The Growth, Ecology and Population Structure of Giant Tortoises on Aldabra

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The growth, ecology and population structure of giant tortoises on Aldabra

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[Plates 24 and 25]

Contents

The giant tortoise of Aldabra, *Geochelone gigantea*, shows quite marked changes in proportions with age, although during growth the relations between the length of the carapace and various measurements of the plastron and scutes involve not only strong but also weak allometry. Certain scutes show a predisposition to split during growth. Accidental damage to the carapace is frequent.

Males reach over 100 cm in carapace length but females are smaller, up to 80 cm. There is no segregation between the sexes in any single measurement investigated, except among the very largest animals. A general appraisal of carapace and tail shape is sufficient to sex only animals above 60 cm in carapace length.

The number of annuli on each scute corresponds to the number of years of age at least up to the formation of the tenth to fifteenth annulus. A general assessment of the pattern of growth is made by plotting body measurements against number of annuli. Growth curves of individual tortoises are reconstructed by relating measurements of successively formed annuli to age. Growth rate is recorded by plotting the difference between successive pairs of annulus measurements against age. The growth rate of ageable tortoises varies between local populations on South Island and between populations of South and Middle Island. Growth rate declines with age, reaching asymptotes at mean values of between 20 and 30 years. Some individuals exhibit sudden increases in growth rate after several years of very slow growth.

There is a well-marked daily cycle of activity, feeding being limited to the early morning and late evening. Agonistic behaviour is virtually absent. Breeding is seasonal and the males select partners from within a limited size range of tortoises. Most mating attempts are unsuccessful.

On Aldabra, tortoises occur in a wide variety of habitats, in each of which they depend on a different plant species or vegetational association for food. On coastal plains the chief source of food is *Sporobolus virginicus*. A variety of small herbs is consumed on the barren stretches of coastal champignon. Distribution in these areas is profoundly affected by the availability of shade. Further inland, the tortoises browse heavily on *Guettarda speciosa* in woods dominated by this tree. They take advantage of seasonal successions in the vegetation associated with freshwater pools, feeding on each community as it develops. Most of the woody plants near the pools are ignored. On the platin, browsing is selective and the regeneration of some trees is held in check. A very important food source here is the 'tortoise turf' (a sward in which *Panicum* sp. is often dominant) developed under conditions of heavy grazing and susceptible to erosion by wind and the tortoises themselves. On Middle Island, where the population is small, the tortoises exert very little effect on the vegetation.

Associations with other animals are mostly casual, but along the south coast dunes *Coenobita rugosus* is dependent on tortoise faeces for food.

Fossilized tortoise bones have been discovered at many points on Aldabra, deposited in brown limestone. They probably date from before the interstadial of about 30 000 years ago.

Some adult tortoises range over 7 km or more, across a variety of habitats, but many individuals appear to be sedentary. The population of South Island is enormous—of the order of 100 000 animals—with a density of about 30 hm^{-2} on the platin. Higher densities are reached in *Guettarda* woodland. Local variation in numbers, size range and age structure depend on habitat preferences, differential movement of age classes and regional differences in growth rate.

Attempts at assessing age class distribution are affected particularly by undersampling of the younger age classes, and the difficulty of counting the worn growth rings in animals with more than about 14. In the census sample, which may itself be an imperfect sample of the whole South Island population, at least 35% of the animals are below 20 years of age and only about 20% can have reached sexual maturity. More than 50 age classes may be present, but this and similar deductions are still speculative.

1. INTRODUCTION

Wild populations of giant tortoises (*Testudo* or *Geochelone gigantea*) formerly occurred on a number of islands in the Indian Ocean, including the Seychelles (see summary in Stoddart & Wright 1967; animals from Madagascar and the Mascarenes are regarded as specifically distinct), but are now confined to the elevated atoll of Aldabra, where they exist on West Island, Middle Island and South Island. They are absent from Ile Polymnie and all the smaller islets in the Lagoon. In company with fruit bats, forest birds of Malagasy origin, geckoes, skinks, rails and immense numbers of land crabs, they contribute to a distinctive faunal association not now duplicated anywhere else in the world. The incredible abundance of the large herbivorous reptiles makes Aldabra a unique island complex, even by comparison with the Galapagos Archipelago, and lends a special attraction to a study of their ecology, already of peculiar interest because of the chelonian's long potential life span.

The Aldabra tortoise belongs to the *Geochelone* group of land tortoises (Williams 1952). Loveridge (in Loveridge & Williams 1957, p. 220) discusses generic nomenclature. The specific name *gigantea*, based on an animal of uncertain origin, but assumed by Rothschild (1915) to have come from the Seychelles, should probably include as synonyms the *Testudo elephantina*, *T. daudinii*, *T. ponderosa*, *T. hololissa*, *T. gouffei* and *T. sumeirei* mentioned by Günther (1877) and Rothschild (1915). None of these names is certainly based on specimens obtained from wild populations of known provenance—indeed in some cases the specimens were tame semi-captive animals. They exhibit no more variation among themselves than can be seen within the present Aldabra population. The names have been associated with tortoises native to particular islands (Rothschild 1915)—*daudini* with the South Island, Aldabra, population and *elephantina* with the Middle Island animals. Hence what is essentially individual variation has been assumed to represent geographical variation and if the latter exists, it has remained undemonstrated (see also Gaymer 1968).

In menageries especially, the Aladabra tortoise may be confused with the giant Galapagos tortoise, *Testudo* or *Geochelone elephantopus*, but illustrations in Gunther (1877) make clear the considerable differences between the two, especially in the form of the head and its scutellation.

The Indian Ocean species is reputed to be the largest terrestrial chelonian. A carapace length of 133 cm is recorded in a '*Testudo daudinii*' obtained from Ile aux Lubines in the Chagos (Rothschild 1915). This specimen is even larger than the one mentioned by Schmidt & Inger (1957), which is the type of *T. gouffei* (Rothschild 1915). During the present study, the largest individual seen was a male with a carapace length (distance between nuchal and supracaudal scutes measured in a straight line) of 105 cm, but a fossil femur found on South Island indicates that larger sizes were attained by the indigenous tortoises in the past.

2. PROCEDURE

The observations on which this paper is based were made during the Royal Society Expedition to Aldabra, phases I to III, 1967 to 1968, and were concerned not only with making a general survey of tortoise ecology, but also with assessing the requirements for adequate conservation of the population.

The season August 1967 to April 1968 was exceptionally dry, so that the annual pattern of events in the life of the tortoise population was possibly atypical. Rainfall in November 1967 led to the filling of solution pans on the platin and to flushing of the vegetation, in turn resulting in a short period of growth among the tortoises. A very dry spell followed in the early part of 1968, though there was some rain at the end of February. Mating—first observed in October—continued on through April. Egg laying was observed in July by Frazier (1968), while hatchlings had been recorded first in October of the previous year.

Tortoises could not be studied from the base camp and most observations were made from camps at Wilson's Well (near Takamaka) and Cinq Cases Well. Other parts of South Island were visited from these camps and short stays were made at Anse Mais, East Channel Camp on Middle Island and Dune Jean-Louis.

The time-table of field trips was as follows:

Takamaka: 22 September to 6 October; 20 October to 4 November; 9 to 17 December (1967).

Anse Mais: 11 to 16 October (1967).

Cinq Cases: 4 to 23 November; 17 to 20 December (1967); 3 January to 25 February; 18 to 24 March (1968).

Middle Island: 20 to 23 December (1967); 10 to 18 March (1968).

(a) *Population samples*

Several samples of the tortoises population were examined and measured. The first sample involved animals at Wilson's Well and Takamaka Grove. All tortoises encountered during work sessions between 22 September and 4 November were marked, but small tortoises found outside these sessions were also noted, introducing a bias into the sampling.

The second sample was of 500 tortoises found within a *Guettarda speciosa–Ficus nautarum* wood seaward of the camp at Cinq Cases, between 7 and 14 November. Every tortoise encountered was examined.

Because of the paucity of small tortoises in these samples a special effort was made to measure animals of about 20 cm carapace length or less, and a sample was collected over 2 days by Seychellois labourers within about 500 m of the Cinq Cases camp.

On Middle Island all tortoises found between 10 and 18 March were measured.

Measurement records were also obtained during the census.

(*b*) *Measurements*

The following routine measurements were taken (see figure 1):

(1) *Carapace length*—The distance between the anterior point of the nuchal scute and the posterior midpoint of the supracaudal scute, measured in a straight line.

(2) *Plastron length*—the distance between the anterior point of junction of the gular scutes and the posterior midpoint of junction of the anal scutes.

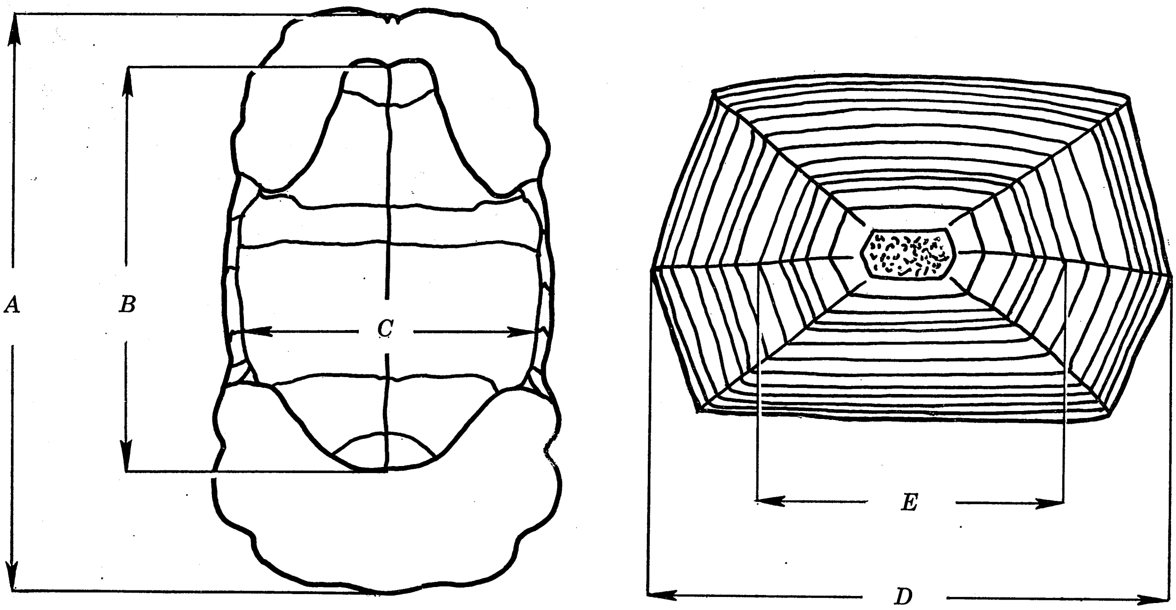

FIGURE 1. Ventral view of carapace and plastron (left) and dorsal view of third vertebral scute (right) to illustrate the methods of measuring carapace length (*A*), plastron length (*B*), plastron width (*C*), width of scute or most recently formed annulus (*D*), and width of fifth annulus (*E*).

(3) *Plastron width*—the distance across the plastron at the point of junction of the abdominal scutes and the sixth and seventh marginal scutes.

(4) *Plastron depth*—this was an assessment of the concavity of the pastron and was made by laying a rule across the plastron at the points mentioned in (3) and measuring the distance between the rule and the point on the carapace perpendicularly below.

(5) *Scute width*—the greatest width across the third vertebral scute. This measurement was used on several occasions as a convenient index of size.

(6) *Annulus width*—width across the growth rings of the third vertebral scute. These measurements could not be made in many cases, for often the scute was worn smooth. The largest measurement of annulus width on a particular scute was the same measurement as 'scute width', except in cases where new growth had started. The distinction between scute width (a single measurement) and annulus width (one of a series of measurements) is nevertheless maintained in this account. The smallest value in the series of annulus measurements was that of the areolar region, that part of the scute ready-formed on hatching.

(7) *Growth increment*—this derived measurement was a record of the increment of growth of the scute between the formation of two annuli and was the difference between measurements of the width of successive annuli.

Measurements of 30 cm or under were made using metal calipers and recording to the nearest millimetre, but larger measurements were made using a wooden caliper reading to the nearest half centimetre. Not all of the described measurements were recorded for each tortoise. Some animals were measured because of their exceptionally large size, or for some other reason of special interest, although they did not contribute to any of the sample populations.

(*c*) *Census*

Pilot counts gave an indication of the numerical concentration of tortoises in open areas but were inadequate as an index of their abundance in areas of scrub and scrub-forest. To overcome this problem, 46 samples of the populations were made at fixed points throughout the eastern half of South Island (figure 2). At each point a 100 m square was paced out, using a compass and marker flags. All tortoises within the area were counted, sexed and aged where possible, and the widths of their third vertebral scutes were measured as indices of size. Sample sites were at $\frac{1}{2}$ km intervals and each was first located on an aerial photograph. It was found possible to identify individual trees and other landmarks on the latter so that each site could be reliably traced in the field.

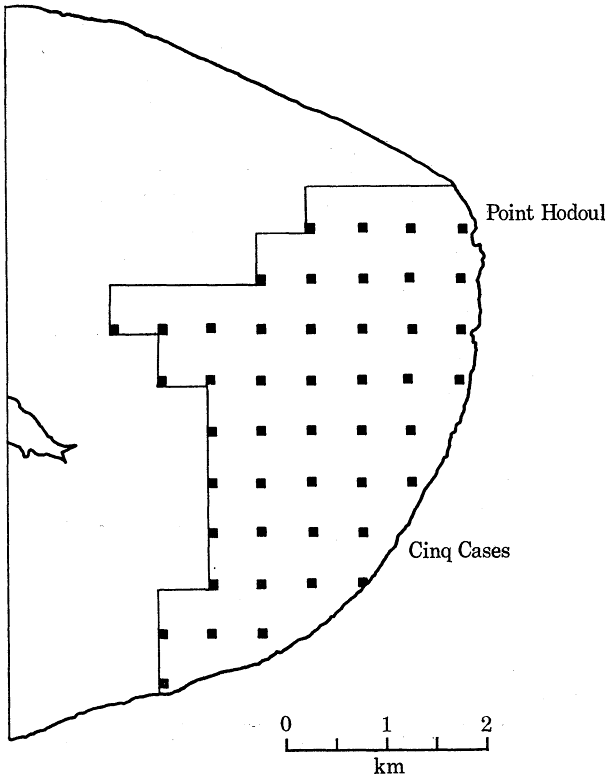

Figure 2. Map of eastern sector of South Island, Aldabra, showing sites of hectare quadrats utilized during the census (black squares). The area whose population was considered to have been sampled is bounded by the narrow line.

3. General appearance

Young and adult Aldabra tortoises are illustrated in figures 3 to 10, plates 24 and 25. The youngest individuals observed had probably been growing for less than a month since hatching. They retained the egg tooth (figure 3, plate 24). In such small tortoises, the carapace is shiny and black. The areolar zone of each polyhedral scute, already formed at hatching, is surrounded by a narrow band of relatively smooth tissue which represents growth since hatching (figure 5, plate 24).

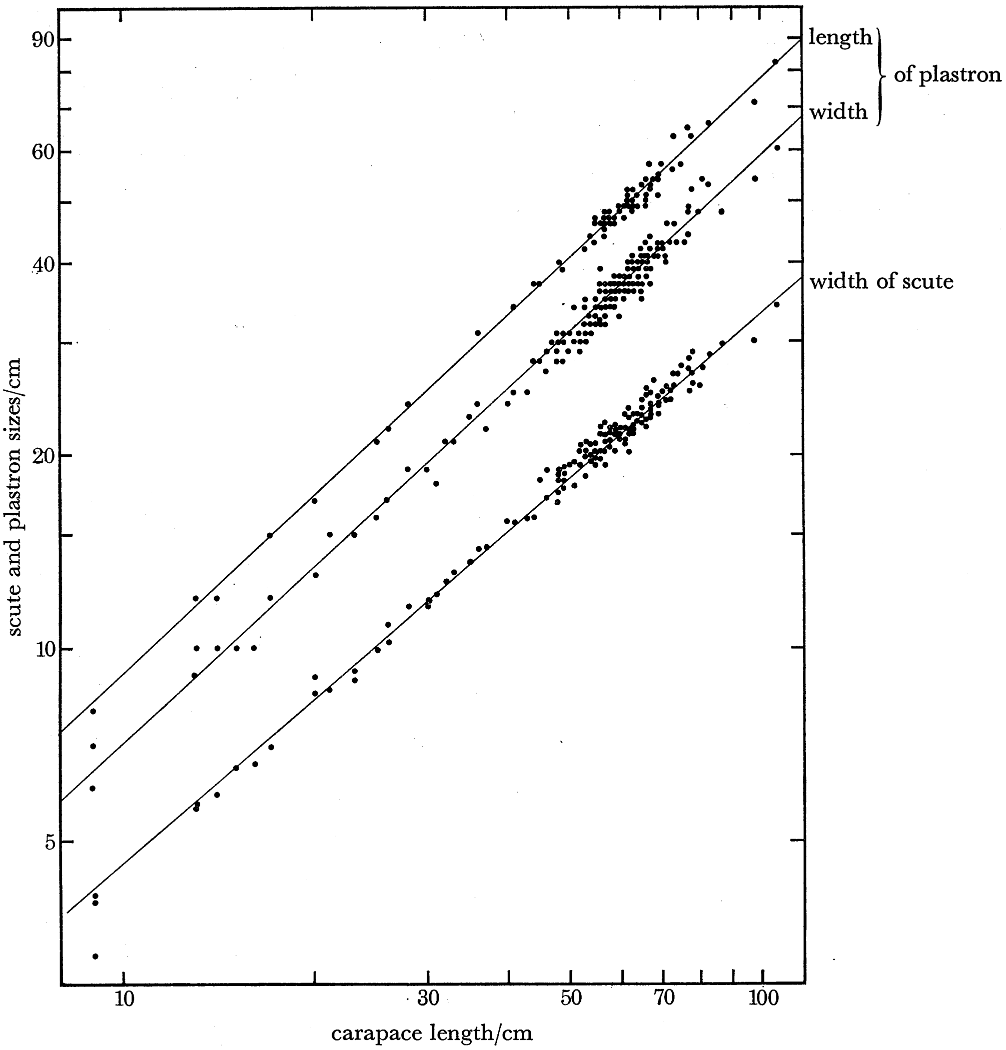

Figure 11. Relation of plastron length (upper regression line), plastron width (middle regression line) and width of the third vertebral scute (lower regression line) to carapace length. For plastron length against carapace length, $\lg y = 0.03 + 0.94 \lg x$ ($n = 80$; $r = 0.99$); for plastron width against carapace length, $\lg y = -0.15 + 0.91 \lg x$ ($n = 244$; $r = 0.99$); and for scute width against carapace length, $\lg y = -0.55 + 0.89 \lg x$ ($n = 244$; $r = 0.99$).

As growth proceeds, more tissue is added concentrically or somewhat eccentrically to the areolae. This tissue varies in thickness (probably reflecting minor changes in growth rate) and it becomes marked by concentric corrugations and major concentric striae or ‘growth rings’, as well as by faint radial ridges (figures 6 to 9, plates 24 and 25).

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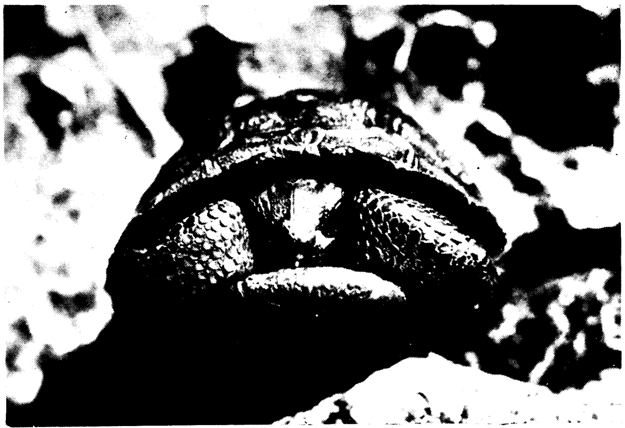

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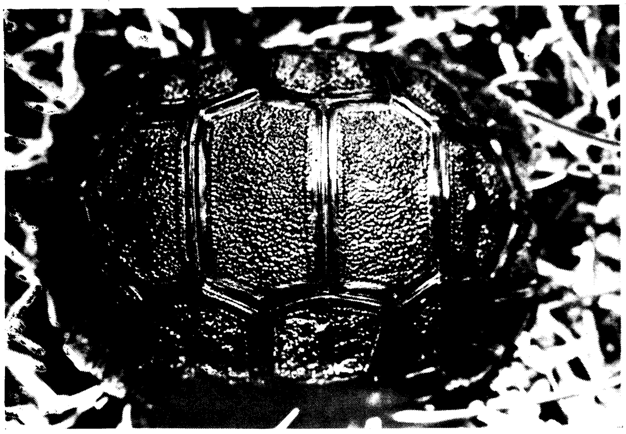

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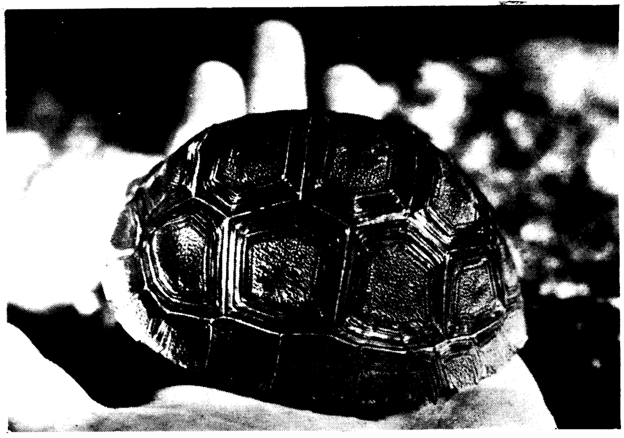

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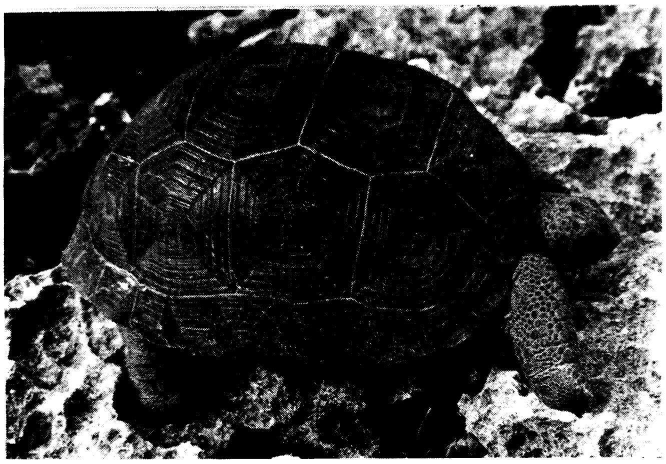

FIGURE 3. Head of young tortoise, probably less than 1 month old, showing the egg tooth.

FIGURE 4. Front view of the tortoise shown in figure 3.

FIGURE 5. Carapace of the tortoise shown in figure 3 to show the relatively large areolar areas on each scute, and the narrow rings of tissue grown since hatching.

FIGURE 6. Carapace of tortoise with a single season's growth on each scute.

FIGURE 7. Young tortoise with four annuli on each scute.

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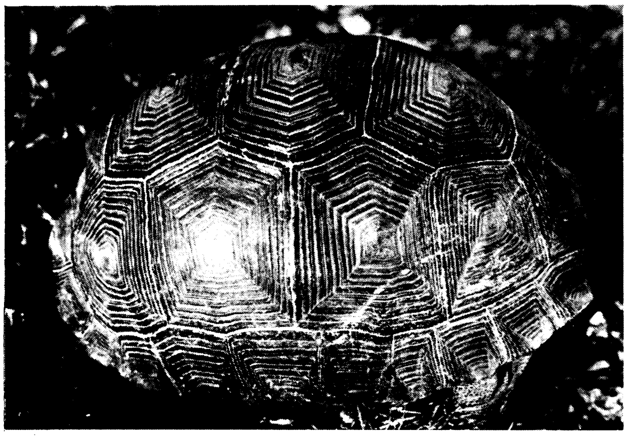

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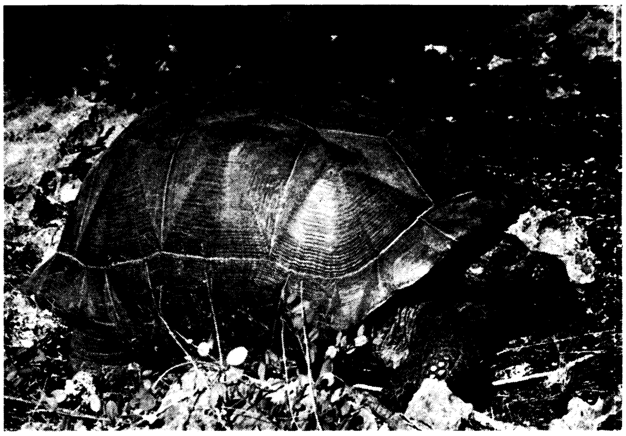

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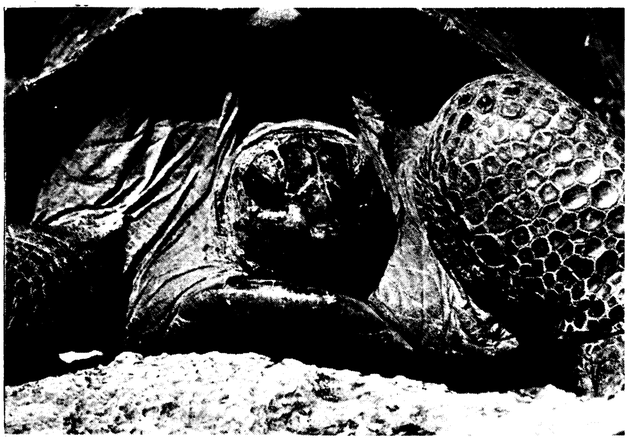

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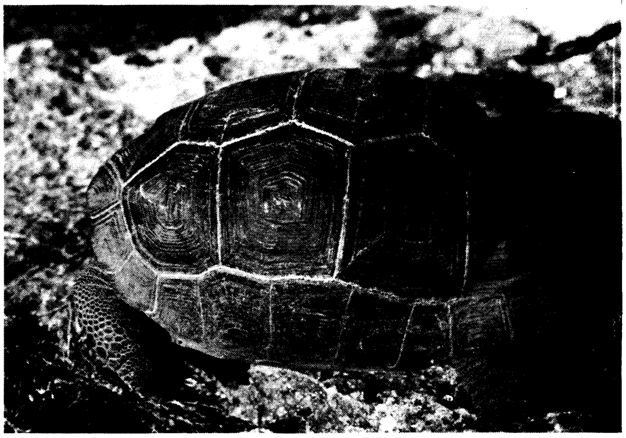

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Figure 8. Carapace of tortoise with ten annuli on each scute.

Figure 9. Tortoise on Middle Island, Aldabra, with about 27 annuli.

Figure 10. Anterior view of adult tortoise for comparison with figure 4.

Figure 26. Carapace of tortoise in which the most recently formed annuli on each scute are much broader than any others, suggesting that there has been a sudden alteration in growth rate.

Figure 33. 'Tortoise turf' showing shoots of *Panicum* sp. (leaves about 1 cm long) and *Ricksia* plants.

Bodily proportions change with age. The head becomes successively more prognathous and relatively smaller, while the limbs become relatively larger (compare plates 24 and 25). Changes occur in the form of the scutes. In some individuals the smooth contours of the juvenile carapace are lost through the strong bossing of the scutes (well illustrated in plate 3 of Günther's 1877 monograph). In all animals the posterior and anterior marginal scutes become somewhat everted and flared. The ridge running along the lateral marginals is obscured. Growth rings can be clearly traced until the formation of the 20th to 30th, after which wear smooths the carapace and plastron and obliterates all surface irregularities. Other changes are associated with sexual maturity.

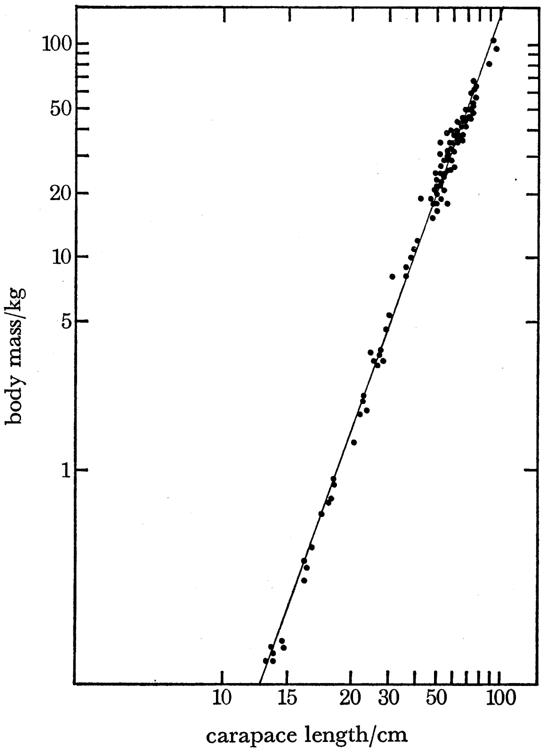


Figure 12. The relation between carapace length and body mass in giant tortoises. The curve has been fitted by eye.

The scutes of the oldest tortoises are dull and very thin, revealing their sinous constituent fibres, and as a result of their semi-transluscency, especially when wet, one can trace the tops of marginal papillae which secure the scute in the bone below. In younger animals, the scutes are attached less intimately to the bone and their margins are etched less deeply in the underlying skeleton.

Variation in the form of the scutes is to be viewed in terms of age, degree of wear and growth rate. There is no racial or regional variation distinguishable, as earlier authors implied (see Gunther 1877, where *Testudo hololissa* is partly identified by its smooth carapace; or Rothschild, 1915, where *elephantina* is separated from *gigantea* on a similar basis).

Growth in the chelonian carapace and plastron has been recognized implicitly as being isometric (see, for instance, Carr & Caldwell 1956). When the large size range available for measurement on Aldabra is examined, the coefficients of allometry indeed prove to be close to unity in the relations between carapace length and the following: scute width, plastron length and plastron breadth (figure 11). However, the relation between carapace length and the concavity of the plastron involves strong allometry (figure 15).

The pattern of growth of the carapace is probably quite complex. The effects of small individual differences in the coefficients of allometry involved will be considerably exaggerated as size increases. This phenomenon accounts for the superficial assessment that large tortoises are more variable in shape than small ones. There is yet no evidence for Gaymer's (1968) view that there is selection for 'one common pattern of growth' in the young tortoises and relaxation of that selection pressure among the subadults.

The relations between mass and size in the Aldabra tortoise is established in figure 12, and from this it is possible to predict the masses of animals whose size only is known.

4. Abnormalities, injuries and effects of disease

Among the various abnormalities in scutellation, it was often difficult to distinguish congenital peculiarities from those arising during growth. Abnormalities associated with the fifth vertebral scute were common and occurred in 25 % of cases out of a sample of 821 tortoises. The scute may have split across transversely, longitudinally or in some other way, to form two, three or more separate scutes with their own centres of growth. In the same sample, two animals had the first vertebral split or splitting. From the examination of very young tortoises it was seen that splitting of a scute could occur before the third year of life.

Gaymer (1968) remarks on the variations in the form of another scute, the supracaudal, which splits into two during growth in about 50 % of tortoises.

Some congenital abnormalities of the scutellation were observed. Twelve out of the sample of 821 tortoises had apparently been born with supernumerary scutes. These were sometimes very small intercalations between the normal scutes, but five animals had six or seven symmetrical vertebrals.

There were also cases where individual scutes were absent. Two remarkable animals were found, with in each case only two, enlarged, costal scutes present on one side. The nuchal was missing in three out of 223 tortoises examined by the Bristol Seychelles Expedition (Gaymer 1968).

Accidents and injuries also affect the scutellation. Many tortoises had punctures in the carapace, usually 2 cm or less across. These probably result from falls in champignon. Some animals had sustained severe injury, including fracture of large areas of carapace and isolation of bone fragments on top of the scar tissue filling the wound. One individual was seen with nearly the whole side covered in a sheet of scar tissue. Bleached skeletons showed how wounds had healed by the formation of a cup-shaped layer of bone below the break in the horny integument. In some skeletons, these healed wounds were surprisingly close to the vertebral column.

The origin of other injuries is less clear. Several animals lacked one of the limbs, some or all of the claws were occasionally missing and one tail-less tortoise was observed.

Disease can afflict the carapace, so that it peels off by the shedding of irregular laminae and is replaced by uneven scar tissue with the scute margins quite obscured. One tortoise had the whole carapace formed of such tissue; in another, even the bone was affected, the projecting anterior and posterior marginal scutes were completely resorbed, and the animal's tail and limbs were fully exposed.

5. Sexing

Adult male and female tortoises are easily distinguished (figure 1). Males tend to be larger. The largest one recorded during the study period reached 106 cm in carapace length, and from figure 12 it can be seen that he must have had a mass of 130 kg. The largest male on record could have attained a mass of 300 kg. The plastron of the male is deeply concave and around its edge the scutes are bowed out to form a prominent ridge, conspicuous along the side of the animal and, even more noticeably, in front of the tail. To house the penis the tail is long (up to 10 cm) and very thick at the base. By superficial comparison with that of the female, the male's carapace appears to be longer, lower and wider towards the rear, with a relatively larger cavity accomodating the tail and hind limbs. Female tortoises are smaller—the largest observed had a carapace length of 79 cm and probably had a mass of about 65 kg. The plastron in the female is flat showing no enlargement of the scutes about its margin. The tail is very short indeed (up to 5 cm) and the carapace appears short and high and is not expanded towards the rear. These assessments of carapace shape are hard to substantiate especially as they reflect largely allometric differences. The other distinctions between the sexes are not evident in tortoises of less than about 55 cm in carapace length.

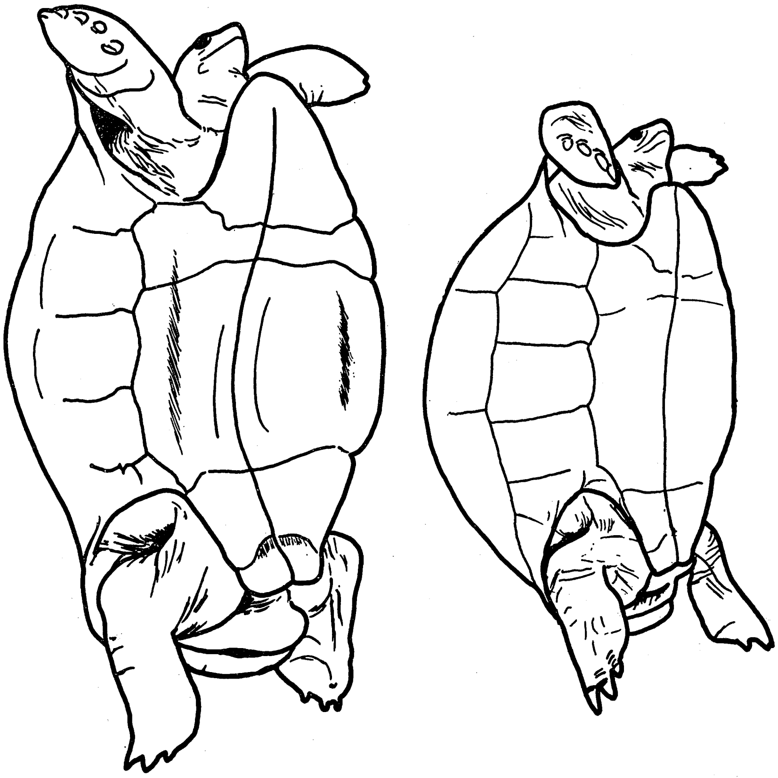


Figure 13. Oblique views of male (left) and female giant tortoises to show secondary sexual differences in the form of the plastron, the tail and the rear margin of the carapace.

It is more easy to identify a male positively than it is to distinguish a female, while around a critical size level of about 60 cm carapace length, whether a tortoise is to be deemed sexable or not becomes arbitrary. The discovery of an objective method for sexing the smaller tortoises was desirable. Several measurements were analysed with this in mind.

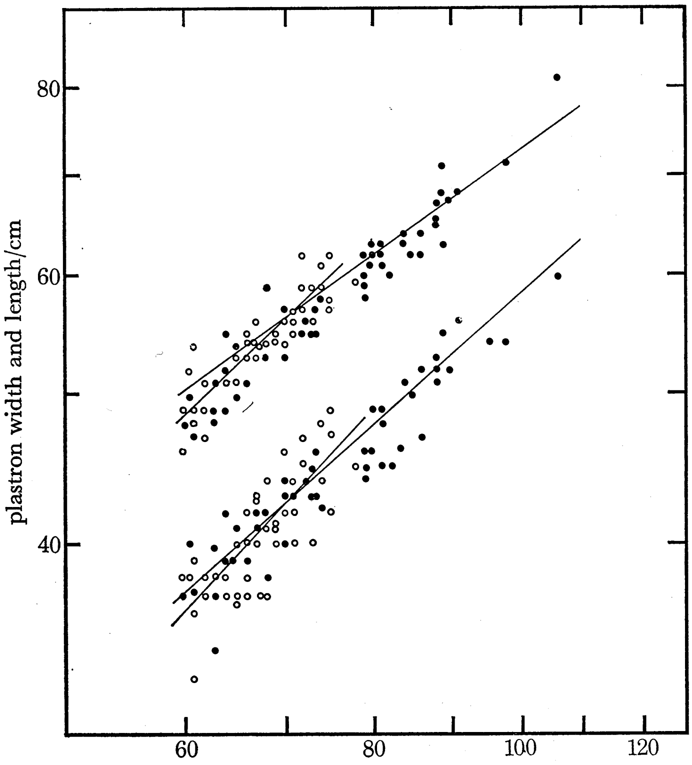


Figure 14

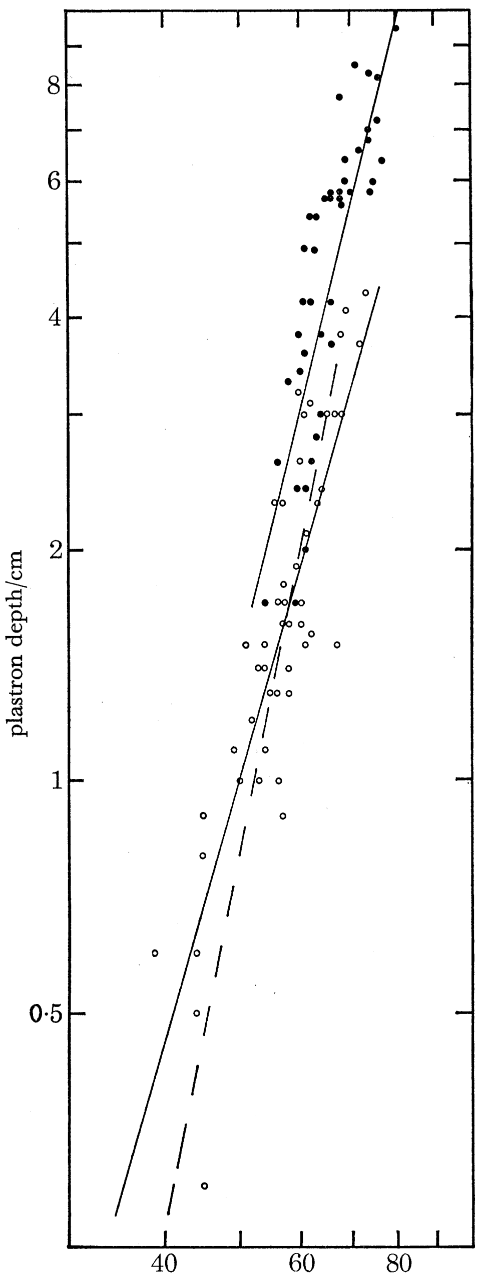


Figure 15

Figure 14. Relation of plastron length (upper regression lines) and plastron width (lower regression lines) to carapace length for male (●) and female (○) tortoises above 60 cm in carapace length. For plastron length against carapace length, $\lg y = 0.52 + 0.82 \lg x$ ($n = 63$; $r = 0.97$) for males, and $\lg y = 0.06 + 0.93 \lg x$ ($n = 59$; $r = 0.89$) for females. For plastron breadth against carapace length, $\lg y = -0.06 + 0.89 \lg x$ ($n = 63$; $r = 0.93$) for males and $\lg y = -0.80 + 1.07 \lg x$ ($n = 59$; $r = 0.73$) for females.

Figure 15. Relation of plastron depth to carapace length for male (●) and female (○) tortoises from Cinq Cases. The broken line is the regression for unsexed animals. For males, $\lg y = -15.47 + 4.06 \lg x$ ($n = 46$; $r = 0.84$); for females, $\lg y = -14.26 + 3.64 \lg x$ ($n = 57$; $r = 0.86$); and for unsexed tortoises, $\lg y = -18.68 + 4.75 \lg x$ ($n = 383$; $r = 0.81$).

It proved impossible to measure the tail to an accuracy of within less than 1 cm because it was difficult to straighten and its length increased with expansion of the cloacal orifice. The distribution of the crude tail measurements for each 10 cm carapace-length class was found to be unimodal except apparently for the very largest animals (70 to 80 cm in carapace length).

Measurements of the carapace were recorded in the hope of demonstrating a segregation between the sexes, of the kind found by Cagle (1948) in *Pseudemys scripta*. There is a suggestion that among the largest animals the females have the plastron relatively wider and longer in relation to the length of the carapace (see figure 14) as one would expect from superficial observation, but even if this were substantiated by examining many more large females, the distinction cannot apply to animals with a carapace length of less than 70 cm and is of no practical value in sexing smaller tortoises.

An assessment of the depth of the plastron concavity also failed to show any segregation of measurements except among the largest tortoises. Possibly an alteration in the coefficient of allometry is involved. Inspection of figure 15 confirms that above a carapace length of 65 cm, females have decidedly less concave plastrons than males of the same length. For animals of less than 65 cm carapace length, no distinctions are evident and again the method does not suffice to sex those animals whose sex cannot be decided by inspection.

Table 1. Measurements of the width of the third vertebral scute in male and female tortoises

	number	mean scute width/mm	standard deviation
mating males	44	244.7	17.45
partners of mating males	44	218.2	15.97
males identified at Cinq Cases	48	236.5	19.25
females identified at Cinq Cases	53	218.7	26.65

Both the validity of the method of sexing and the relationship between the appearance of the secondary sexual characteristics and sexual maturity can be examined by comparing measurements of sexed animals with those both of males making attempts to mate and of their mating partners (table 1). The mean scute width measurements of mating males is significantly greater than that of other males (identified by their appearance) between the 5 and 2 % level, and tentatively it may be suggested that sexual behaviour is first exhibited a little after the development of secondary sexual characteristics. The difference between the means of the measurements of the 'female' mating partners and the Cinq Cases females is not significant below the 10 % level, but this is not any confirmation that mature females were identified correctly, as male tortoises, by attempting to mate what were in some cases obviously other males, were themselves less discriminating than the observer. However their selection was more rigid in terms of size range, the variances of the two samples being significantly different at the 1 % level.

Because of the peculiarities of the various population samples it is not possible to follow the emergence of secondary sexual characters during growth, or to relate their acquisition to age and sexual maturity. It does appear that South Island tortoises attain sexual maturity later than Middle Island animals, in spite of the fact that growth tends towards an asymptote earlier in life in the latter animals, for it was possible to sex most of the Middle Island sample of tortoises (aged 12 to 31 years) but none of the aged group among South Island animals (aged at less than 1 to 24 years).

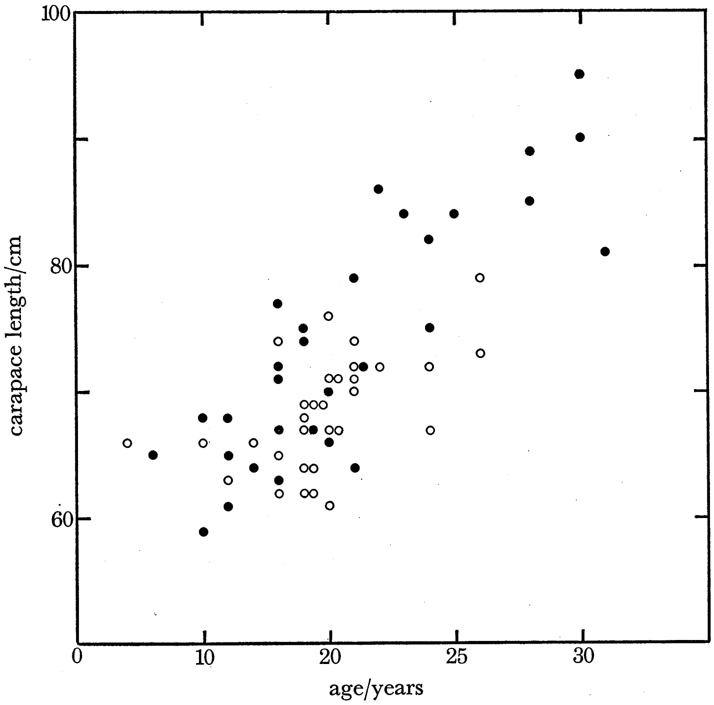


Figure 16. Scatter diagram of carapace length plotted against presumed age (from number of annuli) for male (●) and female (○) tortoises from Middle Island.

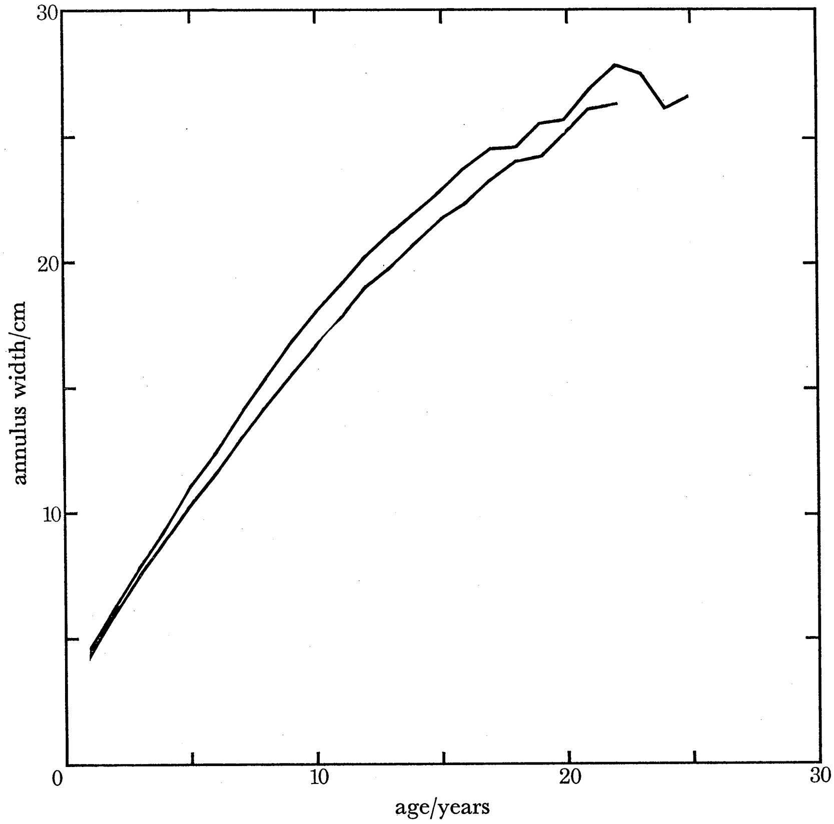


Figure 17. Growth curves for male (upper curve) and female tortoises from Middle Island, derived by plotting mean annulus width against presumed age (the cumulative number of annuli).

Measurements of sexed known-age tortoises are available for Middle Island only (figure 16). There is a very extensive overlap between the measurements of the sexes up at least to the age of 20. Most of the tortoises assessed as being older than 20 are males, but the few records from females do suggest that beyond the age of 20 years, segregation of measurements of males and females of the same age becomes apparent.

Growth curves for males and females have been obtained by plotting mean annulus width against cumulative annulus number (figure 17) and again the lack of data leads to an inadequate record of the last stages in the growth cycle. Initially, growth rate is very similar in the two sexes.

6. Ageing

If the formation of annuli reflects some influence of seasonal cycles on the growth process which is then rendered discontinuous, whole numbers of annuli can correspond to whole numbers of years. On the other hand, if growth is a continuous process, then however precisely annulus formation is related to growth rate, the relation with time need not be such a simple one as to be represented by a fixed ratio, nor may it be possible to evaluate it in the absence of animals of known age.

It is likely that the growth of Aldabra tortoises is indeed discontinuous. The rainy and dry seasons are normally very distinct (though not in 1967–8), so that the breeding season is adaptively limited, presumably as a result of selection against individuals born in the dry season when growth is adversely affected by the poor feeding conditions.

There is also more direct evidence for the discontinuous nature of the growth process. Growth in progress was not observed until November on South Island, at Takamaka. At this time fresh tissue began to be formed at the margins of the scutes. This growth was heralded by the appearance of white lines of keratinous film between the scutes. Otherwise the margin of each scute appeared to correspond to an annulus and this assessment, while conjectural, is assumed here and leads to no anomalies. New growth of the scutes was rarely seen at Cinq Cases but was in progress in 19 out of 79 tortoises observed on Middle Island in March. Growth, then, had either ceased or was recognizably recommencing during the study period.

If growth is indeed episodic, then it would be very surprising if its periodicity were unrelated to the periodicity of annulus formation. At the same time, although the two can hardly be out of phase, one need not expect a perfect correspondence between number of annuli and number of years, for in some seasons there may be no growth and in others possibly there are two growth phases and two annuli are formed. Whichever is the most frequent will determine whether age tends to be over or underestimated. Evidence will be presented later to show that the first supposition at least is likely to be valid only rarely.

Direct but limited corroboration of the annual formation of annuli comes from five tortoises whose scutes had been painted by the Bristol Seychelles Expedition in 1964. These animals were recaptured in 1967, when they were found to be have developed three growth zones three seasons after being marked.

7. Growth

One can now proceed to relate size to age, using either the length of the carapace or the width of the scute that is itself used for assessing age (the third vertebral) as convenient size indices. Measurements are available for three separate population samples—from Cinq Cases and Takamaka, South Island, and from Middle Island.

A disadvantage of the method of procedure is that each set of measurements for a given age (or annulus-number group) comes from a different cohort.

More adequate comparisons can be made by using the measurements of annuli on a single scute as a record of growth in the individual. If annuli mark the limits of annual zones of growth, then the dimensions of successive annuli on one scute plotted against the cumulative number of annuli provide a record of a growth process, with a built-in time scale, for the individual tortoise. Measurements pooled from many individuals can be presented as a plot of mean annulus width for different years of age. Results from several year classes (cohorts) have been used, though the higher the number of the annulus, the fewer are the cohorts from which it can be measured.

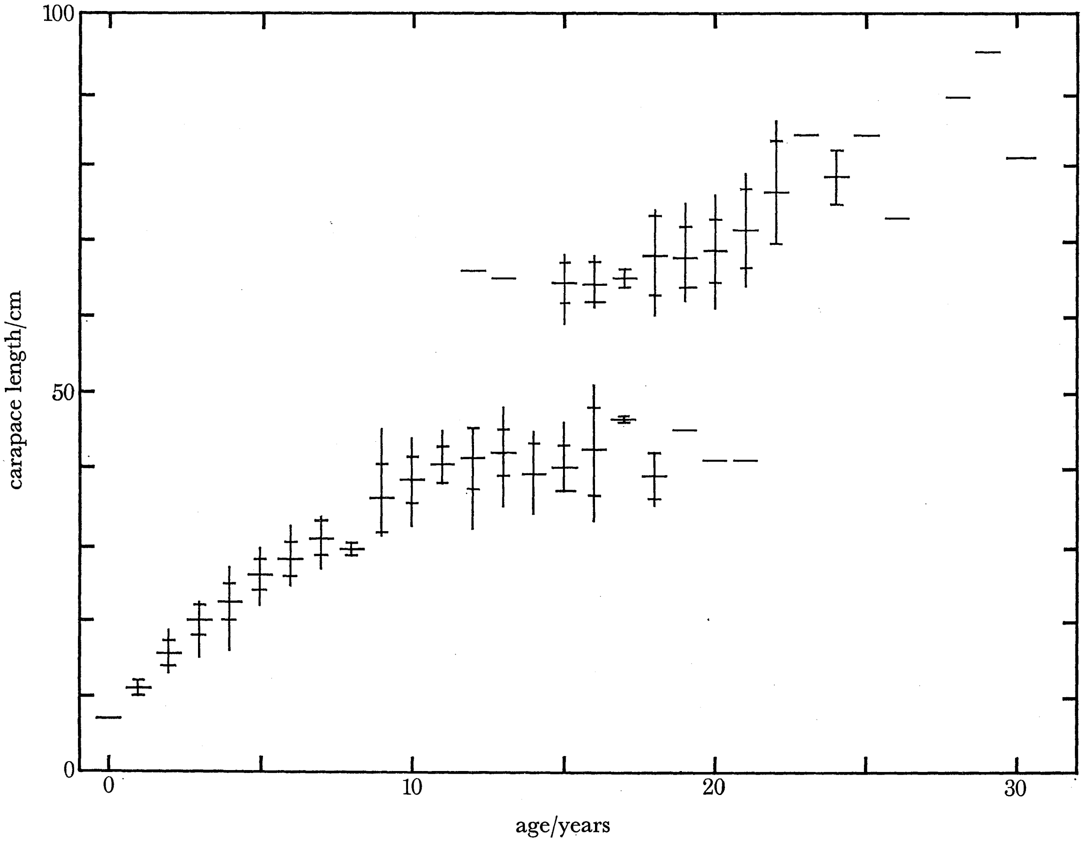


Figure 18. Mean, range and standard deviation of carapace length for different age groups (assessed by the number of annuli) of tortoises from two populations—Cinq Cases (lower series) and Middle Island (upper series). For each age class, the vertical line indicates the range of measurements, the longer horizontal bar the mean and the shorter horizontal bars, one standard deviation from the mean.

It has already been shown how the dimensions of the third vertebral scute are allometrically related to the length of the carapace (figure 12) so it is possible to infer from measurements of the annuli the length of the carapace at the time each was formed.

Recognizing that two different methods are involved in relating body measurements to age, the results will be considered together as they illustrate essentially the same points (figures 18 to 21, and table 2).

Differences in the age class distribution of the samples are apparent from figures 18 and 19.

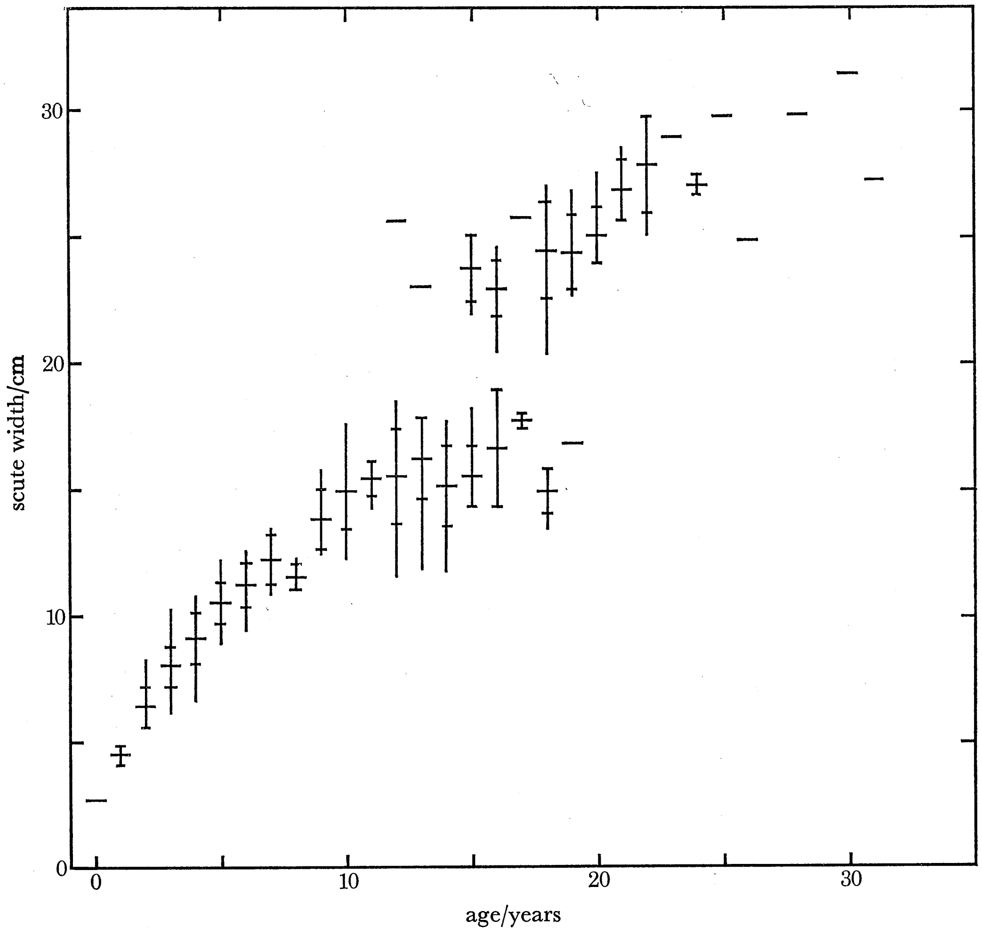


FIGURE 19. Mean, range and standard deviation for measurements of the width of the third vertebral scute in two populations of tortoises. Details as in figure 10.

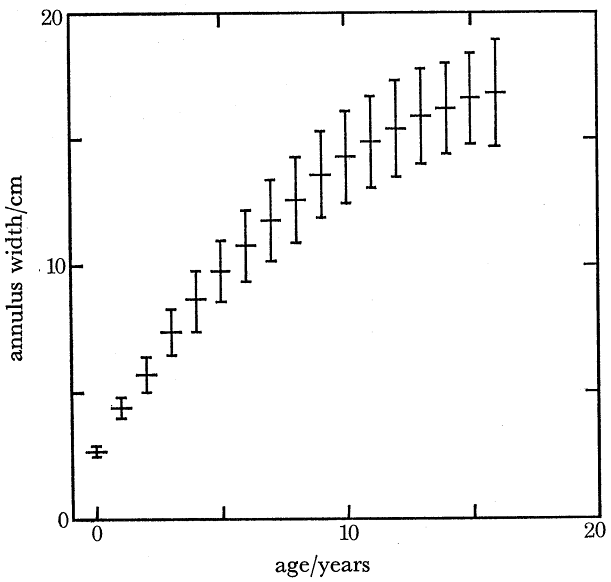


FIGURE 20. Mean and standard deviation of annulus width for different year classes (assessed by the cumulative number of annuli) of tortoises from Cinq Cases. The vertical line indicates one standard deviation from the mean, which is represented by the longer horizontal bar.

This is because the Middle Island sample includes almost no young tortoises and because large animals have been excluded from the other two samples, as these South Island tortoises have such worn scutes that beyond about 20 to 25, the annuli cannot be counted.

The next point of interest is the size distibution of the samples from Takamaka and Cinq Cases, localities only 6 km from each other (table 2). Up to the age of 10 years the Takamaka animals are distinctly smaller than the Cinq Cases tortoises, and for the 3- to 7-year olds and 10-year olds, the difference in mean measurements is significant below the 1 % level.

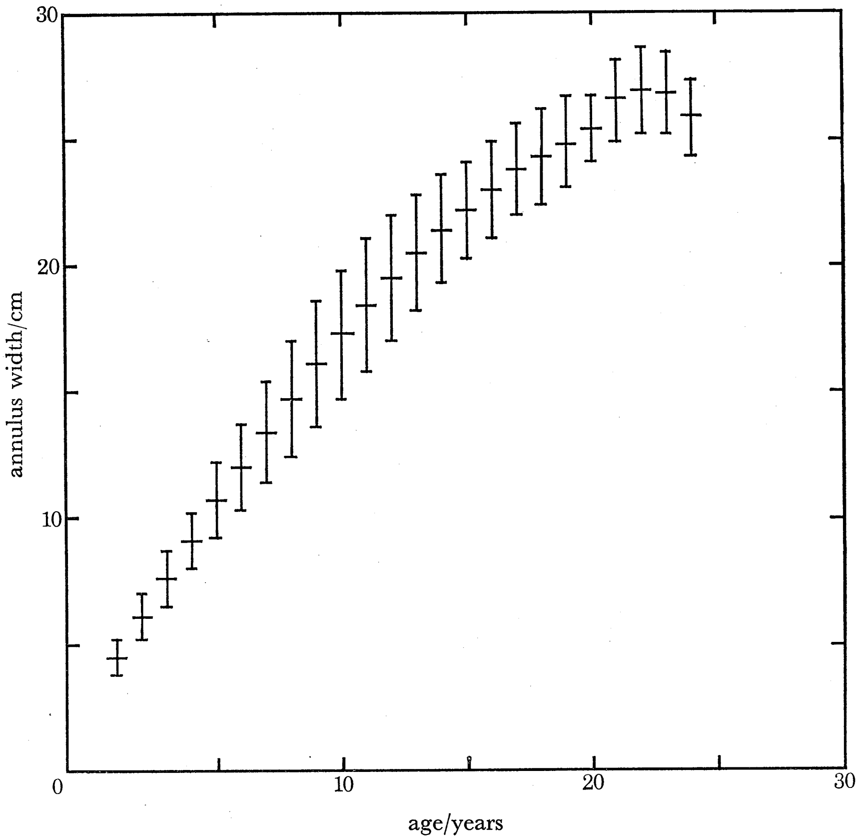


Figure 21. Mean and standard deviation of annulus width for different year classes of tortoises on Middle Island. Details as in figure 20.

Either the growth pattern in Takamaka is different from that in the Cinq Cases area or the different age classes within the Takamaka population have experienced different growth rates. The latter could result from response to changing local conditions.

An even more striking divergence exists between the two South Island populations and the one from Middle Island. Measurements of carapace length or of scute width from these populations do not overlap (at least above the age of 14 years—see figure 18). This can be attributed to the far higher growth rate of the Middle Island tortoises. It is also apparent that growth rate declines with age, and growth probably ceases at some stage (compare figures 20 and 21).

There is no need to assume that very large tortoises are of great age—rather they have experienced exceptionally rapid growth when young.

Measurements of scute width and carapace length are available for young animals only from the South Island populations, and the samples are very small. It is, nevertheless, apparent that the measurements of the lowest annulus-number classes are discrete from each other, suggesting that the size class distribution of young animals may be polymodal, with the modes corresponding to the age classes. This would substantiate the view that growth is discontinuous and annuli provide a record of age.

TABLE 2. MEAN AND STANDARD DEVIATIONS OF CARAPACE LENGTH (MILLIMETRES) FOR DIFFERENT AGE CLASSES IN THREE TORTOISE POPULATIONS

	Takamaka			Cinq Cases			Middle Island		
age class	no.	mean	standard deviation	no.	mean	standard deviation	no.	mean	standard deviation
0	—	—	—	1	70.0	—	—	—	—
1	9	90.7	11.46	4	109.2	7.85	—	—	—
2	2	141.5	8.50	10	154.0	16.49	—	—	—
3	8	146.8	13.90	30	197.5	18.85	—	—	—
4	9	183.4	22.68	44	223.6	24.87	—	—	—
5	7	206.5	30.32	27	260.0	19.99	—	—	—
6	6	225.1	12.15	26	281.1	21.90	—	—	—
7	9	250.4	32.20	6	306.5	22.05	—	—	—
8	7	277.1	31.03	4	293.7	7.85	—	—	—
9	8	308.7	38.54	11	361.3	43.48	—	—	—
10	8	326.2	42.11	11	384.0	28.66	—	—	—
11	4	420.0	96.17	9	405.5	23.14	—	—	—
12	4	331.7	101.60	9	415.5	40.58	1	660.0	—
13	1	440.0	—	21	419.5	30.62	1	650.0	—
14	6	493.3	21.34	24	391.6	39.33	—	—	—
15	5	440.0	70.14	14	430.7	31.04	3	643.3	38.58
16	4	515.0	21.79	8	425.0	55.45	4	642.5	25.86
17	2	570.0	40.00	2	465.0	5.00	2	650.0	10.00
18	2	405.0	85.00	3	390.0	29.43	10	679.0	52.62
19	—	—	—	1	450.0	—	13	677.6	39.25
20	—	—	—	1	410.0	—	8	686.2	41.51
21	2	565.0	25.00	1	410.0	—	5	718.0	49.15
22	—	—	—	—	—	—	3	763.3	68.47
23	—	—	—	—	—	—	1	840.0	—
24	1	540.0	—	—	—	—	2	785.0	35.00
25	—	—	—	—	—	—	1	840.0	—
26	—	—	—	—	—	—	1	730.0	—
27	—	—	—	—	—	—	—	—	—
28	—	—	—	—	—	—	1	890.0	—
29	—	—	—	—	—	—	—	—	—
30	—	—	—	—	—	—	1	950.0	—
31	—	—	—	—	—	—	1	810.0	—

The records of mean annulus width for the early years of life of animals on Middle Island is based on relatively indistinct growth lines from adults with between 12 and 31 annuli. Those for the South Island populations, however, are from much clearer annuli, capable of more precise measurements. They indicate the discreteness of measurements of the first few annulus-number classes.

Further analysis of growth can be made by using measurements of annual growth increments. The growth increment of the individual scute can vary considerably from year to year (figure 24) in spite of the subjective impression that the annuli are evenly spaced. For this reason, the ranges of measurements of successive annuli overlap considerably, though the steady decline in their mean values clearly indicates the manner in which growth rate varies with age (figures 22 and 23). Growth becomes very reduced or ceases at about the 25th and 30th year in the

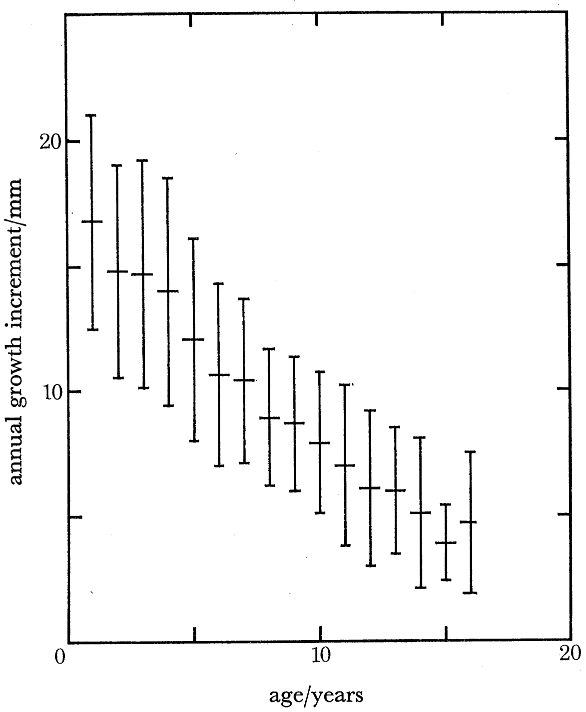


Figure 22. Mean and standard deviation of growth increments plotted against age for tortoises from Cinq Cases. Details as in figure 20.

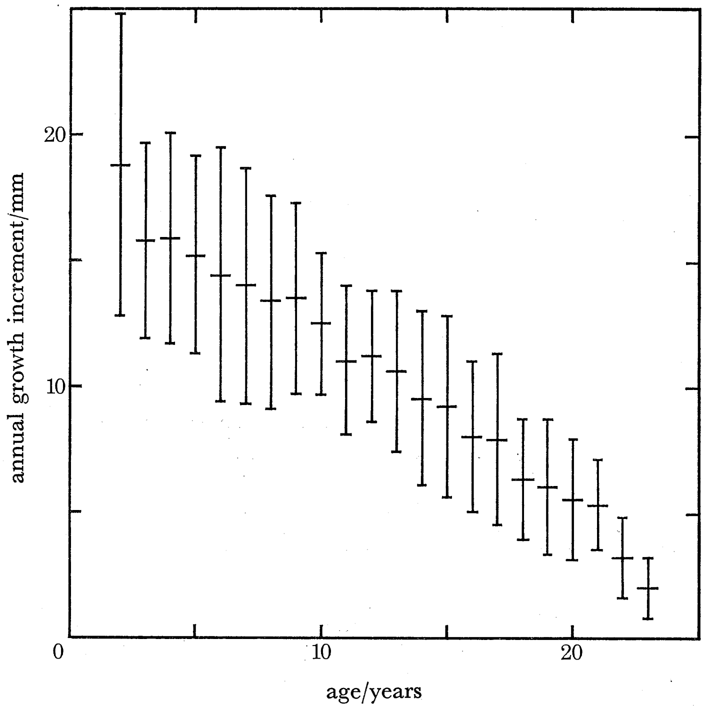
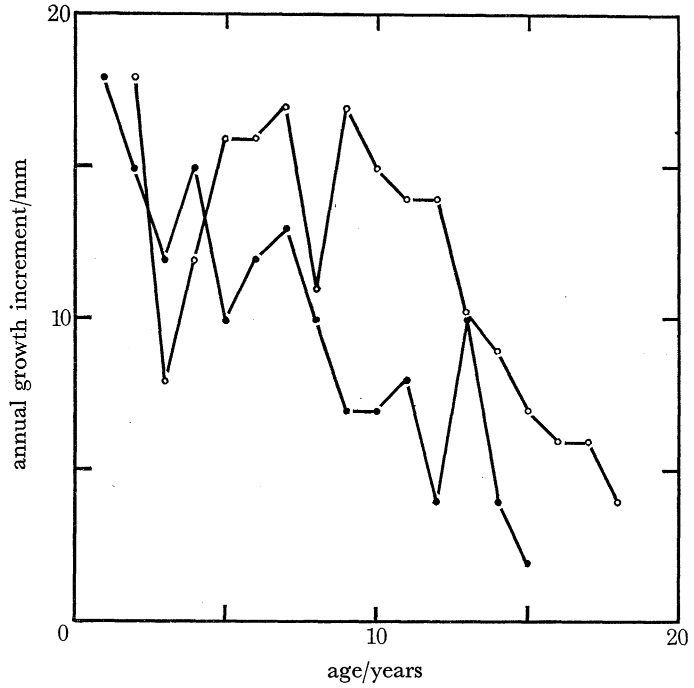


Figure 23. Mean and standard deviation of growth increments plotted against age for tortoises from Middle Island. Details as in figure 20.

Cinq Cases and Middle Island animals respectively. However, lack of measurements for suitable older age groups and the possibility that the ageing method declines in validity with increase in annulus number, both make the later phases of growth unclear.



IGURE 24. Successive growth increments plotted against age for two tortoises, to illustrate the year-to-year variation in growth rate.

The possibility that a single annulus is formed each year deserves re-examination in relation to growth increments. The inherent variation in the size of annuli will make it difficult to distinguish an annulus formed over a whole season from one of two formed over the same period. On the other hand, the frequent failure to produce annuli should be associated with high proportions of values which are close to zero. Inspection of figures 22 and 23 shows that up to the nine annulus class, for the Cinq Cases sample, and up to the twelve annulus class, for the Middle Island animals, the lowest value within the range of two standard deviations from the mean differs from zero by at least one standard deviation, so for these classes at least, it is very unlikely that measurements are being wrongly excluded or included because the tortoises have failed to form an annulus in a particular year. Among classes with a higher annulus number, the range of two standard deviations approaches zero, suggesting that in these age groups annuli are occasionally not formed and annulus number groups are therefore including measurements from older age groups, the assumed correspondence between annulus class and age class no longer being valid. The scale of this error need not be at all great, but evidence from tortoises of known age is needed before it can be assessed.

Some tortoises with anomalous growth of the scutes were observed. An example is illustrated in figure 26, plate 25. The majority of annuli are very closely spaced and may be so worn as to be undiscernible—the outer one or two annuli, in contrast, are very large, black and shiny. It appears that growth has been proceeding very slowly and then a spurt of growth has followed, perhaps reflecting an improvement in feeding conditions after reaching a new habitat. Animals of this kind were not seen away from the census area centering on Cinq Cases. Near Anse Cèdres, several tortoises with very narrow annuli but without the broad marginal annuli were noted. Possibly this region of champignon is the area from which the anomalous animals radiate.

Most tortoises of this type could not be aged, nor could many of the annuli be measured, but two growth patterns are compared with normal ones in figure 25.

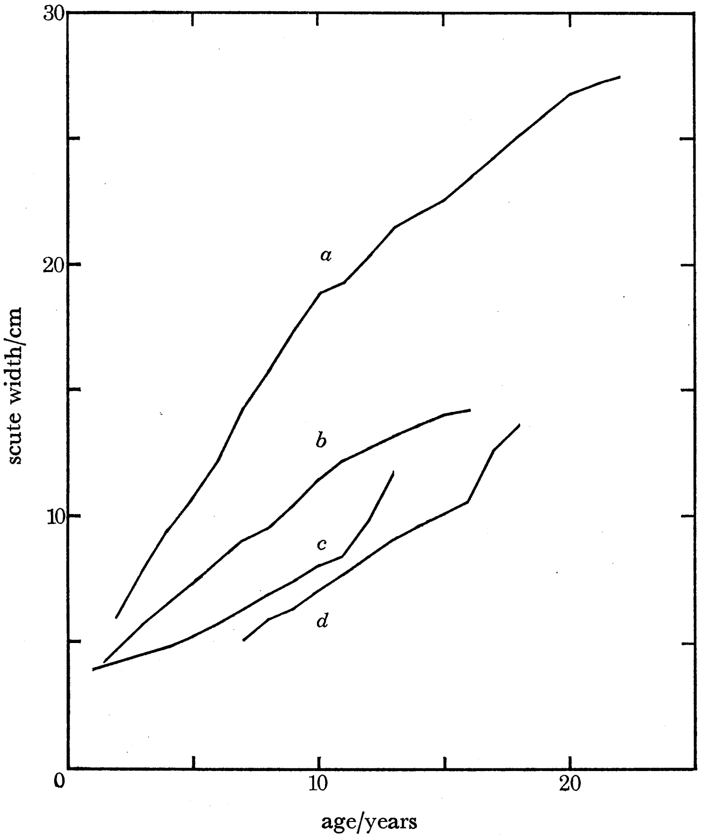


Figure 25. Normal growth curves, based on measurements of successively formed annuli plotted against the cumulative number of annuli, of (*a*) a fast growing, and (*b*) a slow growing tortoise, compared with two growth curves, (*c*) and (*d*), for animals such as the one shown in plate 25.

8. General behaviour

One of the most striking aspects of tortoise behaviour on Aldabra is the restriction of activities to the early morning and late evening, so that the animals are active over a period of 4 h or less, even to some extent on cloudy days. The subject has been carefully studied by Frazier (1968).

Giant tortoises have some well-defined fixed action patterns, but their behavioural repertoire, to be summarized below, is limited even for a chelonian. Some characteristic postures of tortoises are shown in figure 27.

In the resting position, tortoises lie with the plastron on the ground and the limbs and neck somewhat retracted. Movement is initiated by thrusting with both forelegs simultaneously and then the animal takes up a shuffling walk, with the limbs moving in an oblique plane. The large males walk with the carapace raised well off the ground and the limbs fully extended vertically.

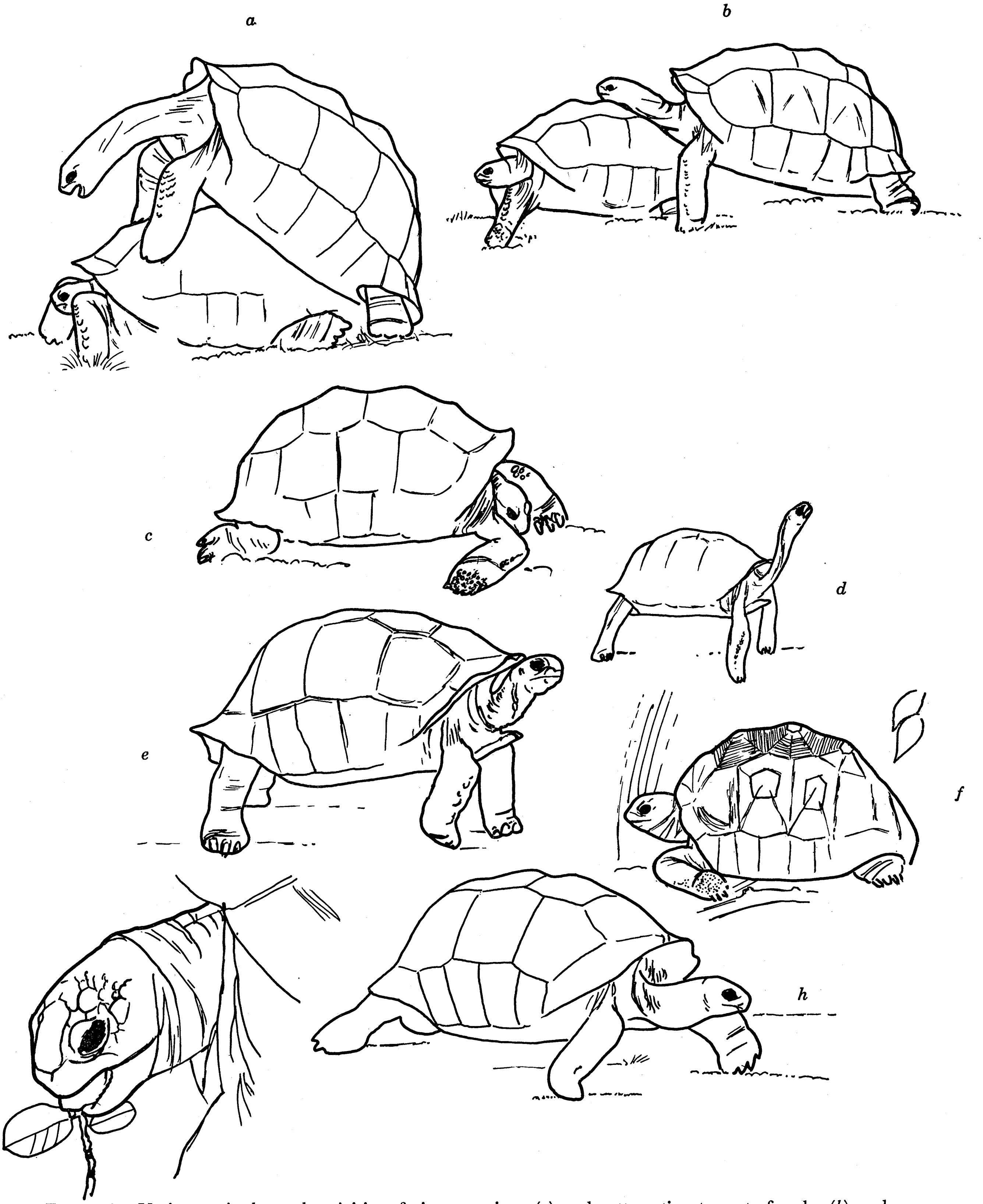


Figure 27. Various attitudes and activities of giant tortoises: (*a*) male attempting to mate female, (*b*) male attempting to mount female; (*c*) adult tortoise sleeping; (*d*) tall stretch posture; (*e*) adult male walking fully erect; (*f*) young tortoise showing typical resting position; (*g*) tortoise feeding, showing extrusion of tongue; (*h*) adult tortoise, walking, with the limbs moving in an oblique plane.

A large tortoise will quickly withdraw the head with a loud expiration if you walk up to it. It may then lie down and rest but more often walks away rapidly. If you keep advancing towards it from one side, it can be induced to move in circles. A strikingly different response can occasionally be elicited both by a direct approach and by tapping the hind legs of a recumbent individual. The animal rises slowly to its full height with the neck extended vertically and the head pointing upwards. This 'tall stretch' posture is held for some minutes before the tortoise relaxes again. A more usual reaction to tapping the rear of the carapace is for the tortoise to rise slowly on the forelegs so as to force the rear margin of the carapace against the ground. These two postures were observed in their natural context during the mating season.

Tortoises of about 30 cm carapace length or less show a passive defensive response to a sudden approach by the observer in which they withdraw the head and limbs under the carapace so that only the forearm and hind feet are exposed. The head is completely hidden, for the carpi are in contact with each other in front of it. The spines on the line of scutes that is brought up to the anterior margin of the carapace, as well as the long claws, possibly act as defensive structures. These are reduced by wear in large tortoises. The defensive posture may be maintained for several hours.

When resting small tortoises probably take up the same position, though this is not certain as they tend to seek cover before resting. Larger tortoises move into shade before resting but do not attempt to conceal themselves. When sleeping they lie with the limbs relaxed and the neck stretched out on the ground. Phases of resting are long but tortoises do not sleep during the whole period and may rise and change position or begin feeding on dead leaves. They commonly stretch the neck upwards and yawn when resting or waking.

Tortoises feed both on small herbs and on large woody plants though the very small individuals are restricted to such items as the minute 'tortoise turf' grasses, the fallen flowers of *Guettarda*, and *Bulbostylis* sp. A feeding animal thrusts its head forward, opens its mouth and extends the tongue. Then as the jaws are closed on the food the lower jaw is retracted. It is brought forward again as the mouth is opened. If the food is difficult to reach or cannot be easily ingested, the tortoise pulls on it with a sideways movement of the head, at the same time pawing past the head with one of the forelimbs. During browsing this serves to bring down a branch to within easier reach of the jaws but the action is stereotyped and is commonly made in situations where it is ineffectual, as when a large leaf becomes caught in the side of the mouth.

During browsing, a tortoise extends its neck to its full length and may gain a little height by rising on three legs, tipping the front of the carapace upwards on one side. Sometimes it rears up against a tree, supported on the lower branches by the forelimbs. It may also climb on to its companions to reach leaves. Accidents during feeding occur. One tortoise was strangled when it slipped and trapped its head in a forked branch. Three tortoises were found which had been trapped by the head in rock crevices while they searched for the small herbs growing there.

Before defaecation, a tortoise raises its hindquarters so that the tail is hanging down vertically. Although there are no special sites for defaecation, faeces tend to accumulate at rest sites. Micturition is not observed in the field, but when handled, tortoises void copious clear liquid and also defaecate.

Tortoises have no grooming or cleaning behaviour, but may occasionally draw in the head and rub it against the soft skin of the body, in an apparent attempt to relieve irritation, possibly caused by mosquito bites.

It is difficult to know whether aggregation represents any sort of social tendency among giant tortoises, for when they gather together it is always for the acquisition of some environmental resource. However, the absence of agonistic behaviour in the animals on Aldabra may be adaptively related to the high population density.

The only non-sexual social behaviour observed was 'nosing'. In this activity one tortoise walks up to another and noses the latter's head or neck, often lying down to do so. The position is held for several minutes and no explanation can at present be offered for it.

Tortoises eat their dead companions, but this cannibalism cannot be said to reflect the breakdown of some social inhibition. Rather, the stench of the rotting corpse creates an attraction which was previously absent.

9. Mating behaviour

Mating behaviour was first observed on 21 October 1967 at Dune d'Messe and then at Takamaka on 30 October, but not until mid-December, at Cinq Cases, were mating attempts noted frequently. Once, near Bras Cinq Cases, 31 mating attempts were heard or seen in a two hour period.

Mating attempts were confined to those times when the tortoises were active. Of 106 mating attempts heard or observed, only five were noted between 11h00 and 15h00 U.T. Mounting often appeared to result from casual encounters, but some males were seen mounting several times during one day, and one nosed or mounted seven animals in succession. Possibly there are phases when adult males are more active sexually than at other times during the mating season.

Mating behaviour involves males with a carapace length of 50 cm or more. Their prospective partners—not necessarily females—were between 45 and 65 cm in length in the sample of 44 measured. The normal procedure during a mating attempt is for the male animal to approach the female and, sometimes after preliminary nosing of her carapace, rise on to her with neck fully extended and tail uncurling (figure 27*b*). As soon as he is positioned on her, he pushes back with one or both forefeet so that his plastron slides down over her carapace and his tail is forced under it. The hind limbs can be raised off the ground with the force of the movement. The male then claws forward again for another thrust. Thrusts are made at about 4 s intervals and during the whole sequence, the neck of the male is fully stretched downwards towards the head of the female, and the mouth is open (figure 27*a*)—indeed on some occasions the male appears to bite at her head. The posture may be a relict of the neck-biting characteristic of the mating behaviour of some other vertebrates, and this view receives support from descriptions of courtship activities in *Malacochersus tornieri* and *Testudo graeca* (Loveridge & Williams 1957, pp. 271, 292).

With each thrust, the male emits a loud groaning roar of considerable carrying power, but if the thrust is not complete the roar is reduced to a grunt. Up to 44 thrusts are made. Usually it is clear that the penis is not erected and often the tail is not even pushed under the carapace of the female.

The female sometimes responds to the mount of the male by attempting to walk off, thus dislodging him. More often she 'jacks' herself up on the forelegs, with the head somewhat withdrawn. This action forces the rear margin of her carapace into the ground and effectively prevents the male achieving intromission. Clearly it is the same response as is elicited by tapping a resting tortoise on the rear of the carapace.

Inappropriate mounting positions are sometimes adopted, in which males rise from the front or side of their partners. One male was observed to mount a corpse while another tortoise fed on the latter.

The most striking aspect of the mating attempts observed was their lack of success. Only very rarely were females seen in a relaxed posture while the male attempted to mate. In the apparent absence of sign stimuli indicating a readiness for mating, a strong libido in the male may be necessary for mating to be achieved efficiently. What was apparently a successful copulation was observed on 22 January. A male of 80 cm carapace length roared and thrust 16 times over a 60 cm female. He next rested on her with his neck outstretched, then grunted and retreated by moving back and to one side over the female, groaning as he did so. Ejaculation probably occurred during the resting phase, as Frazier (1968) confirmed in other cases.

Although the mating activity of males appeared to be promiscuous, there was in fact an element of selection in their choice of prospective partners, even though these occasionally proved to be males also. In only three out of 44 cases where mating partners were measured had the male selected a mate larger than himself. Rutting animals also did not attempt to mount tortoises of less than about 45 cm carapace length, even though these made up as much as 40 % of the local population.

A further conspicuous feature of the mating season was the absence of the aggressive butting behaviour described for instance in *Testudo graeca* and *Geochelone pardalis* (Loveridge & Williams 1957). Only one agonistic fixed-action pattern was observed and this on only two occasions In one instance, two males were seen standing in the 'tall stretch' position, but they soon relaxed and separated. In the second case, a male adopted the same posture when another male walked past him to mount another tortoise. Frazier (1968) considers a similar action in Galapagos tortoises to be a threat display.

10. Tortoise activities and the ecological diversity of Aldabra

Although tortoises move from one habitat to another, their activities in each plant community are best considered separately. Stoddart & Wright (1967) classified habitats on Aldabra into four broad categories—champignon, platin, mangrove and dune—but a finer classification is convenient here, although not every plant community and its possible relevance to tortoise ecology will be considered.

An assessment of vegetation types in the chief study area, including the area of the census, is illustrated in figure 28.

(*a*) Pemphis *scrub*

Dr Fosberg drew the attention of Expedition members to the smooth nature of platin outcrops. Tortoises are abundant on the platin and their trampling and scoring has apparently led to significant abrasion of the limestone. In champignon the rock is so finely crenelated and pinnacled that it is clear that the tortoises exert no erosive influence in this habitat. Indeed they were never observed in the pure stands of *Pemphis* which cover the rougher areas of champignon in the vicinity of Cinq Cases.

(*b*) *Mangrove swamp with* Rhizophora, Bruguiera *and* Ceriops

Tortoises similarly were not seen in this habitat, even where there appears to be free access to the mangroves and the trees are sufficiently spaced to admit progress between them.

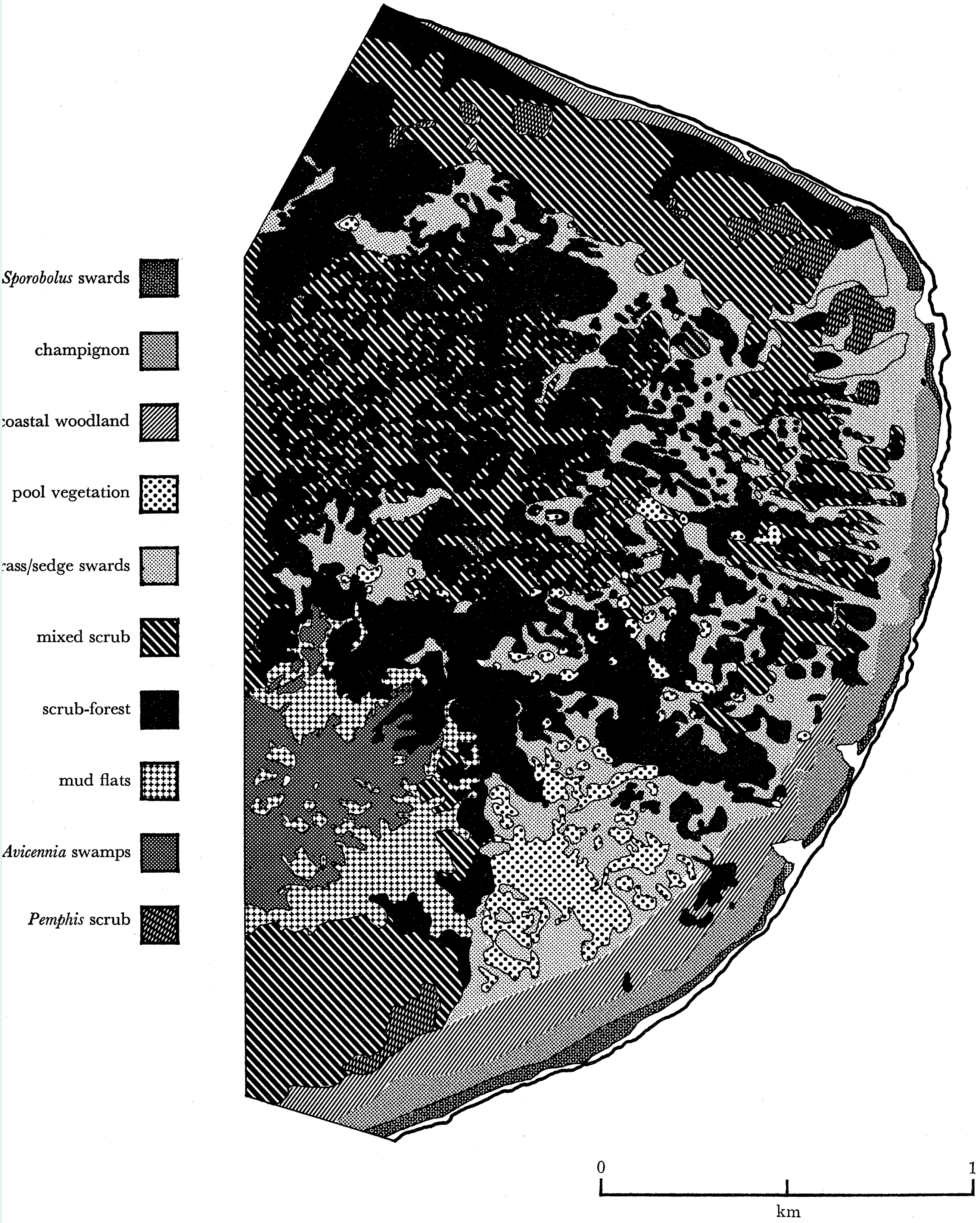


FIGURE 28. Map of the easternmost sector of South Island showing the distribution of vegetation types. This map is provisional and simplified. For instance, the large zones of 'mixed scrub' to the north and to the southwest should perhaps be designated as several separate categories. The segregation of 'grass/sedge sward', 'scrub-forest' and 'mixed scrub' has been somewhat arbitrary, except towards the coast, where these vegetation types are quite discrete from each other. Vegetation which may be described as 'sward, with trees' has been allocated to either sward or scrub-forest, again in a somewhat arbitrary manner. The area under the category of 'pool vegetation' is probably completely flooded for a period each wet season. *Pandanus* and *Guettarda* woodland are included under 'coastal woodland'.

(*c*) Avicennia *swamp and associated mud flats*

Extensive open forests of *A. marina* occur at Bras Cinq Cases and are backed on the landward side by wide mud flats. Most of the trees are about the same size, and may be about 50 years old, judging from a single count of growth rings. The pure stands are flooded regularly but it appears that the mud flats remain emersed for most of the year. No food or other obvious goal is in sight on the flats but there is a continuous traffic of tortoises across them and the tracks of the animals are very conspicuous. They visit the swamps where again they are abundant. At the fortnightly high tide, they rest on rocks or the bases of *Avicennia* trunks and swim freely from one rest site to another. They become more active as the swamp dries out, though where trees are more widely spaced, mud wallows—each usually centred around an *Avicennia* bole—are in regular use. The leaves of the *Avicennia* trees are generally inaccessable to tortoises and only once was a tortoise seen feeding from a branch which it had torn down itself. Feeding on filamentous marine algae dredged from shallow water and from the algal scum scraped from rocks was seen more frequently. These seem very inadequate food sources, and of more significance are the seeds or germinating seedlings of *Avicennia* with their very thick cotyledons. The tortoises collect to feed on these where they have been left densely packed in drift lines by the receding tide. The fruiting season of *Avicennia* is limited to the first few months of the year, so it is not clear what attracts the tortoises to the swamps at other times.

Most tortoises in the *Avicennia* swamps are large and the proportion of males that can be reliably identified as such is high (29 out of a sample of 89). During a period of rain with overcast sky in February and March 1968, there appeared to be a peak of sexual activity in the area, with up to four or five males attempting to mate within earshot at any one time during the day. Whatever factors induce the larger tortoises to cross several hundred metres of open mud to visit the *Avicennia* forest, the resultant concentration of mature individuals leads to an encouragement of mating activity.

(*d*) *Dunes and beaches*

Along the coast of South Island, tortoises utilize sedge and grass swards for food and resort for shelter to small woods lying to the leeward of elevated dunes, or to strips of *Scaevola* or *Suriana* scrub in intervening areas.

The activity pattern of tortoises on the dunes is easily observed. The reptiles emerge from shelter in the late afternoon and disperse over the *Sporobolus* swards, commencing to feed as they go. Although a few individuals do not come out to graze, feeding generally continues till dark and the animals rest in a sleeping posture wherever they happen to be until dawn. According to Dr Lowery, there is some feeding during moonlit nights. At dawn grazing is resumed for a few hours before the tortoises begin seeking shelter. Where shelter sites are isolated the activities of the tortoises are focused in a spectacular manner around particular shade trees, towards which hundreds of animals can be observed streaming at about 10h00 U.T. They concentrate in the small areas of shade available. For instance under one dead wind-blown *Guettarda*, over 130 large tortoises were counted at one time. They were stacked double or propped up almost vertically against each other and the whole mass of animals moved as the shadow of the tree shifted with the movement of the sun.

In the absence of shelter from vegetation tortoises attempt to shade themselves by digging under tree trunks washed up onto the shore or into the sand at the margin of the dune swards. Smaller tortoises ensconce themselves in niches amid the coastal champignon and those that do so regularly are heavily scored by the rock. Where these niches afford the only available shelter, only small animals occur in the area and the size distribution of the local population is thus exceptionally low.

The failure to reach shelter at a critical period leads to distress or death. Several tortoises were observed suffering from heat stroke. The animals foamed at the mouth and frequently threw back the head against the carapace, opening and shutting the mouth. One made immediately for my shadow on sighting me.

Mortality of tortoises along the coast is associated with prolonged exposure to the sun. There was also a higher mortality during the later part of the study period than was evident in October 1967, suggesting other factors are also involved. The dead animals were mostly small individuals (30–40 cm carapace length), perhaps susceptible to more rapid heat exchange. Their remains are consumed not only by hermit crabs but also by other tortoises.

One obtains an exaggerated impression of the extent of mortality for the bleached carapaces, at least of the larger individuals, remain intact for several years and are prominent along the coast of South Island.

The activity patterns of tortoises on the dunes are discussed fully by Frazier (1968).

The various dune swards are each dominated by a single species. These are *Sclerodactylon macrostachyum*, *Sporobolus virginicus* and *Cyperus ligularis* and they occur in that order from the beach inland. This kind of distribution is considerably altered at elevated dunes, where there is no discernable pattern. Sparse *Fimbristylis cymosa* swards and patches of *Lepturus repens* are also present on the dunes but cover relatively small areas.

Along much of the coast *Sporobolus* is dominant to the exclusion of other grasses or sedges. This grass is the favourite food of tortoises in the area and only on swards of this species do they graze gregariously. Grazing reduces the swards to an extremely short and sparse turf.

The situation is different between Anse Takamaka and Cinq Cases, where the *Sporobolus* swards are isolated on the coast by a 300 m wide strip of rough champignon and shelter sites for tortoises are small and few. The latter are rarely seen here and in the absence of grazing, *Sporobolus* grows into a thick cushion with much dead material retained on each shoot below the green leaves.

Grazing on *Fimbristylis* and *Cyperus* was not noticed on the coast, but *Sclerodactylon*, in spite of its sharply pointed leaves, is locally stripped down to the base of the tussock, even though in most areas it is apparently uninfluenced by the activities of tortoises. *Sclerodactylon* spreads by arched runners, yet the border between it and swards of *Sporobolus* is so well defined that it is possibly maintained by the heavy cropping of the latter grass. I do not agree with Stoddart's (1968) view that *Sclerodactylon* is invading the *Sporobolus*. The creation by the tortoises of the very flat swards of procumbent *Sporobolus* plants provides suitable feeding and roosting ground for Great Sand Plovers (*Charadrius leschenaultii*) and curlew sandpipers (*Calidris testacea*), flocks of which were present at, for example, Dune Jean-Louis from August through to March.

Of the dune trees, *Guettarda* shows a prominent browse line and tortoises were often seen feeding on it. *Suriana* also shows a browse line but the procumbent branches of *Tournefortia* with their large tomentose leaves are left alone even though the dried fallen leaves are sometimes eaten. Patches of *Scaevola* also appear unscathed, though the leaves are occasionally consumed.

Although part of the southern coastline of Aldabra consists of a pinnacled cliff of champignon, there are other areas where the open sand seaward of the grass swards is succeeded by a smooth platform of limestone shelving into the sea above which lines of debris thrown up by the surf can collect. Tortoise tracks are conspicuous in all sandy areas but in these places there is access to the sea and tortoises were observed scavenging on pieces of *Sargassum*, *Turbinaria* and other algae in the drift lines.

A conspicuous association exists between land hermit crabs and tortoises. The crabs (mostly *Cœnobita rugosus*; also *C. perlatus*) feed on tidal debris but where none accumulates, they depend largely on tortoise dung for food and converge rapidly on any fresh faecal matter and quickly dismember it. They also feed on the carcasses of tortoises and use the same shelter sites as the reptiles, burying themselves under leaf litter and exposed roots. Two to three hundred could be found under each *Guettarda* tree.

Tortoises on the dunes have ready access to other habitats—either a complex scrub community of dwarfed windblown trees (e.g. at Dune Jean-Louis) or a very sparse herb community on champignon, with adjacent pothole vegetation and *Guettarda* woodland.

(*e*) *Coastal champignon and woodland*

At places where South Island is only 1 km wide, the dunes are quite sharply demarcated from the wind-blown lines of scrub which occur inland. As one proceeds eastward and the island broadens, *Guettarda* woods with fully developed trees begin to differentiate. These woods together with patches of scrub-forest become isolated from the dunes by a broad belt of champignon, almost bare of woody plants.

A seaward band of this champignon is more elevated and especially pinnacled and dissected, forming from Cinq Cases northwards a series of small cliffs. These mark the 8 m ridge (Stoddart 1968) and this region carries a varied scrub flora confined to deep potholes or the labyrinths between coral limestone pinnacles. *Acalypha* dominates, but *Ficus*, *Dracaena*, *Guettarda* and many other woody species are present and eaten by the tortoises wherever accessible. In their efforts to feed, a number of animals fall into the holes. Not all are killed—one adult male was found with the front of the plastron broken after such a fall. Though extremely light in weight from starvation, he had been shaded by the trees in the pothole and had not died from heatstroke.

The less dissected areas of champignon also have a characteristic flora—one of small herbs, confined to solution holes and fissures, with occasional patches of 'tortoise turf' where small pans of soil have accumulated in depressions. The herbs are eaten to the ground by tortoises and only grow to their full size in inaccessible crevices. Those of most significance in the diet of the tortoises are *Boerhavia*, *Evolvulus*, *Hedyotis*, *Hypoestes*, *Lagrezia*, *Phyllanthus*, *Ruellia* and *Sida* (see table 3).

In dwarfed form, the fern *Acrostichum aureum* dominates extensive areas of coastal champignon. It occurs in one locality with extremely abundant *Ficus avi-avi* saplings. Since tortoises normally devour *Ficus* leaves and branches with relish, it is concluded that the absence of shade for the reptiles was the chief factor allowing the community to develop in the area.

Densities of tortoises in the champignon were as low as 14 and 7 per hectare in two samples, but could be greater (up to 77 per hectare) where there was shelter nearby.

Inland from the open champignon is the strip of open woodland dominated by *Guettarda speciosa* and mostly well marked off from other communities. North of Cinq Cases this region becomes less defined, with increasingly abundant thickets of *Pandanus* and encroachments of tall scrub forest. The *Guettarda* woodland appears to offer an optimum habitat for tortoises. They are very abundant (100 or more per hectare) and at midday can be noted in numbers of 20 or so under every tree. The ground cover is virtually restricted to scattered patches of 'tortoise turf' in which the small grass *Eragrostis* sp. is often dominant. This turf is confined to rock depressions and rarely forms extensive patches within the woodland itself. The turf and the *Guettarda* trees provide the main forage for the tortoises. Every tree shows a very well-marked browse line. There is virtually no sign of regeneration of *Guettarda* and the few saplings seen emerged from rock prominences or were outside the woodland zone altogether in the less hospitable mixed scrub. Clearly the tortoises are hindering the maintenance of these woods—not a leaf falls, but it is immediately consumed. Sheltering under the trees tends to expose the roots while browsing on low branches has created swollen calluses on many trees. However, no direct influence of tortoises can explain the high mortality of *Guettarda* trees along the coast, and long-term climatic fluctuations may be involved.

TABLE 3. LIST OF HERBS, GRASSES AND SEDGES ON WHICH TORTOISES HAVE BEEN OBSERVED FEEDING

(*a*) herbs

Bacopa monnieri
Boerhavia elegans
Cassia aldabrensis
Euphorbia prostrata
Evolvulus alsinoides
Hedyotis sp.
Hypoestes aldabrensis
Lagrezia madagascariensis
Mollugo spergula
Naias sp.
Nesogenes sp.
Phyllanthus maderaspatensis
Pleurostelma cernuum
Plumbago aphylla
Portulaca sp.
Ruellia monanthos
Sida parvifolia
Solanum nigrum
Tephrosia pumila
Wedelia sp.

(*b*) sedges

Bulbostylis sp.
Cyperus dubius
C. ligularis
C. obtusiflorus
Fimbristylis cymosa
F. ferruginea

(*c*) grasses

large *Eragrostis* sp.
small *Eragrostis* sp.
Lepturus repens
Panicum sp.
Sclerodactylon macrostachyum
Sporobolus virginicus

(*d*) bryophytes

Ricksia sp.

The thorny bush *Solanum aldabrense* grows abundantly among the *Guettarda* woods. The leaves and stems of this plant are not eaten, but both fruit pigeons and the tortoises feed on the orange berries. The seeds were found in tortoise faeces, though it is not known whether passage through the digestive tract facilitates germination as is the case with the related *Lycopersicum* sp. and the Galapagos tortoise (Rick & Bowman 1961).

(*f*) *Freshwater pools with* Thespesia *and* Lumnitzera *woods and* Pandanus *thickets*

Lumnitzera racemosa or *Thespesia populneoides* with *Fimbristylis ferruginea* are the characteristic species growing by freshwater pools. *Lumnitzera* often grows in water, but the other two form small woods on dry ground.

Tortoises are not abundant either in *Lumnitzera* or *Thespesia* stands, usually only single animals being found sheltering there. *Lumnitzera* is never eaten by tortoises. It often shows a browse line but this is only about 10 cm above mud level and apparently caused by land crabs (*Cardisoma carnifex*). Regeneration of *Lumnitzera* is evident but dwarfed plants are present as well, so that the two may be confused—in any case tortoises do not appear to influence the species.

Thespesia leaves, on the other hand, are taken, but even in areas where tortoises are especially abundant, no browse line is evident and young trees are common, suggesting that there is a steady regeneration in progress, unimpeded by browsing. Fresh and dried fruits of *Thespesia* are however eaten regularly. In the process of digestion, the dry seeds are released from enclosing fibres but are present unharmed in tortoise faeces. Here they are liable to attack by an extremely abundant red and black bug, *Dysdercus fasciatus*, and up to ten nymphs can commonly be seen sucking at a single seed.

Some of the largest *Pandanus* thickets are also associated with freshwater pools, and the *Pandanus* forests along the south coast often enclose small pools or patches of wet mud. The robber crab *Birgus latro* is abundant in these thickets and climbs to feed on the ripe fruit of the *Pandanus*. Tortoises eagerly consume the fallen fruit and can then compete with the crabs—once I saw a crab excluded from access to a fallen *Pandanus* fruit by the mere number of tortoises trying to feed on it. The only instance of direct competition for food between tortoises was seen in such circumstances. The animals pushed on each other in an attempt to reach the fruit and one rammed its companions. No other agonistic behaviour was observed.

Pandanus leaves are occasionally eaten to the base and tortoises have almost destroyed some young plants, but generally the spiny fronds are ignored.

The large fern *Acrostichum aureum* occupies some of the smaller platin sink holes. Tortoises very rarely feed on *Acrostichum* and it must be added to the list of plants associated with surface water which are unaffected by tortoise activity.

In November 1967, the pools were filled by rain, though they dried out gradually over the subsequent months. Following the rain, a rich algal flora built up in the less saline pools, together with the monocot *Naias*. The plants proved especially attractive to the tortoises which waded into the pools and dragged up sheets of this aquatic vegetation. The habit of the animals of wallowing and defaecating in pools probably contributed to the production of the 'bloom' of submerged plants, with its associated insect fauna, poor in species but especially rich in numbers (notably a corixid and a large dytiscid). Drying up of some pools at times proceeded so rapidly that the freshwater fauna became trapped in very small bodies of water and attracted groups of turnstones (*Arenaria interpres*) and reef herons (*Egretta garzetta*). The mud flats left behind were colonized by an ephemeral vegetation of *Mollugo spergula* and *Bacopa monnieri* which in this next stage of a succession again attracted the grazing of the tortoises. Apparently the final stage in the sequence was the conversion of the sward into a tortoise meadow, the initial colonist often being *Euphorbia prostrata*, which also colonized eroding tortoise meadows and was consumed by the animals themselves.

Pools are perhaps most important to the tortoises as places in which to wallow, and all recent visitors to Aldabra (see Stoddart & Wright 1968) have remarked on the large numbers that may be observed half-submerged in the pools at Takamaka or near Anse Cèdres. In the neighbourhood of Cinq Cases it appeared to the author that the largest concentrations of tortoises at a particular pool occurred towards evening, at a time when the value of wallowing for heat exchange would be least.

(*g*) *Platin*

Most of the eastern sector of South Island consists of platin, identified on geomorphological grounds (Stoddart & Wright 1967) and vegetationally a complex community-system of scrub-forest, mixed scrub and open grass and sedge swards.

These vegetation types are most distinct towards the coast. Here rocky spurs, convex in cross-section, run inland from small cliffs formed at the seaward margin of the 8 m ridge. Vegetational zonation reflects slight variations of altitude on these spurs. Their crests are almost bare of shrubs, except for stunted *Maytenus*. Here small tortoises, less than 40 cm in carapace length, are abundant, but larger ones not common. Lower down the slope, windblown lines of dwarf bushes (*Polysphaeria*, *Maytenus*) appear and develop into a thick scrub up to 2 m high, sometimes smothered by *Cassytha*. *Guettarda* saplings are occasionally present and are certainly much commoner than in the *Guettarda* woodland itself, a reflexion of the paucity of tortoises in the scrub. At the bottom of the ridges, there are lines of scrub-forest, 5 m or so high, often in association with pools. This forest provides plentiful shade, unlike the mixed scrub, and is used for shelter by the tortoises. Beyond the scrub-forest are patches of sedge sward (mainly *Cyperus ligularis* and *Fimbristylis cymosa*) in the flat areas between the ridges.

Further inland, this ideal pattern breaks down and the distinctions between the habitat types are less clear. Areas are often composed of a mosaic of plant communities together with the vegetation associated with solution pans.

The mixed scrub became very dry during the latter half of the study period. The dominant woody plants (*Maytenus*, *Mystroxylon*, *Polysphaeria*, *Ochna*, *Apodytes*) are not the most favoured forage plants, pools are absent, the density of the scrub gives no opportunity for the development of sward and shade is not adequate. For these reasons, the most extensive areas of scrub have few tortoises, at densities of as low as 5 per hectare.

In the scrub-forest no species can be classed as dominant, except occasionally for *Ochna*. The trees and bushes of the mixed scrub are all present, often growing to a large size, but many other species are abundant and species composition varies locally. Tall scrub-forest, with for instance, *Ficus nautarum*, *Pandanus*, *Premna*, *Flacourtia*, large *Apodytes* trees, *Terminalia* and *Sideroxylon*, is often so dense that it has no ground flora at all, and is at times virtually impenetrable. Forests of lower trees with fewer low branches are more easily traversed, perhaps by tortoises as well as by man, but they tend to be dominated by 'mango', *Ochna ciliata*. This small tree produces a dense leaf litter, again hindering the development of a ground flora on which tortoises can feed.

Tortoises become more abundant with increasing diversification of the habitat, for instance where the scrub-forest is broken up into blocks of small trees, each block often being associated with a pool or at least a depression in the platin, and the intervening open ground is occupied by sparse scrub and often extensive grass as well as sedge swards. Such an arrangement is typical of the platin. Tortoises use the forest blocks as shelter sites and the swards as feeding grounds. Within the forest they also forage on dead leaves, apparently selecting some and ignoring others. Feeding on leaves is not so intensive as to hinder the development of leaf litter, as in the *Guettarda* woods, and very few tortoises are to be seen feeding on leaves at one time, in contrast to the large numbers which can be found grazing in the early morning or late evening. Grazing schedules on the platin are similar to those on the coast.

Population density on the platin averages about 30 tortoises per hectare. It is at its greatest where there are trees growing somewhat sparsely on open tortoise turf in lines or groves oriented towards the northwest by the trend of the Trade Winds. Common species here include *Ochna*, *Erythroxylon*, *Mystroxylon*, *Maytenus*, *Polysphaeria*, *Terminalia*, *Ficus thonningii*, *Sideroxylon*, *Allophyllus*, and *Phyllanthus cheloniphorbe*. *Clerodendrum*, *Pithecellobium*, *Commiphora*, *Azima*, *Thespesia* and *Tricalysia* are also present. There may be more than 100 tortoises per hectare in these groves.

Table 4. Woody plants and large herbs and their relevance to the diet of tortoises

The presence of a conspicuous browse line indicates that tortoises regularly browse upon the tree in question, and in most cases this was confirmed by direct observation. The species are listed alphabetically.

species	comments
Acalypha claoxyloides	conspicuous browse line
Acrostichum aureum	does not exhibit effects of browsing; leaves very rarely eaten
Allophyllus alnifolia	conspicuous browse line
Apodytes dimidiata	no browse line; eaten rarely
Avicennia marina	no browse line (habit unsuitable); leaves rarely eaten; fallen fruit eaten
Azima tetracantha	conspicuous browse line
Calophyllum inophyllum	cut leaves eaten but mostly ignored
Capparis cartilaginea	rarely shows effects of browsing; rarely eaten
Cassytha filiformis	not eaten
Casuarina equisetifolia	no browse line; not eaten normally; dry needles occasionally eaten
Clerodendrum glabrum	conspicuous browse line
Cocos nucifera	not normally eaten
Colubrina asiatica	does not exhibit effects of browsing; eaten rarely
Commiphora marchandii	conspicuous browse line
Cordia subcordata	leaves eagerly eaten
Dracaena reflexa	shows effects of browsing; leaves eaten
Erythroxylon acranthum	no browse line (habit unsuitable); not eaten
Euphorbia abbotti	no browse line (habit unsuitable); leaves eaten when offered to tortoises
Ficus thonningii, F. avi-avi, F. nautarum	conspicuous browse line in all species; branches as well as leaves eaten
Flacourtia indica	may show browse line; saplings heavily stunted by browsing
Grewia salicifolia	conspicuous browse line
Guettarda speciosa	conspicuous browse line and calluses; fruits, branches, dead and fresh leaves and flowers eaten
Lomatophyllum borbonicum	not eaten
Lumnitzera racemosa	not eaten
Macphersonia madagascariensis	no browse line; not eaten
Maillardia sp.	no browse line (habit unsuitable); browsing only recorded once (species confined to Takamaka)
Maytenus senegalensis	no browse line; eaten rarely
Mystroxylon aethiopicum	no browse line; eaten rarely
Ochna ciliata	no browse line (habit not suitable); fruit eaten and flushing leaves occasionally eaten
Pandanus tectorius/balfourii	may show effects of browsing; leaves occasionally eaten; fruit and male flowers eaten
Pemphis acidula	may show indistinct browse line and calluses; not normally eaten
Phyllanthus casticum	conspicuous browse line
P. cheloniphorbe	conspicuous browse line
Pisonia grandis	conspicuous browse line
Pithecellobium ambiguum	not eaten; no browse line
Polysphaeria multiflora	rarely, a conspicuous browse line; eaten, but not frequently
Premna serratifolia	conspicuous browse line
Scaevola taccada	rarely a conspicuous browse line; not normally eaten
Scutia myrtina	no browse line; not eaten
Secamone fryeri	not eaten
Sideroxylon inerme	no browse line; not eaten
Solanum aldabrense	only ripe fruits eaten
Suriana maritima	apparent browse line but eaten rarely
Terminalia fatrea	conspicuous browse line
Thespesia populneoides	no browse line; mature or developing fruits eaten and flowers eaten; leaves rarely eaten
Tournefortia argentea	no browse line; only dead leaves eaten
Tricalysia cuneifolia	feeding on this species only recorded once

(*h*) *Browsing and its effects on vegetation*

Some of the herbs of the champignon are present in the open platin woods, but they are usually much scarcer here. Effectively the plants in the platin are either grasses and sedges or tall woody plants, including creepers. The relevance of woody plants to the diet of tortoises is summarized in table 4. Some species are readily eaten and if of suitable habit show a conspicuous browse line about a metre from the ground. *Allophyllus*, *Azima*, *Clerodendrum*, *Commiphora*, *Dracaena*, *Ficus* spp., *Flacourtia*, *Grewia*, *Guettarda*, *Phyllanthus* spp., *Premna* and *Terminalia* belong in this category. Isolated *Scaevola* and *Pemphis* trees have browse lines where they grow in the platin and the latter show calluses as well. Where they form pure stands these species appear unaffected by browsing though in such places tortoises are not common in any case. Other species are not browsed on regularly, but among these *Ochna*, *Euphorbia abbotti* and *Erythroxylon* have few or no low branches, so that their susceptibility to browsing is not readily assessed. Some foliage is never eaten at all—*Scutia* perhaps because of its armature of recurved spines, but *Sideroxylon* for no apparent reason. A tortoise was observed to reject dry *Sideroxylon* leaves after taking them into its mouth. Unpalatable trees and bushes and creepers can be grouped together in a list contrasting with the previous one and including *Apodytes*, *Cassytha*, *Erythroxylon*, *Euphorbia*, *Maytenus*, *Mystroxylon*, *Macphersonia*, *Ochna*, *Pandanus*, *Pithecellobium*, *Polysphaeria*, *Scutia*, *Secamone*, *Sideroxylon*, *Thespesia*, possibly *Tricalysia* and perhaps *Canthium*, *Gagnebina*, *Triainolepis*, *Psychotria*, *Tarenna* spp., *Eugenia* and other scrub-forest trees as well, but these latter species were only rarely observed. It is remarkable that so many woody plants on the platin are unattractive to tortoises.

Branches of *Pandanus* are readily eaten once they are cut down, and similarly dry coconut fronds introduced from an area where neither they nor the fresh leaves were eaten, were eagerly consumed. Tortoises attempt to eat all manner of items, from tin cans to tent flaps, and their natural selectivity may be coupled with an attraction to unfamiliar objects including the above-mentioned foliage.

The influence of tortoises on regeneration in the platin can be considerable. Saplings of *Ficus thonningii* and more especially *Flacourtia* are stunted by repeated browsing. In regions where the platin is very open, very few saplings are found and no seedlings can be located at all.

However, in more densely forested areas *Ochna* especially is regenerating conspicuously and seedlings were observed in very large numbers, in spite of the fact that tortoises will eat the flushing leaves. Seedlings of *Polysphaeria*, *Allophyllus* and *Apodytes* were also seen in abundance and locally at least tortoises exert no effect on regeneration.

(*i*) *Grazing and its ecological impact on the platin*

The dominant and most abundant plant of the ground flora is often the sedge *Fimbristylis cymosa* which occurs in mosaics with the 'tortoise turf'. Roughly speaking, the greater the area of a particular open sward, the less is the proportion of it which is covered by this sedge. The plant was green only after the rains in November, when tortoises fed on it to some extent and were seen systematically plucking the flower heads. Generally grazing hardly affects *Fimbristylis* at all, and other more shade tolerant sedges are similarly little eaten.

The chief food plants of tortoises on the platin are the small herbs which contribute to a distinctive plant community termed here 'tortoise turf'. The importance of this as a source of fodder may be gauged from the sample counts listed in table 5, from which it may be seen that between

50 and 85 % of tortoises observed feeding will be eating the plants of this turf. The community consists of minute grasses, herbs and bryophytes growing on a deposit of friable soil amid outcrops and isolated slabs of coral limestone. The soil has an extremely flat surface, giving the impression of being an alluvial deposit.

TABLE 5. PERCENTAGES OF TORTOISES IN SAMPLE COUNTS FEEDING ON DIFFERENT VEGETABLE MATERIAL

The records were obtained by carefully observing as many feeding tortoises as possible and recording what they were eating. In the October counts at Takamaka, the Takamaka grove was included, hence the high percentage of animals feeding on dead leaves. In the December count this area was excluded.

	percentages of tortoises observed feeding on different plants				
				Cinq Cases	
source of food	Takamaka, October	Anse Mais, October	Takamaka, December	open champignon, March	open platin, March
plants of tortoise turf	59	0	51	75	85
dead leaves	25	0	0	0	0
large *Eragrostis* species	0	58	0	0	0
other plants	16	42	49	25	15
	total numbers of tortoises observed				
	163	77	240	167	130

The plants of the community include the often sun-blackened grasses *Eragrostis* sp., *Dactyloctenium pilosum* and *Panicum* sp. (figure 33, plate 25). The last named is the most abundant species of the community though in some localities it is replaced entirely by the small *Eragrostis*. The herbs to be found in champignon holes occur with the tortoise pasture where loose stones or outcroppings of coral rock provide shelter. The minute sedge *Bulbostylis* sp. and the liverwort *Ricksia* sp. appeared in the pasture following the November rain but both became dry and went brown during the droughts of March and April.

The tortoise turf is maintained by the grazing activity of the reptiles themselves. The prostrate form of the grasses in the sward is a direct reflexion of grazing. It appears that virtually all other plants are excluded from the sward and only these resilient species can survive. Exclosures were built in the hope of studying the effect of a relaxation of grazing pressure. Owing to the dry conditions prevailing in the short period available for study, no significant effect was observed except that *Panicum* sp. began to grow more erect and flowered where it was shaded by stakes marking the exclosures.

Where the vigorous *Fimbristylis cymosa* occurs in small patches in the tortoise turf, it is grazed very close to form a compact cushion. It is likely that its complete colonization of the tortoise turf is being held back by grazing, for tortoises graze very close to the ground right up to the tussock bases of the sedge. *Fimbristylis* is often dying off in the neighbourhood of the tortoise turf, with the dead tussocks being scattered by the wind. It is not clear whether grazing accounts for this phenomenon.

Tortoises are in part directly responsible for the degradation of their habitat. So minute and prostrate are the grasses on the swards that the tortoises inevitably ingest soil as they feed. When one considers their great population density, it is apparent that trampling of the soil during grazing must have a considerable direct erosive effect. In addition, tortoises tumble weathered coral fragments over the soil while they walk, further extending their erosive influence.

The dry conditions on the platin during much of the study period restricted the growth of the sward grasses and heavy grazing by the tortoises further prevented them from forming a continuous turf; in most localities, much dry earth was directly exposed. This led to a peculiar sensitivity of the sward to erosion. Heavy rain tended to redistribute pebbles, soil and plant debris. It may have accounted for the terraced appearance of the sward, which forms flat circumscribed patches—each patch at a slightly different elevation from the next—amid the platin outcrops. Wetting and drying of the sward led to cracking, and peeling of the surface, especially in association with crusts of blue-green algae. In a number of localities sheet erosion of the turf was in progress, and the recolonization of old eroded tracts of turf by grasses and *Euphorbia prostrata* was also observed. Any high wind tends to carry clouds of reddish dust off the platin. The best developed tortoise swards lie fully exposed in the track of the southeast Trades but the direct effect of these winds was not studied during the expedition.

Tortoises occasionally dig into the miniature cliffs at the margins of erosion pans, where in any case the soil is readily dispersed. Where erosion has been initiated at a pool margin, the platin rock about the pool is often bared for many square metres and the original earth and vegetation are represented by 'islets' of material isolated on bare limestone. It is possible that wind erosion as well as the action of water accounts for the great area of some of the solution pans.

Tortoises also dig into the turf under trees, in some cases exposing the roots. This activity may contribute to tree-fall in the more open areas of platin where there are virtually no seedlings or saplings. In the absence of regeneration, the direct and indirect effects of the tortoises would seem to involve a progressive and continuing degradation of the habitat, rather than the maintenance of a steady state. It must be emphasized, however, that the areas apparently uninfluenced by tortoises are very extensive and that the impact of wind, desiccation and salt spray on the vegetation appear to be far greater than any biotic effect.

(*j*) *Associations between animals on the platin*

Tortoises exploit the same woody plants as do the frugivorous birds, the Bulbul *Hypsipetes madagascariensis*, and the Blue Pigeon *Alectroenas sganzini* (and the latter comes in direct contact with the reptile where both feed on the berries of *Solanum aldabrense*). More explicit relationships with other animals can be observed on Aldabra. The gecko *Phelsuma abbotti* was often observed lying on tortoises resting in shade. Occasionally one stalked tabanids across a carapace or leapt from one tortoise to another. The association with the tortoise has been described as a symbiosis by Stoddart & Wright (1967). These observers saw the gecko feeding on mosquitoes (*Aedes fryeri*) which themselves were feeding off the tortoises. Mosquitoes were not observed in any great abundance during phase I to III, probably because of the relatively dry conditions that season, although clouds of the insects were seen above the heads of tortoises on a day visit to Anse Mais on 3 December, towards the end of a period of rain.

It is possible that the tortoise carapace offers a smooth warm surface facilitating heat exchange, but as the lizards are strictly arboreal, they probably wander from low branches on to the tortoises by chance except when specifically attracted by biting flies. They also climb over camp furniture and equipment. In contrast the skink *Ablepharus boutonii*, which is terrestrial, was seen only twice running over the backs of tortoises.

The giant land crab, *Cardisoma carnifex*, is the most conspicuous companion of the giant tortoise in the platin, though its local abundance varies in a different manner from that of the reptile. The crabs are especially common round the margins of solution pans, but are also to be found lying apparently amicably with tortoises under their rest trees. They occasionally collect to feed on fresh tortoise faeces but never depend on them in the same way as does *Coenobita rugosus*. Tortoises eat the bodies of *Cardisoma* (or *Birgus*) when these are offered to them and they scavenge on crabs in berry dying on the dunes. The pereiopods of the relatively scarce *Cardisoma frontalis* were found in the faeces of a tortoise. Although the crab and the reptile hardly respond to each other's movements as a rule, a tortoise in camp was once observed making repeated bites at a crab, but without securing a hold. The crab did not retreat more than a few centimetres with each bite by the tortoise.

Cardisoma feeds largely on mud, and it is possible that defaecation by tortoises, by increasing the nutritive value of the mud, serves to benefit the crabs directly. The crabs also feed on dead leaves, and the fresh leaves of *Lumnitzera* and *Fimbristylis* species. All these items are neglected or ignored by the tortoises, and clearly the two species do not compete for food.

Gaymer (1968) has listed the ibis, *Threskiornis aethiopica*, the Crow, *Corvus albus*, and the coconut crab as potential predators of young tortoises. The first-named bird uses a very characteristic nibbling movement during feeding and this and the form of the bill seem unsuited for predation on even new born tortoises. The crow was never observed feeding far from human settlements, and may rarely encounter small tortoises. The formidable decapod is certainly capable of feeding on live tortoises. Two carapaces of small individuals were found which had apparently been opened in scissors fashion through the lateral scutes but this may not have been done by crabs, and there is as yet no confirmation of their predatory activity. The remains of small tortoises (less than 30 cm carapace length) are very rare indeed (four examples found in the whole study period) and this may suggest that predation if at all effective is largely confined to the immediate post-hatching phase.

(*k*) *Anse Mais*

Anse Mais is a beach on the west coast of South Island behind which is a small coconut plantation. The area is of interest because it has been influenced by human activities. Many plants have been introduced to Aldabra, but most of these are at Settlement and tortoises do not normally encounter them. However the ubiquitous rudrules *Stachytarpheta jamaicensis* and *Catharanthus roseus* are present at Anse Mais and are not eaten by tortoises. They show no sign of being grazed. Instead the reptiles feed mainly on a large *Eragrostis* sp. though they have not reduced it to compact turf and most tussocks are about 30 cm high. A few patches of *Sporobolus* are also present, some being close-grazed. In addition, feeding on *Hedyotis* sp., *Sida parvifolia* and *Nesogenes* sp. was recorded.

The tortoises shelter under low coconut palm fronds or in the surrounding bush.

The smallest animal seen in the area was 42 cm long but as only about 80 animals were in the plantation itself over a 5-day period, the absence of very small animals is not of special significance. It still has to be established how freely the tortoises move along the south coast of Aldabra and it is likely that the Anse Mais population is a transient one.

(*l*) *Middle Island*

This island was explored only as far west as a turtle beach just west of Anse Malabar. Tortoises were not seen in the thickest bush between East Channel and Anse Malabar but were present in small numbers in more open terrain between these localities. It is unlikely that they occur outside the scrub which covers the more elevated ground on Middle Island so it is to be concluded that the popultion is small and localized, perhaps being restricted to the easternmost 4 km (none reach Passe Gionnet, where the habitat does not seem unsuitable for them).

There are two habitat types where tortoises were observed on Middle Island. The first is the open cèdre wood, containing *Casuarina* trees some 6 to 10 m high. Many are dead or have been blown over and there are numerous dead branches lying about. The associated flora is sparse and mostly an extension of the scrub occurring farther inland. There is a localized ground flora of *Pleurostelma*, *Sclerodactylon*, *Plumbago* and occasional *Capparis* and *Lomatophyllum*. Scattered *Lepturus* shoots emerge where thick carpets of *Casuarina* needles exclude other herbs. The roots of the fallen *Casuarina* trees are used as shelter sites by the tortoises and they graze the sparse *Lepturus* sward. They were recorded feeding on *Pleurostelma*, *Panicum*, dead *Scaevola* leaves and *Phyllanthus maderaspatensis*, and *Plumbago* showed evidence of grazing. Live *Casuarina* branches are not eaten but the needles were found in tortoise faeces.

Inland from the *Casuarina* groves, on somewhat higher champignon, is a mixed scrub in which *Acalypha*, *Tricalysia*, *Canthium* and *Phyllanthus distichus* are the most common species. *Capparis*, *Polysphaeria*, *Flacourtia*, *Tarenna*, *Apodytes*, *Phyllanthus cheloniphorbe*, *Sideroxylon*, *Clerodendrum* and some others are present. Remarkably, *Phyllanthus distichus* and *Acalypha* grow down to the ground and none of the other shrubs show browse lines or evidence of browsing. Seedlings of *Phyllanthus*, *Polysphaeria*, *Acalypha* and *Canthium* were noted. The ground flora, restricted to the more open scrub, consists largely of *Cyperus* sp., *Fimbristylus cymosa* and *Lepturus*.

The habitat contrasts greatly with that of the platin for the tortoises are at a low population density. Only about 70 were found in the *Casuarina* groves and neighbouring scrub (*ca.* 40 hectares) over a visit of 6 days. They exert no apparent influence on the vegetation which appears to be regenerating normally. There is no development of a 'tortoise turf'.

The reptiles themselves are very large. The largest wild tortoise on recent record from the Indian Ocean was observed on Middle Island (a male with a carapace length of 106 cm) and local rumour spoke of still larger individuals. The most interesting feature of the animals is the retention of growth rings up to the apparent age of 30 years or so. The growth rate of these tortoises has already been discussed.

(*m*) *West Island*

Tortoises are scarce on West Island, and usually they are seen singly. The Seychellois contract labourers occasionally kill them for food but they can still be found near Settlement. Tortoises left the Bassin Cabris area during the dry spell in the spring of 1968, although dry faeces indicated their recent presence there.

Tortoises are brought in to West Island from Anse Mais and other parts of Aldabra for export by the lessee. It may be that in the past some of these have been released on the island. Rothschild (1915) speaks of the transfer of tortoises between Aldabra and the Seychelles.

11. TRANS-OCEANIC DISPERSAL

The colonization of remote islands by giant tortoises has been considered a remarkable and inexplicable phenomenon, but a knowledge of their present-day ecology suggests they are well able to reach remote isolated land masses. Their readiness on Aldabra to traverse the shore or *Avicennia* swamps to feed on washed up debris suggests it is from sites of this kind that dispersal has commenced. The freedom with which tortoises can swim and remain buoyed up when resting in the water indicate a propensity for oceanic transport—the author saw a tortoise floating in the lagoon at Aldabra 0.5 km from land. Tortoises of the *Geochelone* group have made a number of successful crossings of the ocean, reaching more faunistically isolated localities than many other tetrapods. They occur—or occurred during the Pleistocene—not only on Aldabra and neighbouring islands; the Seychelles; the Mascarenes and Madagascar; but also in the West Indies, the Galapagos Islands and across Wallace's line on Celebes, as well as on the Asiatic, African and American land masses.

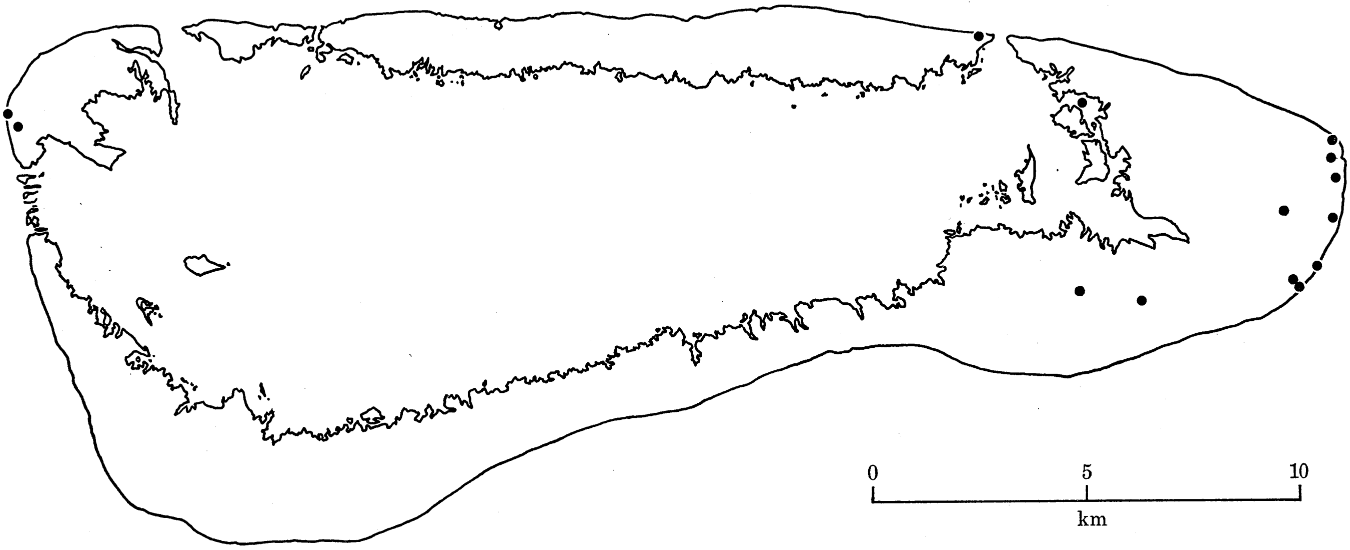


Figure 29. Map of Aldabra showing sites where fossil tortoise bones have been observed or collected.

The chronology of the giant tortoise's colonization of Aldabra can now be studied, for abundant fossil tortoise bones were located during the Royal Society expedition. They consist of bone fragments and of whole limb bones embedded in brown or yellowish grey limestone which in some cases is still clearly plugging a hole in unaltered coral limestone. Bones were not found in the tall brown limestone residuals on the platin and except for some from lagoon islets and a few from solutions pans on the platin, were only observed within about 500 m from the sea (figure 29), in several cases having been exposed on the cliffs by marine erosion. It is yet to be shown whether fossilization continues today or whether conditions were more suitable for it on a less eroded and perhaps more heavily wooded Aldabra. The accumulation of bones is at times remarkable and it is not clear how they were collected—in some examples they have been assembled at the bottom of a deposition of brown limestone and are absent at higher levels in the deposit. The age of the fossils also remains to be assessed, but it is apparent that tortoises colonized Aldabra before the formation of the Upper Limestone (Stoddart 1968) about 30000 years ago. Old beach terraces formed about this time occur above some of the fossil bone sites.

12. MOVEMENTS

Tortoises observed at Takamaka in October 1967 were marked with paint so that they could be speedily identified in the field. Later during the study period, several of these marked animals were observed far from Takamaka, as far away as Dune Jean-Louis or the coast north of Cinq Cases (figure 30). They had covered distances of up to at least 7 or 8 km within 2 months.

Few animals of 30 cm or less in carapace length were marked and none of these were found outside the area where they had been captured. Similarly, many large marked tortoises stayed in the Takamaka area throughout the study period. Tortoises marked by the Bristol Seychelles Expedition in 1964–5 were found both at the site of marking (Takamaka and a neighbouring solution pan) and at well-dispersed localities as far distant as the coast at Cinq Cases.

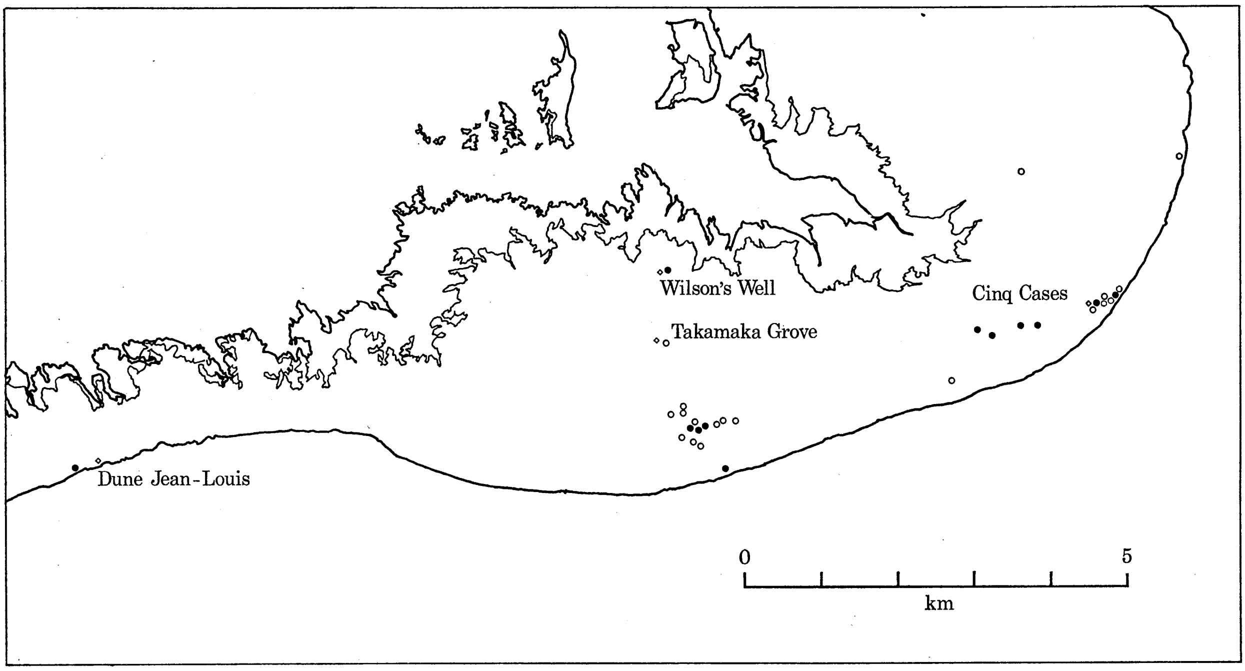


FIGURE 30. Map of the eastern half of South Island, to show where tortoises have been recovered—open circles indicate animals marked at Wilson's Well, and black dots, tortoises marked at Takamaka. Recoveries between these two localities have not been plotted.

There were other trends in the dispersal of the population. For instance, 30 to 40 tortoises were found sheltering at the Takamaka pool and the nearby dry pan on some days, while on other days very few or none were present. A seasonal movement probably occurred at Cinq Cases, since tortoises no longer concentrated in large numbers to feed on tortoise turf during the drought in 1968. Movements of marked animals or the regular influx at the *Avicennia* swamps indicate the turnover that must exist in the population at any one locality. At each camp, individually identifiable animals would remain about the site for a few days and then leave. In some cases this departure involved the use of successively more distant rest sites from one day to the next. While such individuals may move over almost the whole of their potential range, others may be relatively sedentary. The behavioural norm has yet to be determined and the factors which determine apparently random movement in one individual and the establishment of a 'home range' in another still remain to be studied.

13. POPULATION DENSITY

The number of tortoises in hectare samples recorded during the census lay between 0 and 160, with a mean of 38.5. If these samples are taken to be representative of 0.25 km squares (figure 2) then the area surveyed covered a total of 10.6 km^2. In this area, it is estimated that there were as many as 40830 tortoises.

Although most hectare samples were from platin, some were from coastal communities—*Guettarda* woodland for instance—and if these samples are excluded, the mean density of tortoises is estimated as 23.0 per hectare. The total area of platin on South Island is approximately 30.7 km^2 so that it could carry as many as 98240 animals. While some localities outside the surveyed area included large concentrations of tortoises, the scrub forest to the north and west was thought to have relatively fewer animals than the censused area. The estimate of the platin population may thus be rather too high, but it is likely that many small tortoises were overlooked during the census, so the balance is to some extent redressed. The population of the whole atoll, including the animals of habitats other than platin, is certainly of immense size, and of the order of 100000 tortoises.

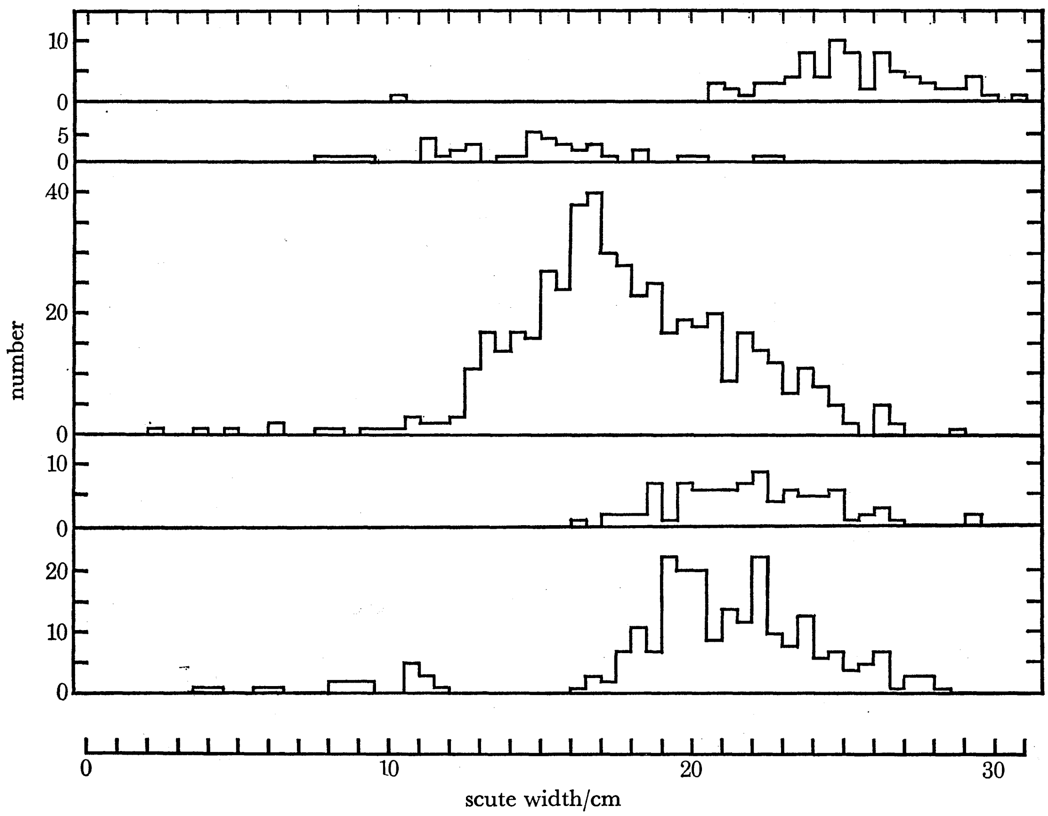


FIGURE 31. Frequency distribution of the width of the third vertebral scute in a number of population samples. These are, from top to bottom: (1) Middle Island—all animals encountered; (2) coastal champignon, South Island—two sample quadrats from the census; (3) *Guettarda*/*Ficus* wood at Cinq Cases—first 500 animals encountered; (4) *Avicennia* forest near Bras Cinq Cases—first 91 animals encountered; (5) neighbourhood of Takamaka and Wilson's Well—all animals encountered between 27 and 31 October 1967.

14. LOCAL VARIATION IN ABUNDANCE, SIZE AND AGE STRUCTURE

The population density of tortoises and their size range and age-class distribution vary over Aldabra in a complex manner. The census was not primarily concerned with relating this variation to environmental differences, but from the data collected rough assessments of densities in several habitats have already been made and further analysis does give some insight into the kinds of variables involved. The analysis cannot be carried too far as very few of the census quadrats covered areas that were typified by one habitat type only.

Two-thirds of the census quadrats—i.e. 29 out of 46—had between four and fifty tortoises of mean scute width (used as an index of size) of between 170 and 210 mm (45 to 58 cm in carapace length) and the majority of these samples were located in platin. For the remaining quadrats, the mean scute width or the number of tortoises, fell outside these ranges, and the extremes can be related to two habitat types (table 6). First, samples from open coastal champignon had low numbers of rather small, young tortoises, and secondly samples from *Guettarda* woodland had large numbers of animals, mostly of medium size. As these two habitats are juxtaposed along a front of many kilometres they illustrate how the character of the population can vary strikingly over a small distance, so considerably are the tortoises influenced by properties of the environment.

TABLE 6. CHARACTERISTICS OF SOME POPULATIONS OF TORTOISES FROM DIFFERENT PARTS OF SOUTH ISLAND

sample	number	scute width/mm mean	scute width/mm standard deviation	percentage aged at 20 years or younger	percentage of adult males
census survey, 46 quadrats	1771	190.1	38.9	28	11
census quadrat, *Guettarda* woodland	103	178.4	43.4	47	13
	114	196.3	29.7	25	10
	116	189.9	38.2	39	15
census quadrat, coastal champignon	27	148.7	28.1	89	0
	14	152.2	43.3	79	(1 animal)
	7	162.2	27.0	57	0
all tortoises encountered at Takamaka 27 to 31 October 1967	230	209.3	43.3	21	20
the first 89 tortoises encountered in in *Avicennia* swamp	89	222.2	25.89	0	33

Tortoises from the *Avicennia* swamps averaged larger than in any census quadrat and tortoises measured at Takamaka also tended to be larger than those in the census area (figures 31 and 32).

Local variation in size range results from differences in age structure, presumably the consequence of trends in the emigration or immigration of particular age classes. For instance, there are relatively few animals from the first 20-year classes at Takamaka, many more at Cinq Cases and none in the *Avicennia* swamps (compare figures 31 and 32). On the other hand, most tortoises from coastal champignon fall within this age range. As the number of 20-year-old or younger tortoises decreases, the proportion of adult males increases (table 6). Differences in growth rate can also affect the size range of populations—compare the measurements of Middle Island animals with those from Takamaka (figure 3) which if anything include older animals. The ageable tortoises from Cinq Cases and Takamaka also differ in growth rate, and for this to be the case, they must be relatively isolated from each other, probably because young tortoises range over rather short distances.

15. POPULATION STRUCTURE

There are five separate samples from which one can assess age-class distribution of tortoises on Aldabra (table 7). The Takamaka sample is biased because small tortoises were selectively examined, and the same is true of the Cinq Cases sample of small tortoises, in which animals below about 30 cm in length were specially chosen for measurement. The other Cinq Cases sample, obtained from a small area, cannot be regarded as representative and the census sample will chiefly be considered, though the high proportion of large tortoises outside the census area (figure 31) does imply that older animals might be somewhat under-represented in the census area, and that the census sample is not as representative of the total population as is desirable.

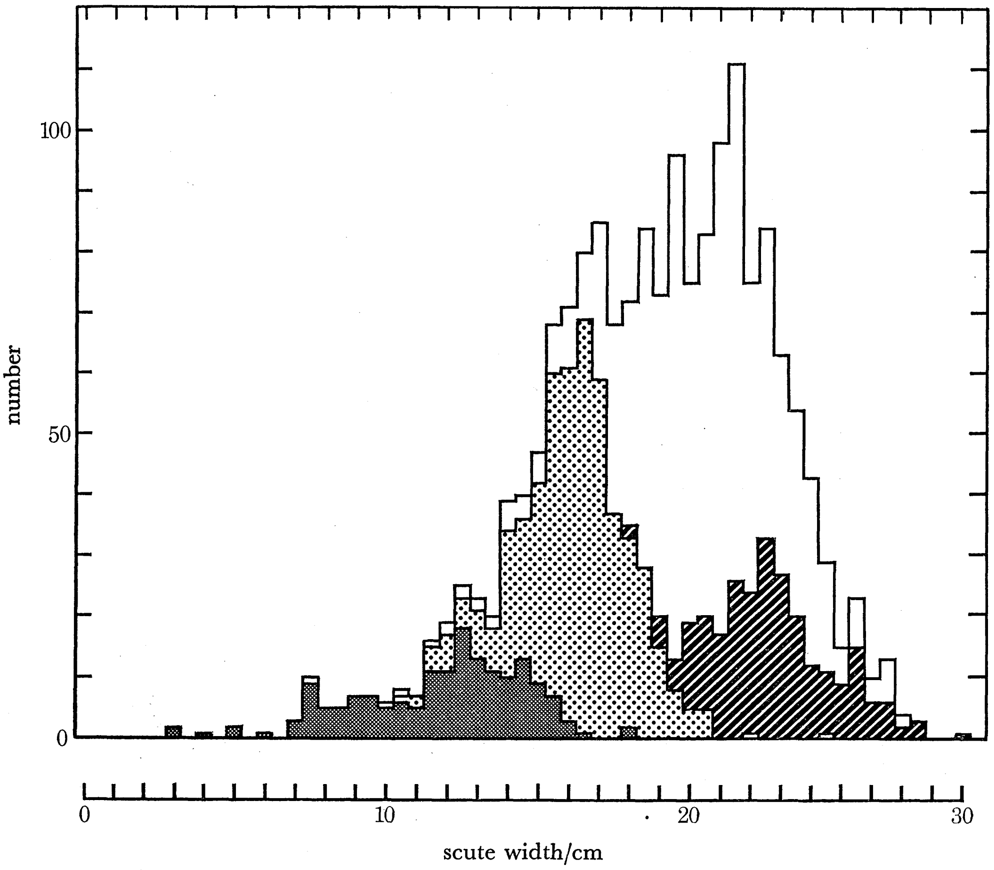


FIGURE 32. Frequency distribution of the width of the third vertebral scute in the 1771 tortoises examined during the census. Four categories are distinguished—tortoises up to 10 years old (heavy stipple), tortoises of between 11 and 20 years of age (light stipple), adult unaged males (oblique shading) and unaged, unsexed animals, including females (blank).

Four categories compose this sample (figure 32)—first, animals believed to have been aged accurately, then a group aged only roughly, thirdly a number of unaged and unsexed animals, and finally, sexed, unaged tortoises.

In considering the first of these categories it is apparent that the age-frequency distribution shows a peak at 13 to 14 years of age, with numbers dropping off in both older and younger age classes. The older the tortoise, the less likely will it be possible to age it from the scutes, so that this factor could account for the decrease in numbers from the 14th to 25th age class. There are several explanations for the paucity of numbers in the younger classes. Possibly there has been a big increase in mortality at an early stage of development in recent years, or recruitment has actually decreased, or the smaller tortoises have been grossly undersampled. The last explanation seems to be the likely one. When a special search was made for small tortoises at Cinq Cases over a 4 h period the resulting sample contained many 3-year olds (table 7) so these at least do not appear to be particularly rare. It may be that differences in activity pattern and the habit of hiding themselves when resting make the smallest tortoises difficult to find, even in this respect differentiating the first and second year individuals from the 3-year olds in the last-named sample.

Table 7. Age-class distribution in six population samples of Aldabra tortoises

Accurately (A) and inaccurately (B) aged animals are listed separately

age/ years	Middle Island		Takamaka	Cinq Cases		Cinq Cases (small tortoises)		census	
	A	B	A	A	B	A	B	A	B
0	—	—	3	—	—	—	—	3	—
1	—	—	1	2	—	1	—	1	1
2	—	—	5	2	—	8	—	2	—
3	—	—	3	—	—	30	—	6	—
4	—	—	4	1	—	43	—	24	—
5	—	—	5	3	—	23	2	20	—
6	—	—	10	1	—	23	2	24	1
7	—	—	7	1	—	7	2	15	—
8	—	—	4	—	—	4	1	20	1
9	—	—	7	11	3	1	1	27	2
10	—	—	1	12	3	—	1	15	7
11	—	—	2	9	1	—	—	32	11
12	1	—	5	14	5	—	2	44	13
13	1	—	6	26	8	1	—	46	19
14	—	—	2	24	9	1	1	46	19
15	3	—	2	20	10	—	—	35	25
16	4	—	2	8	6	—	1	35	17
17	2	1	—	6	7	—	—	22	8
18	10	—	1	6	11	—	—	19	15
19	13	—	1	4	9	—	—	5	8
20	8	—	1	5	11	—	—	13	14
21	5	—	—	4	3	—	—	7	8
22	4	—	—	1	9	—	—	3	5
23	1	—	—	—	5	—	—	1	5
24	2	2	—	4	3	—	—	1	1
25	1	—	—	—	3	—	—	1	3
26	1	—	—	—	1	—	—	1	1
27	—	—	—	1	2	—	—	—	—
28	1	—	—	—	—	—	—	—	—
29	—	—	—	—	—	—	—	—	—
30	1	—	—	1	—	—	—	—	—
31	1	—	—	—	—	—	—	—	—

The animals which were roughly aged had retained many annuli but some of the first-formed ones had been worn away, making an accurate age assessment impossible. These tortoises present a special problem, for it is difficult to know what proportion has been correctly aged.

Since females were not distinguished as reliably as adult males, they were relegated to the unsexed, unaged category, so that the sexed category includes adult males only.

Taking the census sample at its face value, a high proportion of the population—at least 35 % (613 animals out of 1771)—is found to be less than 20 years old. Of the remaining 1158 tortoises, only 188 were with certainty distinguished as males, implying the existence of at least 376 sexually mature beasts if the sex ratio is assumed to be unity. This still leaves at the most 782 non-mature tortoises above the age of 20 years.

Further speculation on population structure is for the moment hazardous. In attempting to assess the real age-class distribution of the South Island tortoises, one has to assume that the ageing method is reliable, that the census sample is representative of the population as a whole, that the population is a stable one, and so on. Many different models can be postulated. If the population is indeed stable and we assume that the largest age class is the most accurately known, then with a constant mortality rate, the proportion of the population believed to be of greater age determines the number of age classes which are present. This next raises the possibility that the number of tortoises in the first 10 or 12 classes that have been missed in censusing is very great, a point yet to be established.

Assuming there are about 50 animals in the 14-year class, then at a constant rate of mortality, there should be more than 90 age classes all told. However, if mortality rate alters drastically with old age, there might be no more than 40 or 50 age classes, and the likelihood in any case is that the population has not remained at a steady level.

The sample from Middle Island is small, but the older age classes are probably fairly represented in it. There are 35 animals below 20 years of age, most in the 18- and 19-year group, but there are 43 animals of 21 years or more (17 of these are unaged). This suggests that tortoises of more than 30 years of age are very scarce on Middle Island, a contrast with the situation on South Island which may be the result of removing the largest tortoises from Anse Malabar for export.

16. Conclusion

In the Indian Ocean, tortoises are likely to have dispersed from Madagascar to Aldabra, rather than from the Seychelles to Aldabra, and one would expect there to be a very close affinity between the Aldabra tortoises and the now extinct *Geochelone grandidieri* of Madagascar. However, this tortoise has a very flattened carapace (Rothschild 1915, plate 37) and it is the Seychelles animals that have the closest affinity with the Aldabra form. The only distinction between the two may lie in the shape of the anterior marginal scutes which tend to be downcurved in the Seychelles tortoises (M. J. Penny, personal communication) although with mixing of local populations and semidomestication, the characters of pure strains of Seychelles tortoises cannot now be identified with any certainty.

In the past, the number of species of Indian Ocean tortoises has been exaggerated and from what factual information that can be assembled, a provisional assessment of tortoise evolution in the area still remains to be developed and contrasted with the history of the giant tortoises on the Galapagos archipelago.

Studies of the living animals in their natural environment are perhaps the more rewarding. Their abundance on Aldabra suggests that very detailed information on all aspects of their biology will be readily obtainable and prime interest will probably centre on the relation of the population to its food supply. It is instructive that domestic goats, which have caused such ecological havoc on the Galapagos, should be just maintaining themselves and no more on Aldabra, while the tortoises are so ebulliently proliferating. The energy budget of the reptiles must be closely examined and compared with what is known of the way ungulate herds exploit their grazing grounds, in order to explain the success of the tortoises in their inhospitable home. There can be few more interesting reptilian populations deserving investigation and none which can provide such an illuminating comparative study. The population appears to be in a state of flux. Though regional variation in density, age structure and size range is maintained, some individuals or age groups are constantly on the move, affected both by seasonal changes and by selection of particular habitat types. A quantitative approach to such topics as the scale of emigration and immigration in different habitats or the differential mobility of size classes is necessary for clarifying the properties of the apparently non-territorial population.

One other topic of special importance is the way in which numbers are kept in check. As Stoddart (1968) has pointed out, there are doubts that the population has maintained its present high level throughout the last 200 years and natural processes as well as human interference must be taken into account in explaining how decreases and increases may occur. Tortoises are prone to fatal accidents but it is not certain whether such factors can hold back population increase. The mortality rate seems low in relation to the vast numbers of animals present.

In considering the way in which food supply might effect population dynamics, it must be remembered that tortoises can apparently resist food shortage by quite considerable reductions in growth rate—if this is at least a partial explanation of local differences in growth rate on Aldabra—and possibly they are also well able to withstand drastic seasonal shortages of fodder. Nevertheless, at some state a proportion of the population will be sufficiently undernourished for mortality to ensue. There is some indication of the extremes of variation in physical condition on which mortality factors may act differentially. During February 1968, both very thin and very fat tortoises were seen, though unfortunately it was not possible to weigh them. The former had thin limbs and very loose skin about the throat and pelvic regions. The latter in contrast were so fat that the body bulged from the carapace and the limbs were thick and firm.

The special problem of population control in giant tortoises is that any large-scale mortality cannot be compensated for by recruitment. The sexually mature sector of the population is surprisingly small, if the census gives a fair indication of it, and even if a great many eggs are laid, the age-class distribution suggests that annual recruitment can only be of the order of about 5 % of the total population. Following a population slump, a return to former numbers could not be other than an extremely long-term process, unless there were quite massive change in the scale of recruitment. The relation between clutch size, egg loss, mortality at hatching and juvenile mortality have still to be evaluated, but by reference to Gibbons's (1968) study of *Chrysemys picta*, we might expect egg mortality to be very high, the main factor affecting recruitment and one possibly not susceptible to changes in population density.

Gibbons (1967) also found that variation in growth rate between different populations of painted turtles could be explained by the variable quality of the food available to them. On Aldabra, the same factor may be partly involved in accounting for a somewhat less remarkable variation in growth rate. In spite of the diversity of the diet on Aldabra, two food plants are of pre-eminent importance, *Sporobolus virginicus* and *Panicum* sp. The standing crop of these and allied species may be limited but grass is not only very accessible to tortoises, its productivity is probably far greater than that of woody plant material, at least in normal wet seasons, and at the same time it is more resistent to cropping. In curbing the growth of woody plants tortoises locally create what to them may be peculiarly valuable plant communities, but as these are also particularly subject to erosion, the tortoises begin to risk local destruction of all food sources. At this time it is hard to know to what extent their activities as agents of erosion are effective over a long period.

Much worthwhile information on other aspects of tortoise ecology should emanate from further studies, some of which are in progress, and allusion to the most urgently needed data has already been made. It is to be hoped that the tortoises will always remain outstandingly abundant on Aldabra and not suffer some modern repetition of the slaughter on Mauritius and Rodriguez.

I am very grateful to Dr D. R. Stoddart and The Royal Society for the opportunity to visit Aldabra. I should also like to thank W. Pople, who was instrumental in dealing with the computation, T. Graham, who assisted in the census work, and Dr F. R. Fosberg and S. Renvoize, who identified the plants.

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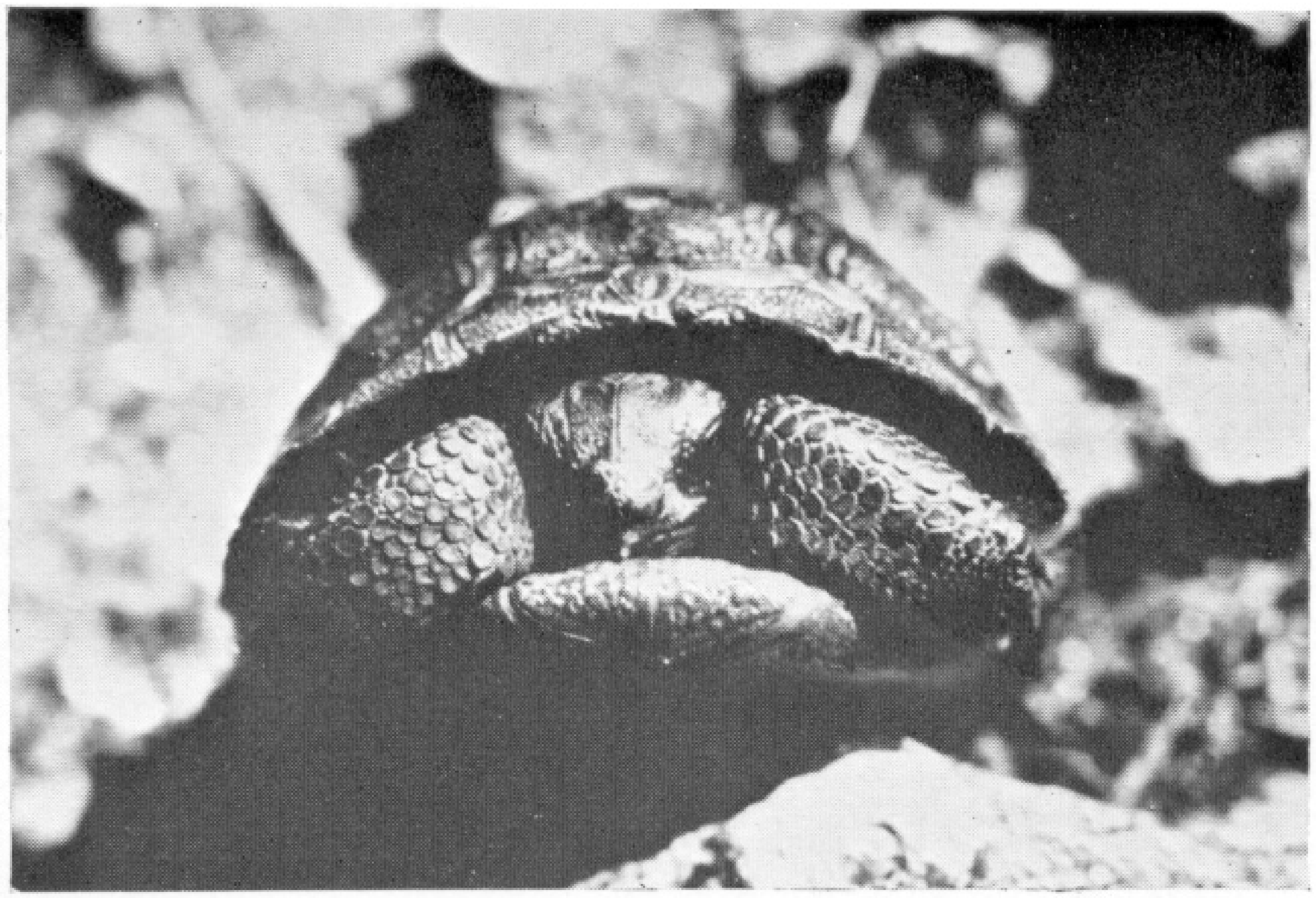

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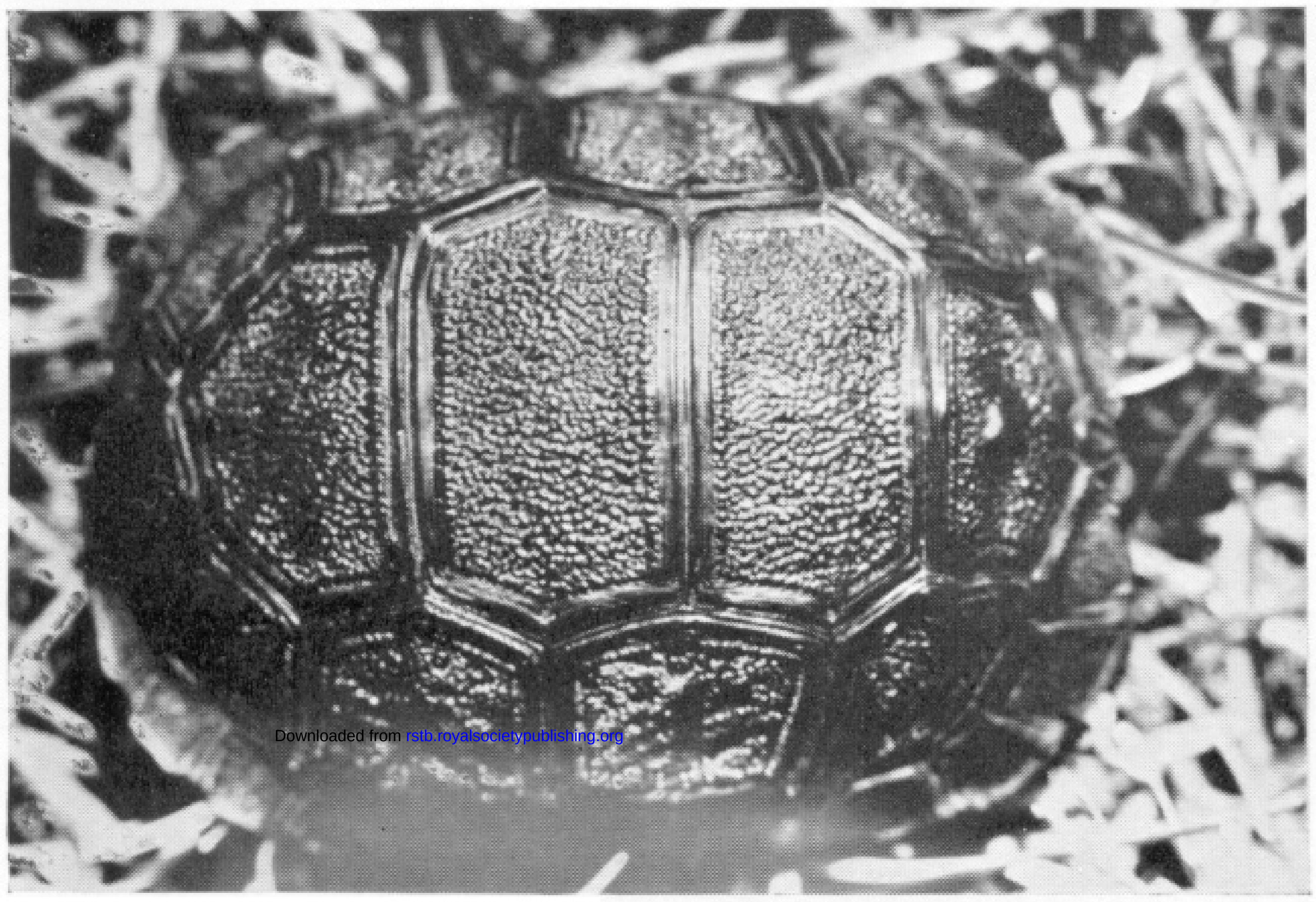

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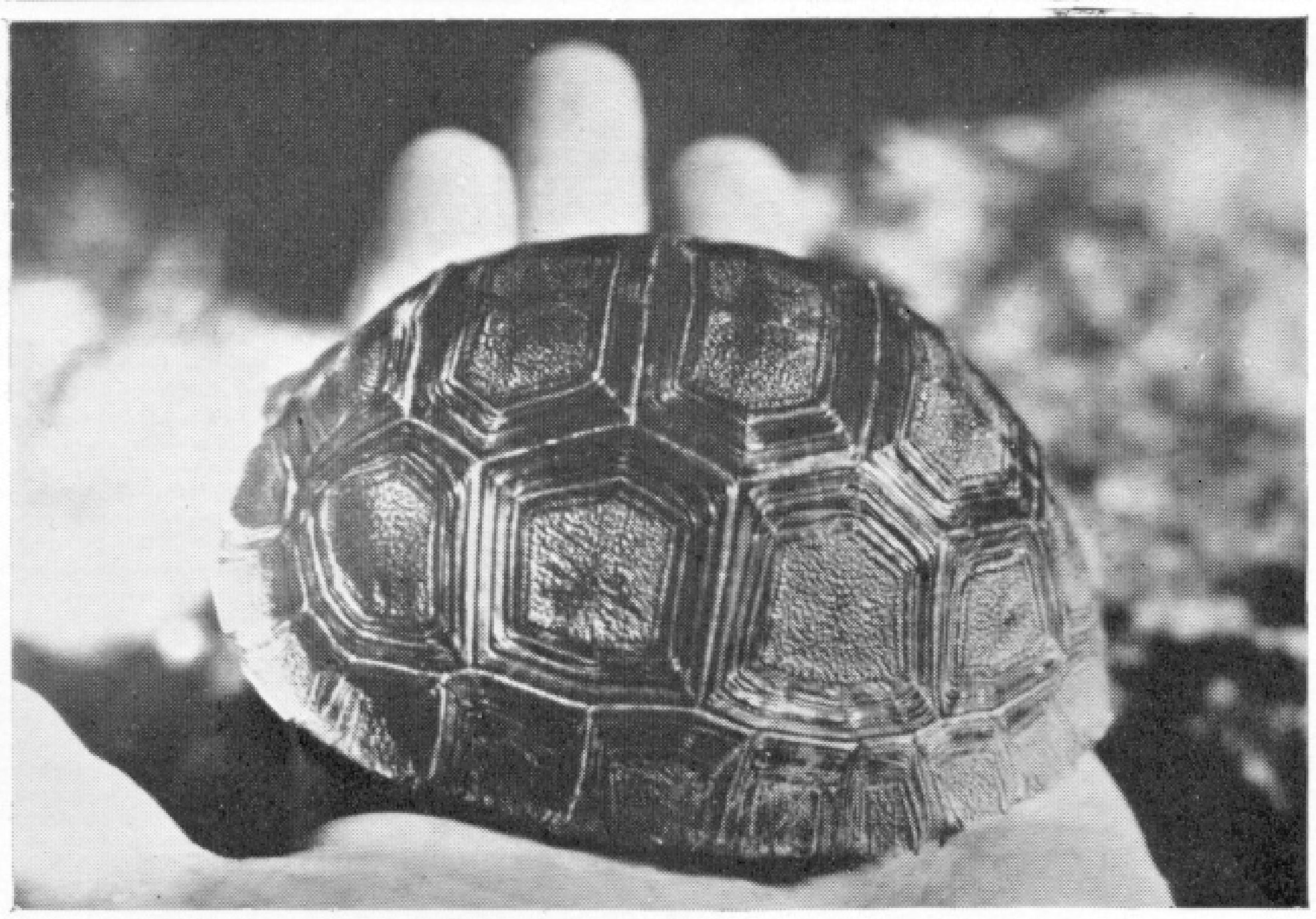

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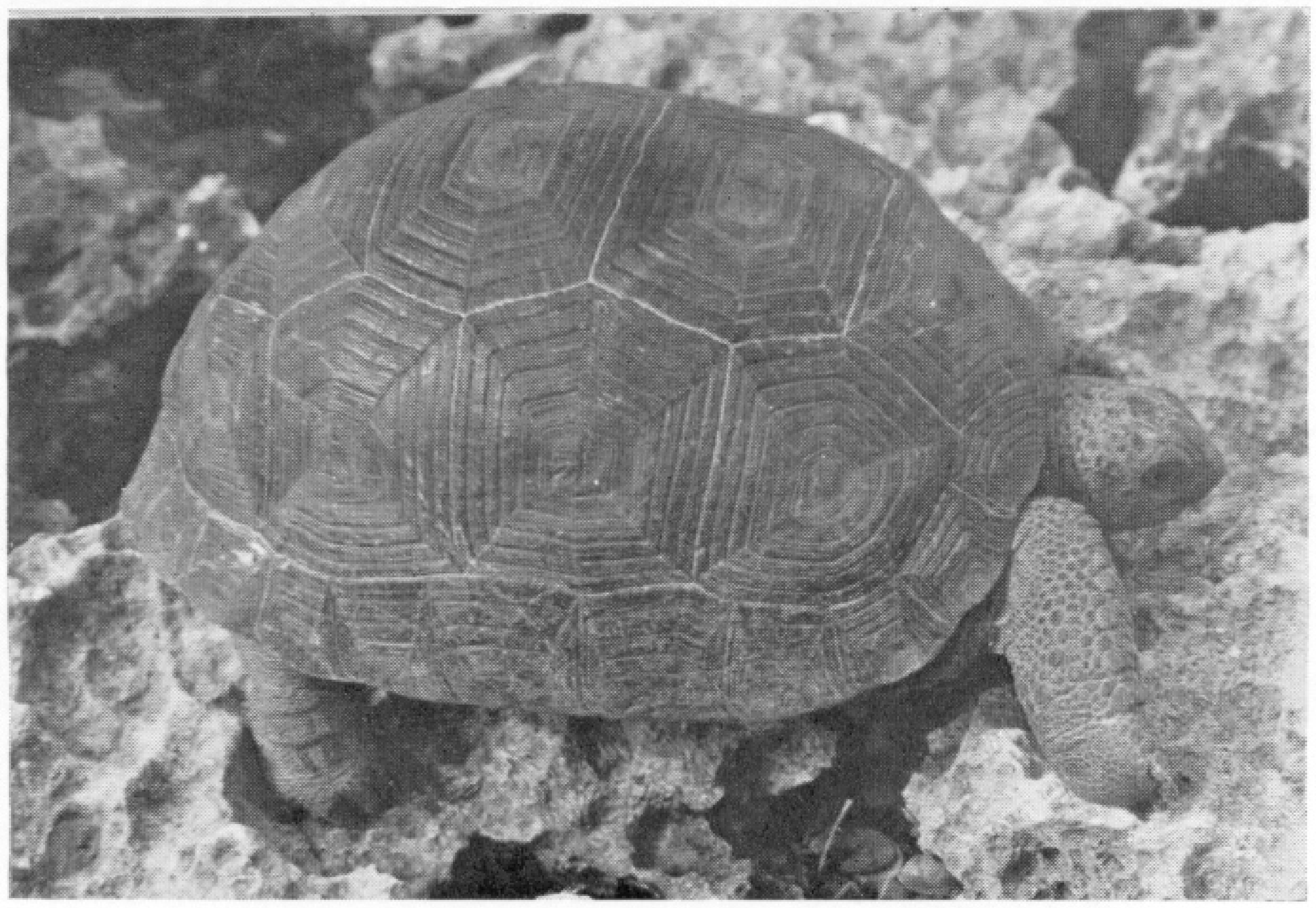

FIGURE 3. Head of young tortoise, probably less than 1 month old, showing the egg tooth.

FIGURE 4. Front view of the tortoise shown in figure 3.

FIGURE 5. Carapace of the tortoise shown in figure 3 to show the relatively large areolar areas on each scute, and the narrow rings of tissue grown since hatching.

FIGURE 6. Carapace of tortoise with a single season's growth on each scute.

FIGURE 7. Young tortoise with four annuli on each scute.

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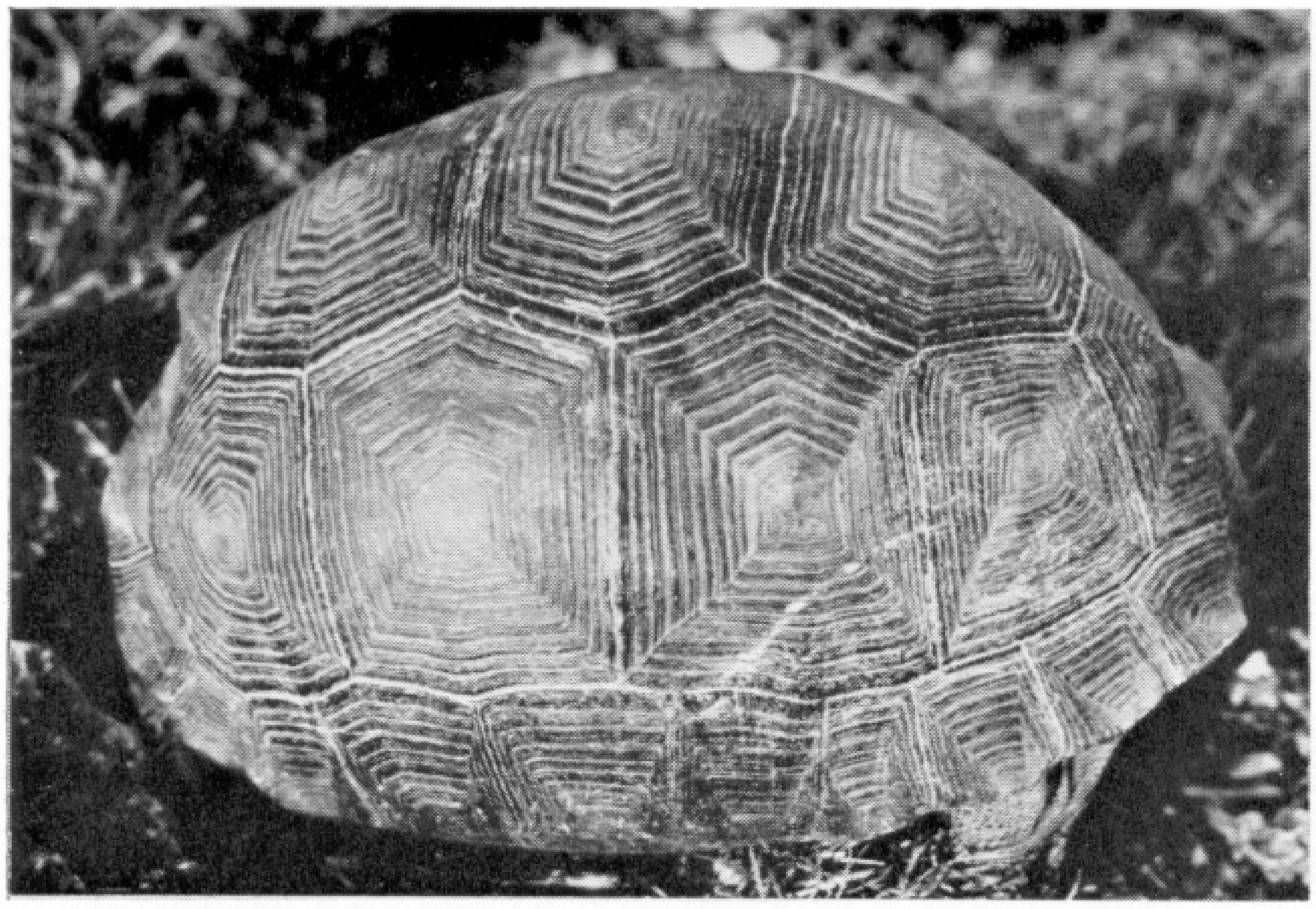

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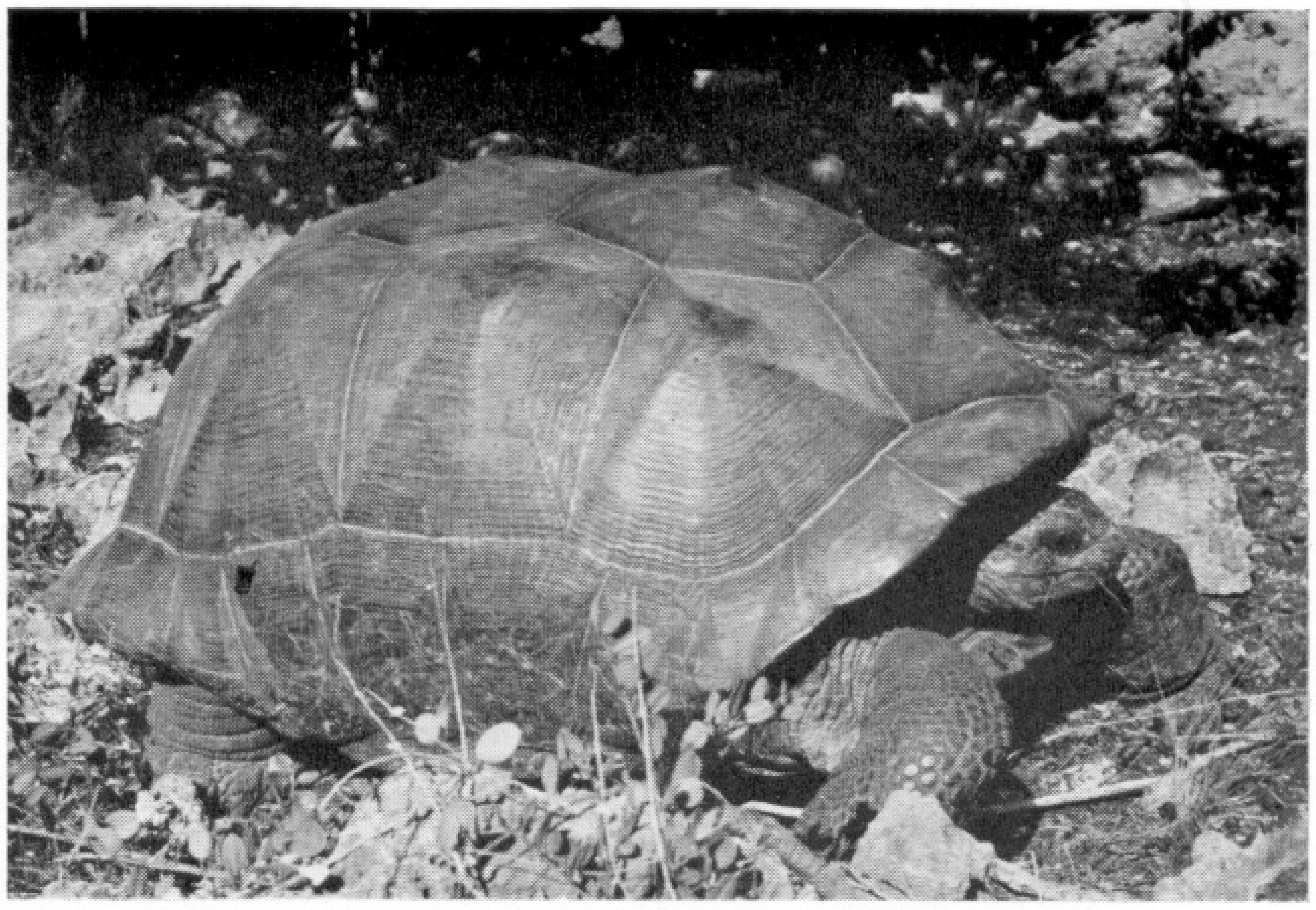

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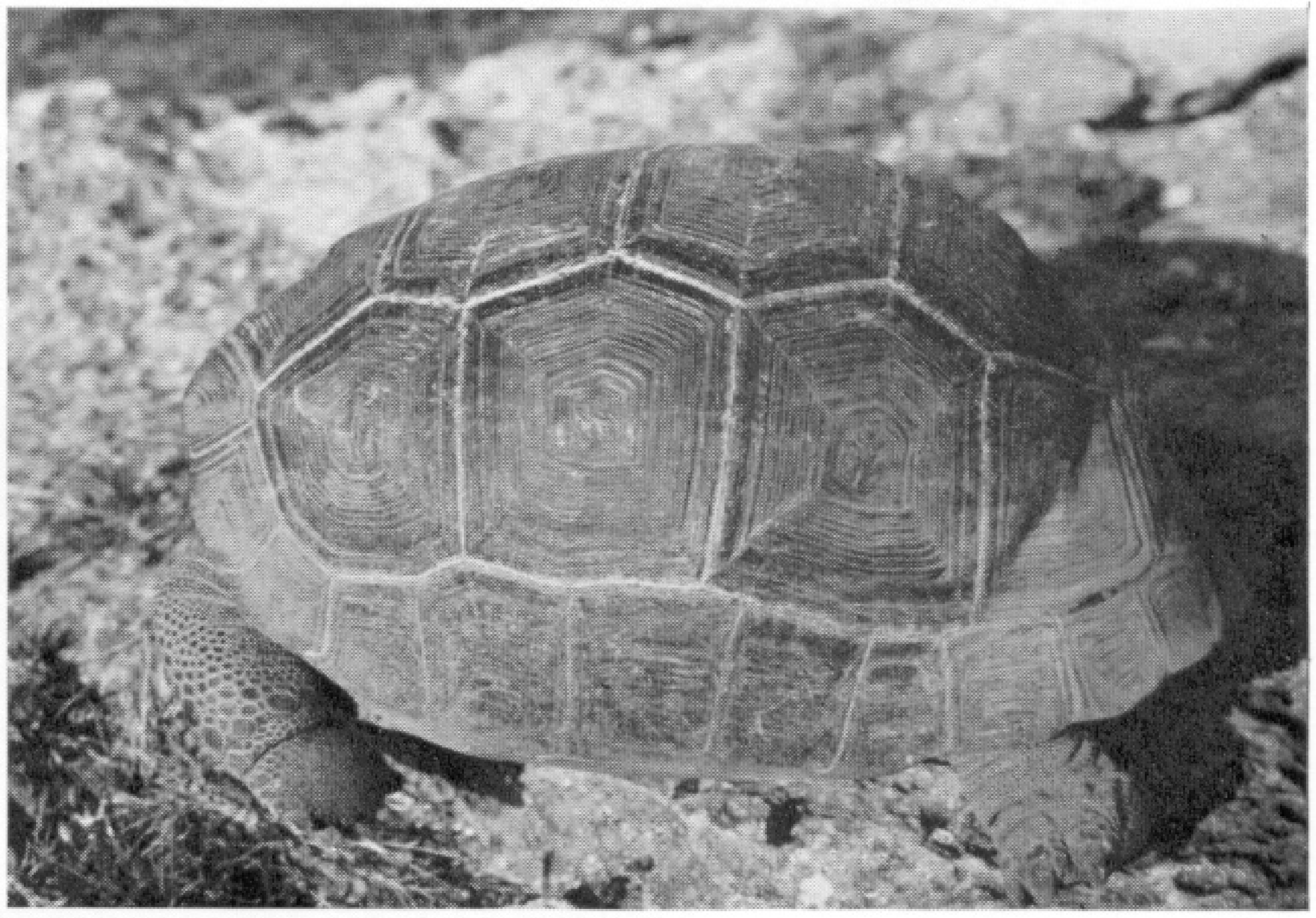

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FIGURE 8. Carapace of tortoise with ten annuli on each scute.

FIGURE 9. Tortoise on Middle Island, Aldabra, with about 27 annuli.

FIGURE 10. Anterior view of adult tortoise for comparison with figure 4.

FIGURE 26. Carapace of tortoise in which the most recently formed annuli on each scute are much broader than any others, suggesting that there has been a sudden alteration in growth rate.

FIGURE 33. 'Tortoise turf' showing shoots of *Panicum* sp. (leaves about 1 cm long) and *Ricksia* plants.