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Notes on the courtship of the land tortoise *Geochelone travancorica* (Boulenger)¹

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(With two plates and a text-figure)

INTRODUCTION

Geochelone travancorica, a species of land tortoise endemic to south-western India, is very rarely encountered in European and American zoological gardens and museums. Therefore, I was particularly fortunate in obtaining a number of live specimens for studying certain features of both its behaviour and its anatomy. My sincere appreciation is extended to those individuals and institutions who have aided me in obtaining the specimens. In particular I wish to thank the Bombay Natural History Society and Mr. Sane of Sachetan, Bombay.

Though the herpetological literature is sprinkled with observations on the courtship of tortoises (see Loveridge & Williams 1957 for most recent discussion of many Old World species) only a few reports have dealt with the comparative aspects of this behaviour and most publications are based on casual observations of a few tortoises in captivity.

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As part of a broader study of the fossil and Recent land tortoises of the family Testudinidae I have had an opportunity to observe the combat and courtship behaviour of a number of species, and to record these activities on movie film for later comparative analyses. The present report is the first contribution resulting from these studies (Auffenberg MS.), and is based on the behaviour of nine adult males and nine adult females of *G. travancorica* (probably more living specimens of this species than have ever been accumulated in one place before), maintained for a period of up to one year at the time of this writing. All the specimens were taken in Kerala State, India. Some were collected by myself in January 1963, while others were sent to me after my return to the United States.

To date it has been possible to observe only courtship behaviour in this species. Though several sexually active adult males were confined in the same large enclosure for long periods of time no combat was observed.

THE COURTSHIP PATTERN

The courtship behaviour of all tortoises can usually be divided into three phases or steps. These are: (1) the behavioural pattern involved in sex and species recognition, (2) the technique whereby the female is 'immobilized' by the male, to allow (3) mounting and intromission. Each of these major steps in the courtship of *Geochelone travancorica* is briefly described below.

1. *Sex and species recognition.* The use of a sequential combination of specific visual and olfactory signals that together provide a means of sex and species recognition in two sympatric South American species of tortoises has been observed (Auffenberg MS.). Only the olfactory signal is found in *Geochelone travancorica*. Apparently there are no visual signals important in courtship. Thus, being based only on an olfactory signal the behavioural pattern involved in sex recognition is very simple. When a sexually active male approaches the posterior portion of the shell of a potential breeding partner the neck is extended and the head moved in a fashion identical to that used in olfactory investigation of food items.

Eglis (1962) has described the olfactory motor patterns of several genera and species of land tortoise, concluding that these patterns are characteristic of particular taxa. His observations suggested that the characteristic olfactory motor pattern in the genus *Geochelone* is one in which the head is moved in a vertical plane, though the precise

nature of the movement is interspecifically variable. However, the present writer has shown (in MS.) that not all species of *Geochelone* possess a vertical pattern, since in at least *G. carbonaria* and *G. denticulata* (not seen by Eglis) it is horizontal.

In *Geochelone travancorica* the olfactory motor pattern is essentially vertical. First the neck is extended in a single, continuous motion, bringing the head near the object to be investigated. The head is then moved through a short vertical arc, frequently followed by a small and rapid curlicue (Plate I, Fig. A). This olfactory behavioural pattern is very similar to that reported for other species of *Geochelone*, as well as the closely related genus *Testudo*.

2. *Immobilization Technique.* Courting males of all species of tortoise observed, either in captivity or in the wild, seem to encounter difficulty in mounting a moving female. This is particularly characteristic of those species which possess a high, vaulted shell, such as *Geochelone elegans*. A correlative morphologic modification in species with a highly-vaulted shell seems to be that the plastron of the male is more concave on its lower surface. Among other things this arrangement increases the stability of an otherwise one-point contact between a sphere and a plane. More specialized modifications in addition to this one seem to allow easier mounting in other kinds of highly-vaulted land turtles. As an example, in the terrestrial North American emydid genus *Terrapene* the hind feet of the males are apparently specially modified so that they can be inserted into the space between the movable rear portion of the plastron and immovable carapace of the female, where they are secured by the female hooking her own legs around them, or closing her shell on them (Evans 1953, Legler 1960, Cohn 1937, *et al.*). This behaviour apparently serves several functions. It assures that intromission remains possible in a species that has the ability to completely close its shell, and is a device whereby the male is kept from falling off the high-vaulted shell of the female. In marine turtles, a single enlarged claw on each flipper of the male grasps the shell of the female, and in kinosternids patches of enlarged scales on the hind legs of the males are apparently used to grasp the females (Carr 1952, *et al.*).

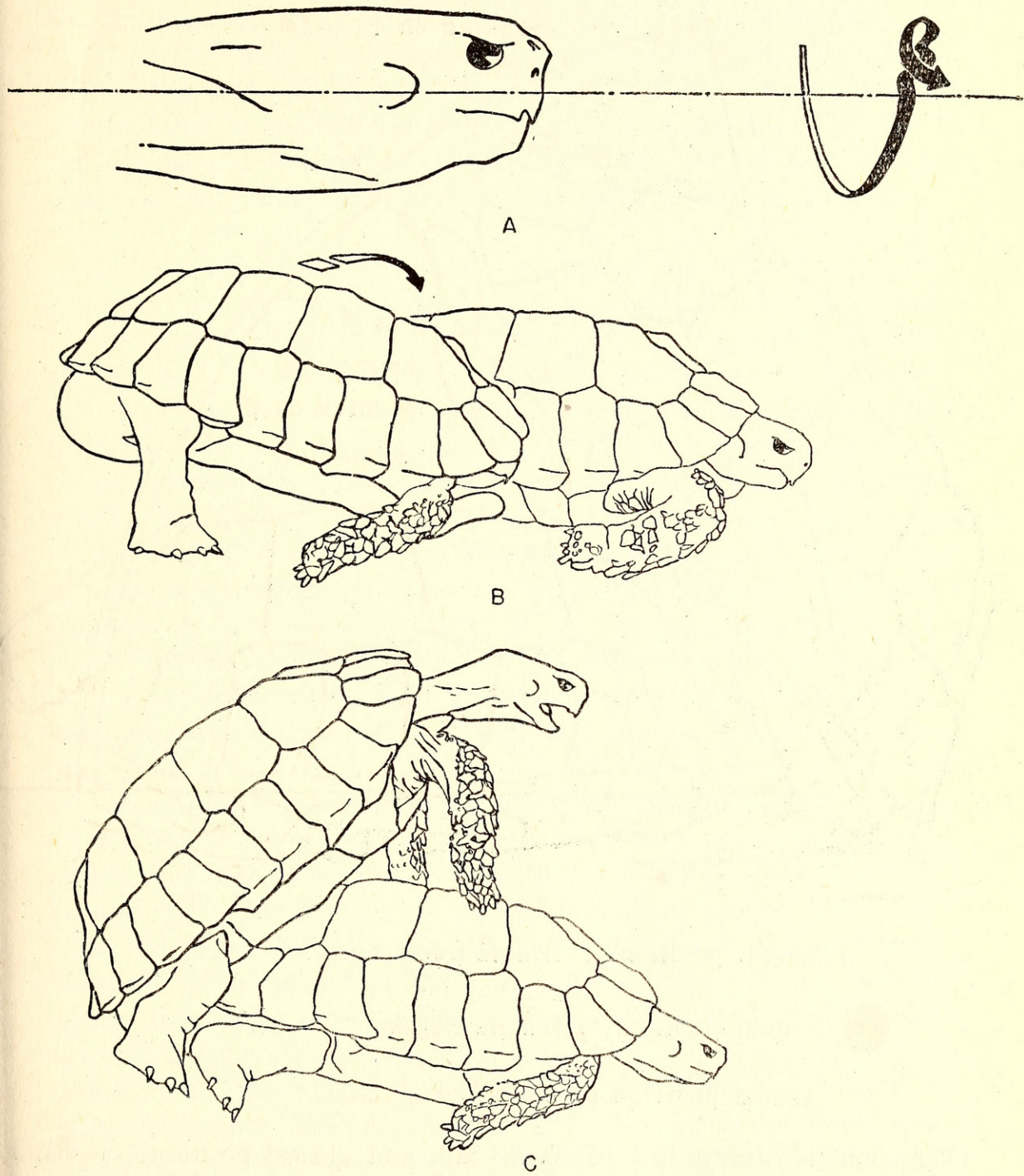
However, in *Geochelone travancorica* there are no apparent anatomical features that assure proper and continuous positioning of the male even though the female walks away, as in *Terrapene*. Thus, immobilization of the female is of considerable importance in this species. In all other turtles in which immobilization plays a role it is usually accomplished by the male either biting the head and legs of

the female so that these parts are kept withdrawn; or by a vigorous ramming of the shell of the female by the male with the anterior projection of his plastron. Somewhat similar tactics by male specimens of the emydid turtle *Terrapene ornata* have been interpreted by Brumwell (1940) as a method of sex recognition. Though sex-recognition is certainly a result of this behavioural pattern, immobilization is probably the primary function. Shell-tapping or ramming (presumably with the same function) is also known in one genus of aquatic turtles (Taylor 1933, for *Kinosternon flavescens flavescens*).

Some species of land tortoises are known to practise only one of these devices—others both. In *Geochelone travancorica* immobilization of the female is accomplished by shell-ramming alone. Leg- or head-biting has never been observed.

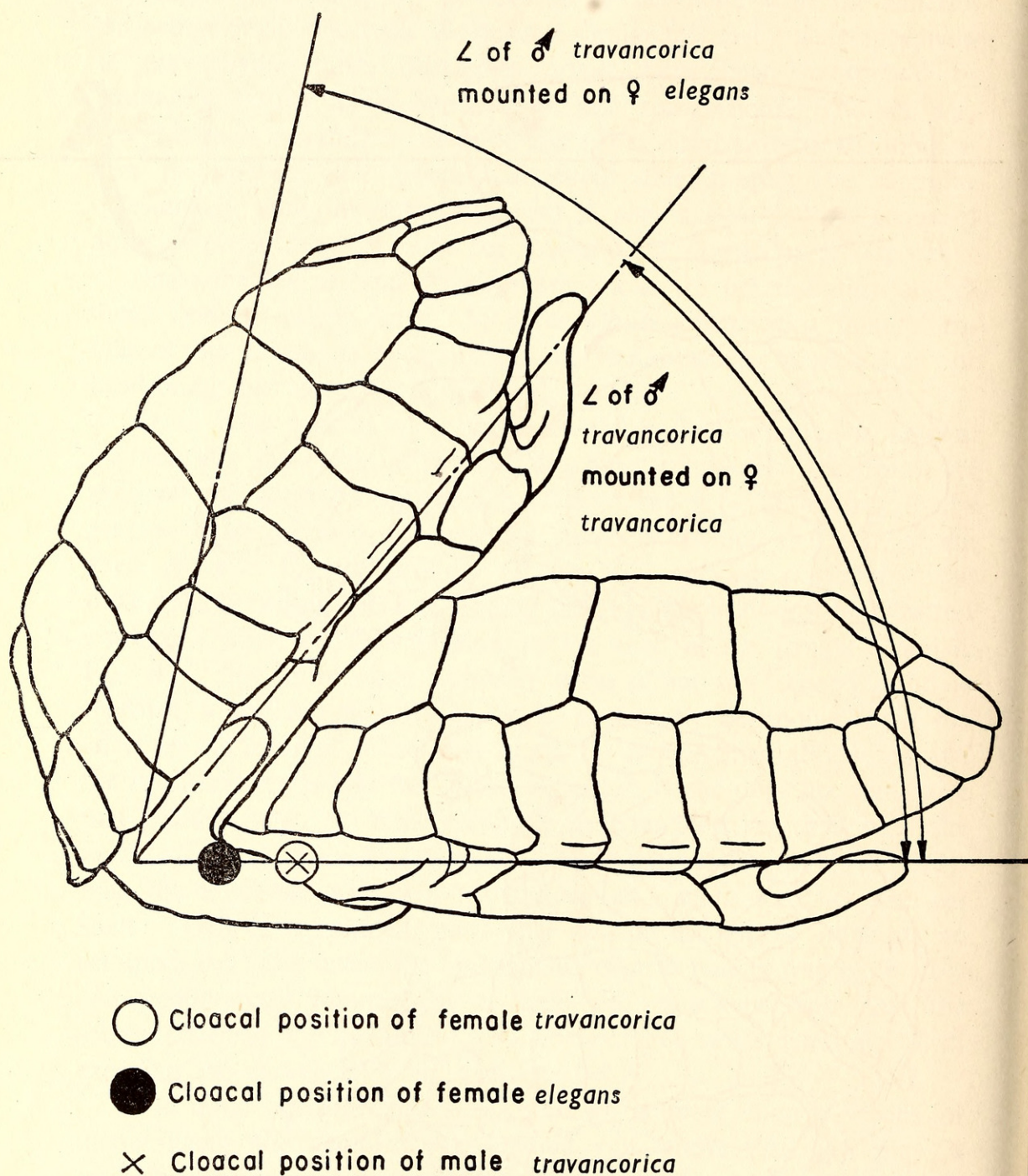
As in other species of tortoises in which shell-ramming is known, the courting male first withdraws the head completely and raises its shell off the ground by extending all four limbs. The anterior limbs are less extended than the posterior members, so that the front of the shell is closer to the ground. Then, after rocking posteriorly, the male quickly lunges forward, sending the gular projection of his plastron crashing against the side or back of the shell of the female (Plate I, Fig. B). The entire cycle normally takes about two seconds, and is repeated a variable number of times, apparently depending upon the effect on the female. When first struck the female invariably withdraws the head and limbs into the shell. However, if she does not remain in that position long, the male continues to pound on her shell until she seems unwilling to walk away. If the female starts to move away, then the mounted male will slide down and again start to ram her shell. This is continued until the female no longer attempts to scramble out from under the male. One captive female was so forcibly and continuously rammed by a large and persistent male that the scutes covering the posterior part of her shell were later sloughed, exposing the carapacial bony elements below.

It is quite possible that shell-ramming is more than a means of immobilizing the female. As pointed out above, it may play a secondary role in sex recognition. It may also be important in hormonal balance and reproductive periodicity. The ramming normally occupies the attention of the adult males for a long period of time before a successful mounting and intromission is actually accomplished. Thus, a male tortoise may attempt to immobilize a female for days, or even weeks, before prolonged mounting is possible. The repeated vigorous ramming of the shell could easily provide an important tactile stimulus whereby the reproductive cycle of the female is ultimately



The three phases of courtship behaviour of *Geochelone travancorica*

Fig. A. Sex recognition by olfaction, in which the males utilize an olfactory motor pattern characteristic of the species; B. Immobilization of the female by shell-ramming; C. Mounting and intromission



Diagrammatic illustration of shell, tail, and cloacal positions of males of *Geochelone travancorica* mounted on females of *G. travancorica* and *G. elegans*

brought into synchrony with that of the male. It has been observed that after prolonged ramming the female seems less inclined to walk away than initially. Thus, successful mating may, at least in the earlier part of the breeding season, depend upon such activity. Similar situations have been described for several other organisms.

That the male courtship behavioural pattern of *Geochelone travancorica* is largely initiated by the scent of the female alone is clearly shown by the fact that when the cloacal exudation of a sexually active female is smeared on a block of wood, box, or any similar object, sexually active males will often ram and mount the object.

3. *Mounting and intromission.* As pointed out above, successful mounting in most tortoises demands that the female remains passive for a relatively long period of time. This is apparently initially effected by the physical shock of the shell-ramming, and later by the probable effect of constant mating attempts on the reproductive hormonal balance of the female. Proper mounting is also dependent on such mechanical features as shell shape of both pairing members (Plate I, Fig. C).

The shell of *Geochelone travancorica* is not as high-vaulted as that of many other tortoises, such as the sympatric *G. elegans*. Thus, the plastron of *G. travancorica* males is less concave than that of *G. elegans* males. The angle formed by the longitudinal axis of the shell of a male *travancorica* mounted on an immobilized female of the same species is approximately 50 degrees. Due to differences in shell shape this same angle is approximately 80 degrees when a male of *G. travancorica* is mounted on a female of *G. elegans* (Plate II).

The tip of the tail of adult males of *G. travancorica* is provided with a scute-covered hook (Text-fig.). When the tail is held in a normal position the tip of the hook is directed toward the ground. However, when the male is mounted and attempting to breed the tail is directed anteriorly under the shell of the female, and the tip is directed upward against the ventral surface of the plastron. When fully extended and in position for copulation the tip of the hook contacts the femoro-anal suture of the plastron of the female, in which there is frequently a slight depression. This depression receives the tip of the hook, and presumably aids the male in maintaining a mounting posture (Plate II). A similar hook-like structure is apparently employed in the same manner by mounted male kinosternid turtles (Carr 1952, Taylor 1933).

When mounting an adult female of the sympatric species *Geochelone elegans*, the tail of the male of *G. travancorica* is too far forward, and cloacal contact is apparently very rare (Plate II). Furthermore the



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