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Tortoises, Not Dodos, and the Tambalacoque Tree

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It has been suggested (Temple, 1977) that an obligatory mutualism existed between the extinct dodo (*Raphus cucullatus*) and the endangered "tambalacoque" tree [*Calvaria major* according to Owadally (1979), but actually a composite of two species (*Sideroxylon sessiliflorum* and *S. grandiflorum*) according to Friedmann (1981)]. Although some of the evidence on which that hypothesis was based is disputed (Owadally, 1979; Temple, 1979), the apparent near absence of natural germination and the thickened structure of the endocarp of the seeds suggest that the tambalacoques (*sensu lato*) are very specialized plants, requiring some mechanism of endocarp abrasion to facilitate germination. Temple (1977) suggested that the dodo's gizzard accomplished this, and that since that bird's final extirpation in 1681, there has been no natural germination.

One test of Temple's hypothesis would be an accurate aging of the remaining trees, especially since there is disagreement between Temple and Owadally as to the age of those trees. They suggest the trees are 300 and 75-100 years old, respectively, even though their information apparently came from the same source. Friedmann (1981) has recently aged one specimen at between 30 and 50 years, and if other trees are significantly less than 300 years of age, any dodo-tambalacoque mutualism would at best have been facultative. However, the aspect of the Temple-Owadally debate that is most surprising to me is the total neglect of an even more logical group of organisms in response to which the thickened tambalacoque endocarp may have evolved. These are the testudinid tortoises of the genus *Cylindraspis* (Bour, 1984, 1985; *Geochelone*, according to some authors).

The significant enhancement of germination of the Galapagos tomato (*Lycopersicon esculentum*; Rick and Bowman, 1961) and the prickly pear (*Opuntia* sp.) by passage through the digestive tracts of the Galapagos tortoise (*Geochelone elephantopus*), and Berlandier's tortoise (*Gopherus berlandieri*; Rose and Judd, 1982), respectively, have already been documented. In addition, seeds of many Aldabra Island plant species germinate readily after passing through the gut of the Aldabra tortoise [*Geochelone gigantea* (= *Dipsochelys elephantina* according to Bour, 1984); Hnatiuk, 1978] and germination may even be enhanced in some (Stoddart and Savy, 1983). Further, tortoises were undoubtedly abundant herbivorous inhabitants of Mauritius through the Pleistocene (Bour, 1979, 1985; Pritchard, 1979) and until their extirpation in the early 19th century (Auffenberg, 1974; Pritchard, 1979). Closely related species on Rodrigues Island (now extinct) were even observed eating "apples," "dates," and "seeds from trees" 300 years ago (review in Bour, 1981).

There is, however, considerable difference of opinion as to how many tortoise species lived on Mauritius into Recent times. At least one species apparently went extinct on Mauritius shortly before humans arrived, and another shortly after (Auffenberg, 1974; Pritchard, 1979). In all, at least seven Pleistocene-Recent tortoise species have been described from Mauritius (Auffenberg, 1974), but it is currently believed that these were variants (primarily sexual and ontogenetic) of only two (or possibly three) species (Auffenberg, 1974; Bour, 1979, 1984).

Ecologically it is very interesting that two (or more) herbivorous tortoise species could coexist on Mauritius, an island of only 1865 km². They must have had very different habits as Arnold (1979) suggested was the case for the two closely related tortoise species living on nearby Reunion Island. Based on morphology he speculated that one species (more saddle-backed) occupied more open habitats and browsed higher than the other (more dome-shelled) species. Similar differences probably also characterized the species on Mauritius. It is therefore just as logical to suggest a tortoise-tambalacoque seed coevolution as one involving the dodo. Experimentation with tambalacoque seed germination following mastication and passage through tortoise guts (for example, those from nearby Madagascar or the Aldabra islands in the Seychelles Archipelago) is clearly warranted. Enhancement of germination in such experiments would argue strongly in favor of the natural existence of a tortoise-tambalacoque mutualism prior to the former's disappearance. It would also provide the Mauritius Forest Service with a more natural alternative to the mechanical seed abrasion now used to induce germination (Temple, 1979).

Finally, it should be mentioned that monkeys were also introduced to Mauritius in the 16th century and they may also have figured in the decline of the Mauritius tambalacoques (Bour, pers. comm.). However, neither they nor dodos occurred on Rodrigues, yet another tree of the same genus (*Sideroxylon galeatum*) is apparently vanishing on that island (Bour, pers. comm; Friedmann, 1981). The historic presence of tortoises there argues against a mutualism involving dodos and in favor of one involving tortoises. The decline in other potential tortoise mutualists (especially the palms, as well as almost 300 other threatened plant species; Strahm, 1985) may well be linked to the disappearance of the tortoises as well as to direct human destruction. The near collapse of the natural ecology of the Mascarene Island due to human intervention makes it difficult to determine what (if any) organisms may have been involved mutualistically.

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Effect of Temperature on the Incubation Period and Hatchability of *Trionyx sinensis* Wiegmann Eggs

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Incubation times of the eggs of the soft-shell turtle *Trionyx sinensis* Wiegmann under natural conditions in Japan were reported by Mitsukuri (1895 and 1904) and Okada (1931). The average incubation period for

T. sinensis eggs were 60 days (Mitsukuri, 1904). Okada (1931) documented that the incubation period of *T. sinensis* in the Japanese provinces of Honshu, Skikoku and Kyoushu, varied from 50 to 60 days and 60 to 70 days when ground temperatures were approximately 30 and 22°C, respectively. *Trionyx sinensis*, a native species of Japan, Taiwan and China, is commercially cultured in Singapore. In the farms, the eggs are collected daily from the egg-laying sites and later transferred to sand beds which are sheltered from the sun and rain. The incubation period of the eggs under this semi-natural condition is approximately 60 days (Choo and Chou, 1983). It is generally accepted that temperature accelerates development in ectotherms and that morphogenesis can be normal over a range of several degrees Celsius despite the varying rate (Ewert, 1979). Thus the incubation times of the eggs of *Trionyx sinensis* at various constant temperatures were investigated with a view to shorten the relatively long incubation period under semi-natural conditions.

In the farm, the spawners' tanks were provided with egg-laying sites which were raised rectangular or square platforms containing sand to a depth varying between 15 and 25 cm. Newly-laid eggs were collected from these egg-laying sites and transported to the laboratory in sand trays. Egg viability was checked by candling. To eliminate brood effect, fertilised eggs within a brood were distributed equally among the treatment temperatures.

In the first experiment, no substrate was used so that the egg was clean and translucent during incubation, making it possible to examine the embryo by transmitted light. The fertilised eggs were set in 2 cm diameter hemispherical cups on a tray which was then placed in a polythene bag with a small dish of water so that the eggs were incubated in an atmosphere of humid air. The polythene bag was opened at least twice weekly to replenish the oxygen. Incubators and refrigerators were regulated to within 0.5°C of the following temperatures: 18, 25, 28, 31, 34 and 37°C. Some of the eggs were also incubated at a room temperature of $23 \pm 1^\circ\text{C}$. Dates of hatching were recorded. Eggs were inspected for embryonic development at the first sign of spoilage. The embryos were fixed and stained with borax carmine.

In a second experiment, we investigated incubation under semi-natural conditions. The set-up of this experiment was similar to the incubation bed used in the local farm (Chou and Choo, 1983). Sand was used as a substrate. The eggs were buried individually at a depth of 4 cm in the sand. This depth was shallower than the natural nest of approximately 10 cm (Breckenbridge, 1960; Vose, 1964; Ewert, 1979) to ensure easy emergence of the hatchlings from the sand. The trays of sand were provided with opaque roofing to prevent overheating by solar radiation and flooding by rain. We also tried using transparent plastic roofing to determine whether incubation time could be shortened with increased exposure to solar radiation. Temperature of the sand at the level of the eggs and air temperature under the different roofings were measured with mercury thermometers (accurate to 0.5°C). The sand was moistened daily. Hatching dates