrals, four paired costals, 11 paired marginals, a single supracaudal and a single nuchal scute. The plastron consists of a large, protruding, undivided gular scute, and paired humerals, pectorals, abdominals, femorals and anals. Each side has one or two axillary scutes and one inguinal scute. The front and hind limbs have five and four claws, respectively. There are no buttock tubercles, nor a terminal spine on the tail.

Figure 3. Old adult female *Chersina angulata*, from Dassen Island, South Africa, with faded color pattern and burn scars. Photo by M.D. Hofmeyr.

Figure 4. Hatchling *Chersina angulata*, from the West Coast National Park, South Africa. Photo by M.D. Hofmeyr.

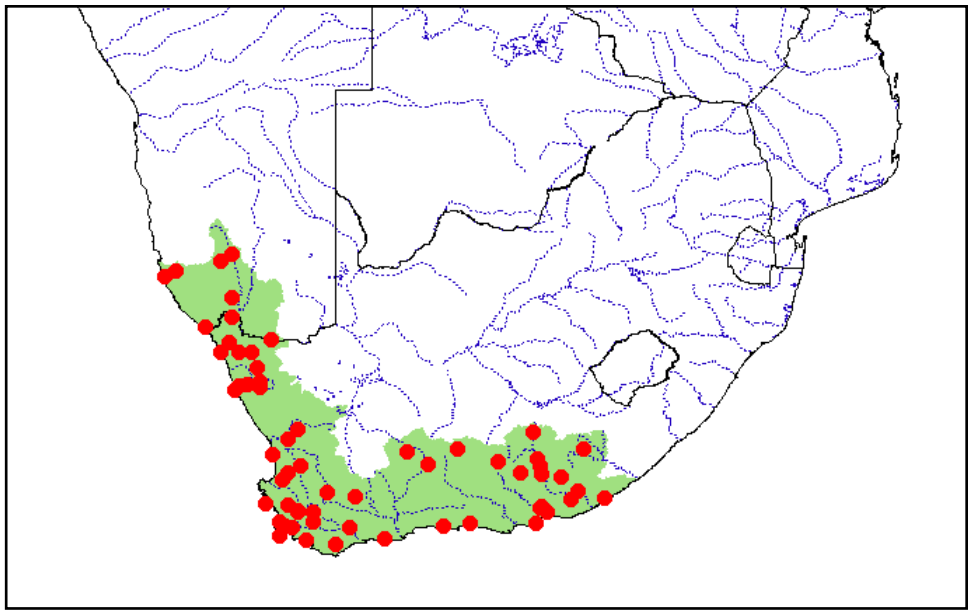

Figure 5. Distribution of *Chersina angulata* in southern Africa (Namibia and South Africa). Red points = museum and literature occurrence records based on Iverson (1992) plus more recent and author's data; green shading = projected distribution based on GIS-defined hydrologic unit compartments (HUCs) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs (Buhlmann et al., in press), and adjusted based on author's data.

Angulate tortoises are sexually dimorphic with males being larger than females. In the southwestern Cape, mean straight carapace length (CL) for males and females, respectively, is 187 and 168 mm, and mean body mass is 916 and 813 g (M.D. Hofmeyr and B.T. Henen, unpubl. data). Hatchlings weigh 12–18 g and measure 30–39 mm in CL (Branch 1989). Tortoises on Dassen Island off the coast of South Africa are significantly larger than on the mainland (Lesia 2001). One exceptionally large male on Dassen Island had a CL of 351 mm and a body mass of 3939 g (M.D. Hofmeyr and B.T. Henen, unpubl. data). Males and females differ in shape with males being flatter, longer, and often wider than females. Compared to females, males have a longer gular scute and tail, a more bulging supracaudal scute, and a plastral concavity.

Color patterns can vary substantially over the species' range and within a region. The marginal scutes characteristically have a light yellow color with a dark, broad-based triangle. The light-colored areolae of the vertebral and costal scutes usually have dark centers, and the growth rings around the areolae are dark-brown to black. The ratio of dark to light color on the carapace varies geographically, and in some regions the shell appears nearly black. Dark colors often fade with age, and older individuals can have a nearly uniform straw color. The plastron has a dark, irregular central pattern on a straw-colored background. In some regions, the plastral background color acquires an orange to red tint, which explains the Afrikaans vernacular name "rooipens" (red-bellied) tortoise.

Distribution. — *Chersina angulata* is endemic to southern Africa; its distribution falls mainly within South Africa (ca. 90%) and extends marginally into southwestern Namibia. In South Africa, the species occurs from East London in the Eastern Cape Province, westwards through most of the Western Cape Province, into the western region of the Northern Cape Province. Its range extends across the Orange River into Namibia, where it is found in the Sperrgebiet and surroundings, possibly as far north as Lüderitz and Aus (Griffen 2003). The species occurs on several offshore islands, and reaches high densities on Dassen and Robben islands off the southwestern coast of South Africa.

Habitat and Ecology. — Angulate tortoises occur from the coastal plains, all along the escarpment, to altitudes of approximately 1200 m, but do not penetrate the interior of southern Africa. They live in regions with low annual rainfall (< 100 to 600 mm) although annual rainfall along the south coast can exceed 1000 mm in some areas. The west receives winter rains whereas rainfall in the south is non-seasonal. Temperatures are mild to very hot in summer, with no or little frost in winter, except at high altitudes beyond the escarpment. The species' range covers several biomes such as Fynbos, Albany Thicket, Succulent Karoo, and Nama Karoo.

Fynbos consists of an open to dense, fire-prone shrubland, covered with ericoid and asteraceous shrubs, restios and grasses (Rebelo et al. 2006). Albany Thicket has dense, semi-succulent and thorny vegetation, which includes large and small shrubs, geophytes, annuals and grasses (Hoare et al. 2006). Tortoises are excluded from dense thicket, but high population densities can occur in partially cleared areas (Branch 1989). The Succulent and Nama Karoo biomes have dwarf, open shrublands, with annuals, grasses and geophytes (Mucina et al. 2006a, b). *Chersina angulata* seems to prefer a sandy substratum, where the tortoises half-bury themselves into the sand when taking refuge under vegetation. They

nevertheless also occur in rocky areas, where they hide under large boulders or among rocks.

Angulate tortoises can reach high densities in some regions (30–35 individuals/ha) and sex ratios often approach 1:1 (Branch 1984; Van Heezik et al. 1994). Population structure is skewed towards large, adult individuals (Branch 1984; Van Heezik et al. 1994), probably because young individuals suffer high mortality. Several mammalian (e.g., viverrids, jackals, mongooses, and baboons) and avian (e.g., ravens, crows, kelp gulls, black eagles, and secretary birds) species predate young angulate tortoises (Branch 1989; Boycott and Bourquin 2000). Adult tortoises have few enemies but wild fires can kill large numbers of tortoises (Baard et al. 2001).

Males and females reach sexual maturity at approximately 10–12 yrs and may live for more than 30 yrs (Branch 1989). Female angulate tortoises produce one egg at a time and can produce up to six clutches per year under favorable conditions (Branch 1989; Hofmeyr 2004). Females in the southwestern Cape are gravid through most of the year and nesting takes place from late summer to late spring (Hofmeyr 2004). Ambient temperature and rainfall influence egg retention time, which varies between 23 and 212 days (Hofmeyr 2004). Rainfall, but not temperature, stimulates oviposition, possibly, because the wet ground facilitates nesting (Hofmeyr 2004). Egg size and mass (n = 104) range from 38.7 x 27.6 mm (17.6 g) to 45.5 x 37.5 mm (38.6 g) (M.D. Hofmeyr, unpubl. data). Incubation time can vary between 94 and 198 days (Branch 1989), and eggs hatch in early autumn (March to April) in the southwestern Cape (pers. obs.).

Chersina angulata has a diverse diet and consumes a wide range of angiosperms, as well as mosses, mushrooms, insects, snail shells, and animal feces (Joshua 2008). Herbs and grasses are the most important growth forms in the diet in the southwestern (Joshua 2008) and southeastern (Branch 1989) regions of South Africa. The tortoises are food generalists but select dietary items out of proportion to availability, in both pristine (e.g., West Coast National Park) and disturbed (e.g., Dassen Island) habitats (Joshua 2008). The depauperate vegetation of Dassen Island and shortage of food plants during the dry season may explain why rabbit feces contributed nearly 30% to angulate tortoise diet in autumn 1999 and summer 2000. Rabbit feces may not only provide a source of nutrients but may also supplement the microflora that is required to digest cellulose in the gut (Joshua 2008). The Dassen Island tortoises also practice lithophagy, possibly because sand may provide important minerals that are deficient in food plants, or because the abrasive action of sand may help with the digestion of tough plants (Joshua 2008). In Dassen Island and the West Coast National Park, diet composition and principal food items of angulate tortoises change with season (Joshua 2008).

Chersina angulata is active throughout the year and its activity pattern shifts between unimodal and bimodal, depending on temperature (Ramsay et al. 2002). In winter-rainfall regions, activity is low during summer and autumn, but fog or rain dramatically increases activity (Ramsay et al. 2002). The tortoises have an unusual drinking pattern to make optimal use of small amounts of water in the dry season. When conditions become wet, a tortoise extends its hind limbs to raise its posterior shell, and pushes its head into the substratum. Water runs down the carapace to accumulate around the head, and the tortoise then sucks water up through its nose.

Both sexes spend long hours basking in spring, and 90% of the basking time is spent in the cover of sparse vegetation (Keswick et al. 2006). Heating rate exceeds cooling rate (Els et al. 1988), which would allow the tortoises to maintain optimal body temperatures for longer during cool conditions in winter and spring. In the southwestern Cape, feeding activity is high in winter and spring when rainfall increases food availability. Active behaviors such as feeding, courtship, and fighting occur within narrow, high temperature ranges (Ramsay et al. 2002). Male fighting activity increases in spring, probably to establish dominance hierarchies, and most courtship activities occur in spring and on cool summer days (Ramsay et al. 2002). Males use their long gular scute to overturn rival males, and the peanut-shape of some males apparently holds an advantage because males with wider posterior carapace widths win more fights (Mann et al. 2006). Males are more active than females during spring and summer, but not in winter (Ramsay et al. 2002; Keswick et al. 2006).

Angulate tortoises have small home ranges and home range size for males and females at Sardinia Downs in the Eastern Cape is similar (mean ± SE = 0.28 ± 0.06 ha; Els 1989). In the southwestern Cape, however, females have larger annual home ranges than males have, both on Dassen Island (median = 1.6 ha for females and 0.25 ha for males) and in the West Coast National Park (median = 1.0 ha for females and 0.11 ha for males; S.R. Ramsey and M.D. Hofmeyr, unpubl. data).

Population Status. — *Chersina angulata* is common over most of its range in South Africa. In Namibia, the species is considered Peripheral and receives special protection.

Threats to Survival. — There is no indication that this species is currently threatened. Angulate tortoises have been an important source of food since antiquity. Their remains at archaeological sites along the coastline indicate that these tortoises have been exploited from the Middle Stone Age to the Holocene (Klein and Cruz-Uribe 2000; Halkett et al. 2003). This practice continues today but is no longer widespread. *Chersina angulata* is commonly kept as pets, but trade is limited by strict regulations.

Urban and agricultural developments have affected significant proportions of the species' habitat, but *C. angulata* seems to be relatively tolerant of habitat degradation (Branch 1989). Large parts of its natural habitat are fire-prone and there are indications that angulate tortoises may survive fire by burrowing into the sand (Stuart and Meakin 1983), or taking refuge among rocks (Wright 1988).

Invasive alien plants in the Fynbos biome increase the frequency and intensity of fires (Van Wilgen and Richardson 1985), which may devastate tortoise populations. Intensive surveys showed that approximately 98,000 to 275,000 angulate tortoises were killed after a runaway wildfire destroyed

ca. 18,000 ha of coastal Fynbos habitat in January 2000 (Baard et al. 2001).

Conservation Measures Taken. — *Chersina angulata* is listed on CITES Appendix II, similar to most other tortoises, and as protected wildlife in both South Africa and Namibia. Permits are required for the collection, exportation or killing of tortoises. The species is not listed in either the South African Red Data Book or the IUCN Red List.

In South Africa, *C. angulata* occurs in eight National Parks: Addo Elephant, Agulhas, Bontebok, Karoo, Table Mountain, Tsitsikamma, West Coast, and Wilderness, and more than 10 major Nature Reserves: e.g., Anysberg, Baviaanskloof, Cederberg Wilderness Area, De Hoop, Great Fish River, Goegab, Hottentots Holland, Kogelberg, Riverlands, and Vrolijkheid, spread throughout the species' range.

In Namibia, the species occurs in the Ai-Ais/Hunsberg Reserve (now part of the Ai-Ais/Richtersveld Transfrontier Park), Namib-Naukluft NP, National Diamond Coast Recreation Area, and the Sperrgebiet NP (Griffen 2003).

Conservation Measures Proposed. — No conservation action is needed at the present time, but translocation of individuals among the defined mtDNA clades and subclades should be strongly discouraged.

Captive Husbandry. — There is no official captive breeding program for *C. angulata*, but the species is a popular pet in South Africa, and reproduces successfully in captivity. The tortoises should be kept in large, outdoor enclosures, with ample shelter and open space for basking. The diet should preferably include plants from the species' natural habitat, but the tortoises are quite partial to vegetables and salads from the kitchen. Little is known about disease of tortoises in South Africa, but there have been reports of mass mortalities due to an unknown respiratory ailment of angulate tortoises from the Eastern Cape (Branch 1989).

Current Research. — In order to clarify the taxonomic status of mtDNA lineages, more sampling is being done in regions where the different clades overlap. In both Dassen Island and the West Coast National Park, more than 1000 tortoises have been marked and measured for long-term studies. These populations should be monitored on a regular basis to gain an understanding of population dynamics in these conserved areas. Future research should focus on the ecology of populations in the arid northwest, which is particularly threatened by predicted climate change.

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