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Features of tortoise mortality and decomposition on Aldabra

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[Plate 1]

Apart from predation on tortoise eggs and young tortoises by crabs and birds, the Aldabran giant tortoise population is virtually unaffected by predators. The decomposition of a series of tortoise bodies, with known dates of death, was monitored for periods up to 18 months. The rate of carapace disintegration provides a useful means of introducing a temporal component to the analysis of mortality data.

Introduction

During a study of the population dynamics of the giant tortoise (*Geochelone gigantea* Schweigger) on Aldabra it became apparent that while a series of marked animals provided valuable data on the numbers and distribution of living animals, this information would be incomplete unless an attempt could be made to assess mortality. The remains of adult animals are a conspicuous feature of the arid Aldabra landscape and their apparent persistence for long periods indicated a possible means of obtaining a measure of mortality. In particular the presence of this skeletal material offered the opportunity of introducing a temporal component to the study of mortality provided a time series for decomposition could be established.

The persistence of tortoise remains can be attributed to the almost complete absence of predators on the atoll. At present, land crabs, birds and feral cats are probably important agents of predation on both eggs and young but adults are not affected, although all these creatures perform an important scavenging rôle on carrion. Feral dogs, once present on Aldabra, are now extinct. Thus for animals with carapaces greater than 50–60 cm (curved length) the skeletal remains are virtually unaffected by these agencies.

The tortoise carapace is composed of an outer series of keratinous scutes and an inner layer of bony plates which in adult animals are well ossified and fused together. During decomposition the outer scutes become detached from the body plates and fall off, leaving the carapace bones to become bleached by sunlight. The presence of these remains provides an excellent marker whether above ground or in holes and crevices in the broken limestone champignon. Hence during transect and hectare surveys for living animals it is also possible to record the presence of skeletal remains.

Provided a time scale can be constructed for the time taken for tortoise skeletons to break down, the comparatively long-term persistence of these remains makes it possible to assess the mortality rate for the adult tortoise population. During the course of investigations of the dynamics of the tortoise population (Bourn 1976, 1978; Bourn & Coe 1978), individuals whose date of death was known were monitored for up to 18 months. At present, I. Swingland, who is investigating tortoise reproduction and recruitment, is recording further information on mortality. This paper describes a number of time-related stages of the breakdown process and gives estimates of the time elapsed since death.

Method

Between January 1973 and September 1974, during the course of an extensive tortoise census and marking programme, most areas of the atoll were visited on a number of occasions. The remains of many dead tortoises in various stages of breakdown were located and recorded. The fresh, unbloated appearance of certain remains and the absence of putrescent odours indicated that some animals had died very recently. In such cases carcases were marked and their position recorded. In addition, various other data were recorded, including the size and sex of the individual, its location in relation to the nearest available shade, the degree of exposure, whether or not the tortoise appeared to have been trapped in holes or fissures, and the general condition of the carcase. Subsequently, as the marking programme permitted, the remains of these animals, whose date of death was known to within a few days, were revisited and notes kept on the progress of the decay process. The presence of scavengers on or near the remains was also recorded.

As part of a preliminary reproductive study a limited number of tortoise post-mortems were performed (Bourn 1978). After post-mortem examinations had been completed a number of carcases were laid out and monitored to assess the rates of breakdown and to determine qualitatively the importance of various scavenger species. However, as these observations progressed it became apparent that post-mortem remains were not decaying at the same rate or manner as those of natural intact carcases. In order to gain access to the tortoise's internal organs during post-mortem examination the plastron had been entirely removed so that prematurely dismembered bodies were laid out for observation. Necrophagous species therefore had relatively easy access to the fleshy remains. In addition, the removal of the plastron meant that the dorsal carapace bones were subject to somewhat different contraction and expansion stresses, than in natural mortalities with an integral plastron. Breakdown rates of these unnatural mortalities could not therefore be regarded as typical. However, it is considered that the scavenger species seen are likely to be the most important under natural conditions.

Results

(*a*) *Carapace breakdown*

The remains of 31 natural tortoise mortalities were monitored for periods of up to 18 months after death. A total of 146 visits were made to these remains. Initially detailed descriptions were made of the status of each carcase, but after a period of familiarization with the breakdown sequence it was possible to define eight recognizable stages in the process. These are described in table 1 and photographs of the various stages are shown in figures 1–8, plate 1. Of the 31 tortoises monitored, only 6 were located in shaded positions. It was not therefore possible to determine with confidence whether these broke down less rapidly than those in the open, although shaded remains usually became discoloured by algal/bacterial growth more readily than those in open positions. Presumably the shaded positions afforded less extreme microclimatic conditions for microbial growth to take place. It must be emphasized that although every effort was made to visit tortoise remains as frequently as possible, especially in the early stages of breakdown, when the process was relatively rapid, the observations and the estimates of the duration of each stage, especially the more attenuated later stages, are inevitably rather imprecise and the ranges are wide and sometimes overlap. There is obviously a considerable

degree of individual variation and in any case the phases described compose a decay continuum. Nevertheless, useful criteria may be established from these results.

Table 2 summarizes the results; the duration of each stage is given in terms of days elapsed since death, along with the number of observations that were made, given in parentheses. The early stages of breakdown (stages 1–3) were reasonably consistent regardless of the size in the range considered. During the first 48 h after death there is little or no smell, while in the subsequent 2 weeks or so the processes of putrefaction proceed; first the limbs become bloated, the skin tissue splits and foul smelling liquid oozes from orifices and sites of scavenger activity.

Table 1. Breakdown stages of tortoise carcases arising from natural mortality

stage	description
1	*Freshly dead*. No bloat. No smell. Limbs entire, fleshy and covered with skin. Scutes all in place and firmly attached.
2	*Putrid*. Initially bloated with oozing orifices. Subsequently skin may begin to peel. Fleshy parts drying out and blackening. Foul putrid odour throughout. Scutes firmly attached.
3	*Soft parts absent*. Fleshy remains and entrails removed or thoroughly dried out and mummified. All scutes attached although some marginals may have become detached. Little or no smell.
4	*Scutes attached*. Most or all dorsal scutes in place, although often raised off underlying carapace bones and separated from each other. Where scutes have fallen off, exposed carapace bone usually has connective tissue still visible and attached.
5	*Scutes shed*. Most dorsal scutes detached. Exposed carapace bones usually bleached white. Initially some connective tissue between scutes and carapace may be evident. Carapace bone sutures still holding.
6	*Sutures opening*. Individual carapace bones starting to separate along sutures. Depending on exposure, bones may be more or less darkened by algal/bacterial growth.
7	*Collapse*. Carapace collapsing, with individual bones collapsing inside.
8	*Disintegration*. Carapace structure lost. Complete disintegration. Remaining bones usually grey and powdery.

Gradually the remains begin to dry out, the fleshy parts are consumed by the activity of dipterous larvae, and some limb bones are removed by scavengers. The carapace scutes usually remain firmly attached. During the following 2 weeks (until approximately 1 month after death) flesh, connective tissue and keratinous skin remains that persist become thoroughly dried out and mummified. Some scutes may begin to lift off the underlying carapace bones. The durations of subsequent stages are much more variable; in part this appears to be a reflexion of the size of the individual and probably the degree of ossification and thickness of the carapace bones. Smaller tortoises with a curved length of 61–71 cm with less robust carapace structures reach the stage of disintegration in which individual carapace bones begin to collapse after a period of between 4 and 7 months, while tortoises of 71–80 cm curved length took between 7 and 15 months to reach the same stage. Unfortunately the period of observation was too short to give a clear indication of the time required for larger individuals to reach this stage of disintegration, although it would seem likely to be about 2 years, or possibly, in the largest individuals, in excess of 3 years.

(*b*) *Predators and scavengers*

As has already been pointed out, the long-term rates of breakdown of tortoise remains laid out after post-mortem examinations were thought to be accelerated. However, the records of scavengers visiting the remains are probably a fair indication of those animals playing the most significant rôle in the initial stages of decay under natural conditions. Ten carcases were monitored at 3 h intervals for 4 days and thereafter twice a day until 1 week after death.

These qualitative observations indicated that by far the most important agents of initial decomposition were various species of dipteran larvae, which were evident within the first 24 h and were active throughout the carcase within 36–48 h. Large red ants swarmed over the remains during the hours of darkness and large black ants were evident during the day. Of the Crustacea, which were regarded as scavengers of major importance, *Birgus latro* (the robber or coconut crab) was the most frequent visitor, with as many as 14 in the vicinity of the body at a time. They were almost exclusively active at night and the very early morning and could be seen tearing off the fleshy remains, dragging away limb bones and entrails and even gnawing at the carapace with their chelae. They were thought to be responsible for the complete disappearance of the remains of one small tortoise with an incompletely ossified carapace (38.5 cm curved length). *Cardisoma carnifex* was also a common visitor at night, and where they occurred *C. cavipes* were also frequently to be seen at night and during the day. *C. hilgendorfi*, *C. perlatus* and *Geograpsis grayi* were occasional visitors.

Pied crows (*Corvus albus*) were often observed feeding on the remains and sacred ibis (*Threskiornis aethiopica abbotti*) were also often present in the vicinity. The latter were observed feeding on insect larvae and pupae as well as small particles of flesh. Grey and green herons were also occasionally seen close to the remains. No flightless rails (*Dryolimnas cuvieri*) occurred in the areas where the tortoise carcases were laid out. Where present they would have almost certainly taken advantage of the abundant insect food source associated with a tortoise corpse. Swingland

TABLE 2. RELATIVE RATES OF BREAKDOWN FOR NATURAL MORTALITIES OF TORTOISES IN DIFFERENT SIZE CLASSES

curved length / cm	number of remains	duration of each breakdown stage/day						
		stage 1	stage 2	stage 3	stage 4	stage 5	stage 6	stage 7
61–70	6	1–2 (6)	2 (3)	3 (0)	14–150 (6)	60–180 (2)	90–180 (2)	120–210 (3)
71–80	7	1–2 (7)	2–12 (9)	14–30 (8)	60–210 (8)	180 (1)	180–270 (2)	210–450 (2)
81–90	10	1–2 (10)	2–12 (10)	14–17 (8)	30–210 (16)	90–180 (2)	150–270 (2)	150 (1)
91+	8	1–2 (8)	2–16 (8)	10–30 (7)	60–540 (14)	— (0)	450 (1)	— (0)

DESCRIPTION OF PLATE 1

FIGURE 1. Bloated remains of a tortoise 4 days after death (stage 2).

FIGURE 2. Mummified remains of a tortoise some 20 days after death (stage 3).

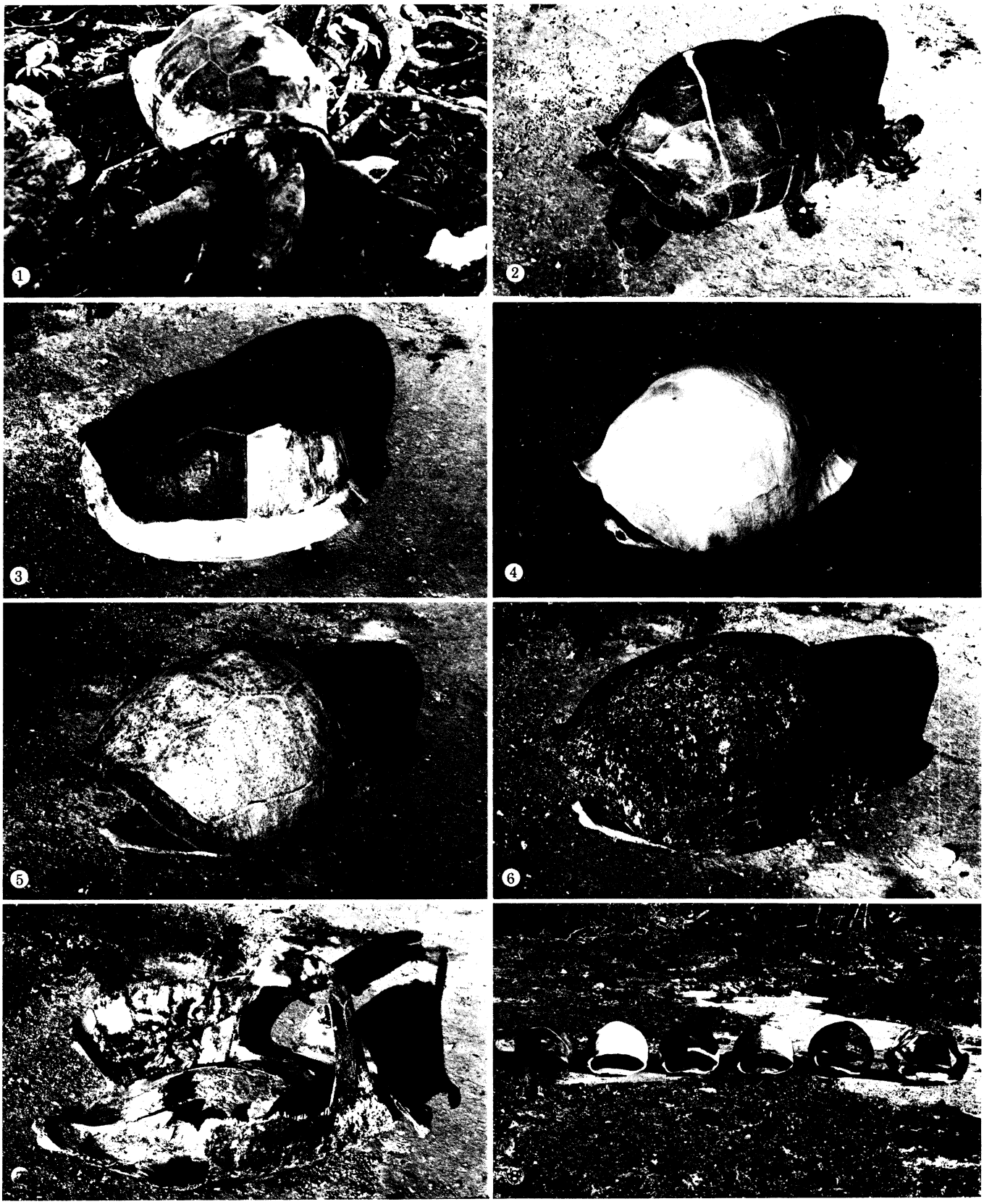
FIGURE 3. Tortoise remains approximately 3 months after death. Most scutes still in place, some lateral and marginal scutes detached, revealing discoloured carapace bones beneath (stage 4).

FIGURE 4. After about 5 months all scutes have been removed and the carapace bones have been bleached white by the sun. This example is typical of remains found in exposed positions (stage 5).

FIGURES 5 AND 6. The initial phase of carapace disintegration can be seen: transverse cracks in the carapace are developing along the sutures (stage 6). The two photographs also show varying degrees of algal/bacterial invasion and growth. The carapace in figure 6 was found in a sheltered, well shaded position.

FIGURE 7. Tortoise remains in an advanced state of carapace disintegration (stage 7).

FIGURE 8. Stages 1–7 are here illustrated for comparison.



FIGURES 1–8. For description see opposite.

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has demonstrated that these birds compose an important element of predation on young tortoises and hatchlings (Swingland 1976, personal communication). Finally, in the field it was not uncommon to find tortoises feeding on the putrid remains of natural tortoise mortalities.

Conclusions

There is considerable variation in the rates of breakdown of tortoise carcases on Aldabra. In part this variation is closely related to the size of the individual, larger animals having more highly ossified carapace bones which break down more slowly than those of smaller individuals. It is also likely that the degree of exposure of the remains and the general condition of the tortoise at the time of death are both important contributors to the observed variation in the rates of breakdown. In spite of the small number of carcases monitored in shade, Coe (1978) has demonstrated that the carcases of elephants dying in this position show delayed bone exfoliation compared with exposed material.

Tortoises in the size range 61–70 cm curved length took up to 7 months for their carapaces to disintegrate; those in the size range 71–80 cm curved length took up to 15 months and larger individuals had not reached this stage after 18 months when observations were terminated. It may therefore be conservatively estimated that the average persistence of the remains of adult tortoises is about 2 years. This is the figure used by Bourn & Coe (1978) in their treatment of mortality data collected during a sample census of the giant tortoise population of Aldabra. Live tortoise density was found to be 26.95/ha in the southeast of the atoll; 77% of this population were larger than 60 cm curved length. The mortality density in the same area was 1.2/ha. If tortoise remains persist on average for about 2 years this represents a mortality of 0.6/ha/a. By proportion this is equivalent to an annual mortality rate of 29/1000 individuals. We are well aware that this procedure will underestimate the mortality rates of smaller tortoises and overestimate that of larger individuals. When, however, further data become available from the continuing monitoring programme on Aldabra we will be in the unique position of being able to determine within acceptable limits the mortality rates of a large proportion of the size ranges of tortoises present in the population.

We should like to thank the Natural Environment Research Council for funding this work on Aldabra and the Royal Society for providing facilities at the Aldabra Research Station which made life in this difficult terrain bearable and work possible. We have continuously been encouraged by members of the Animal Ecology Research Group in Oxford. Dr John Phillipson and Dr Ian Swingland have greatly assisted us both in general and specific discussions.

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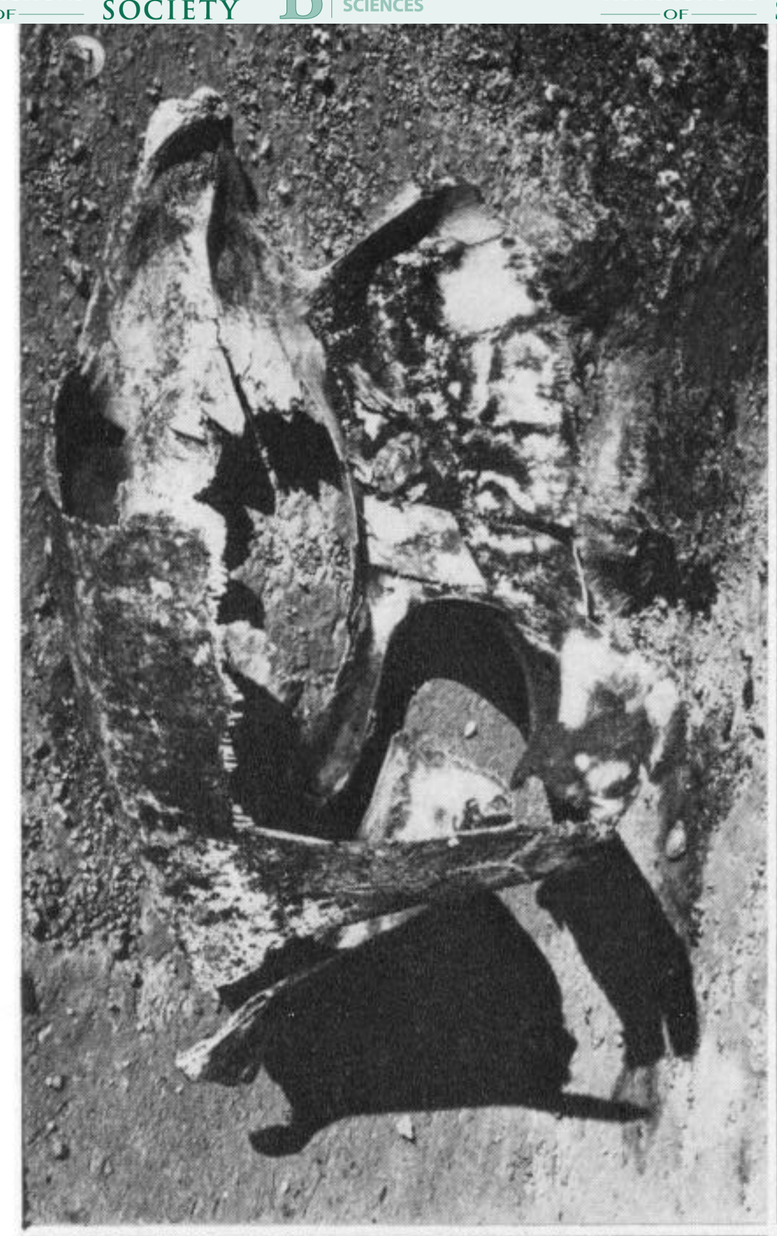

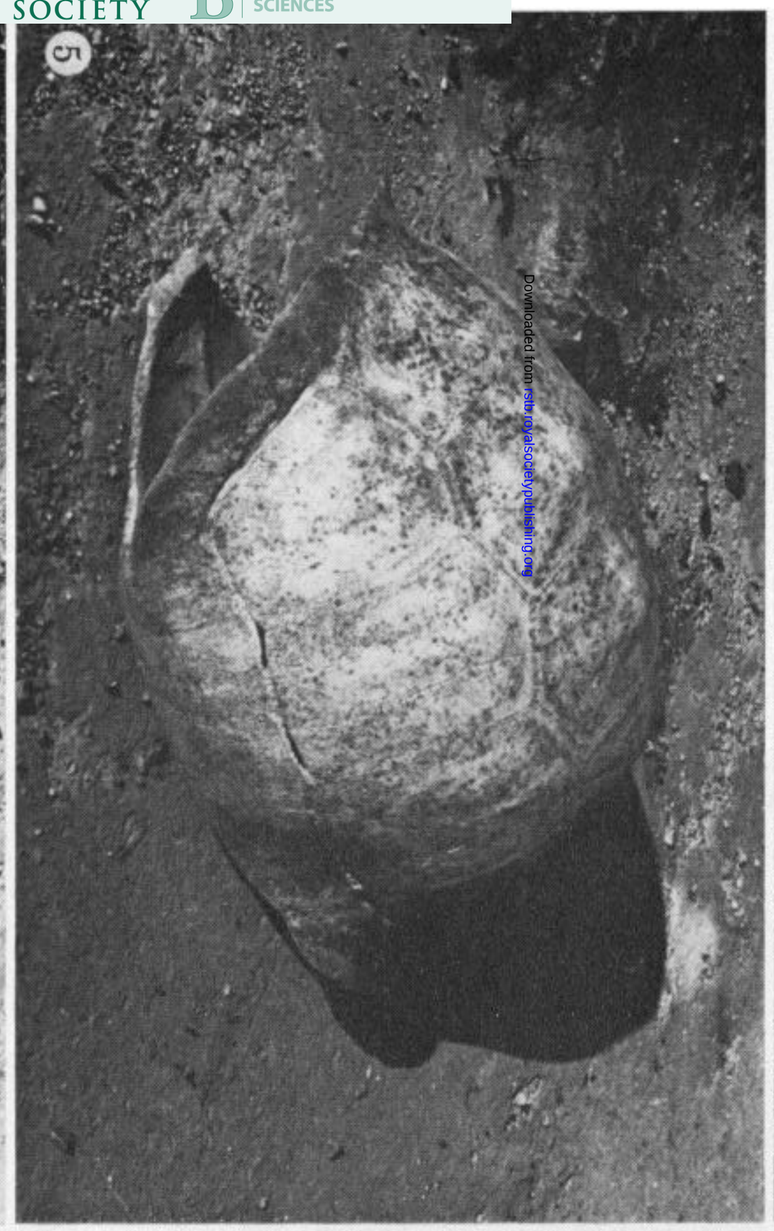

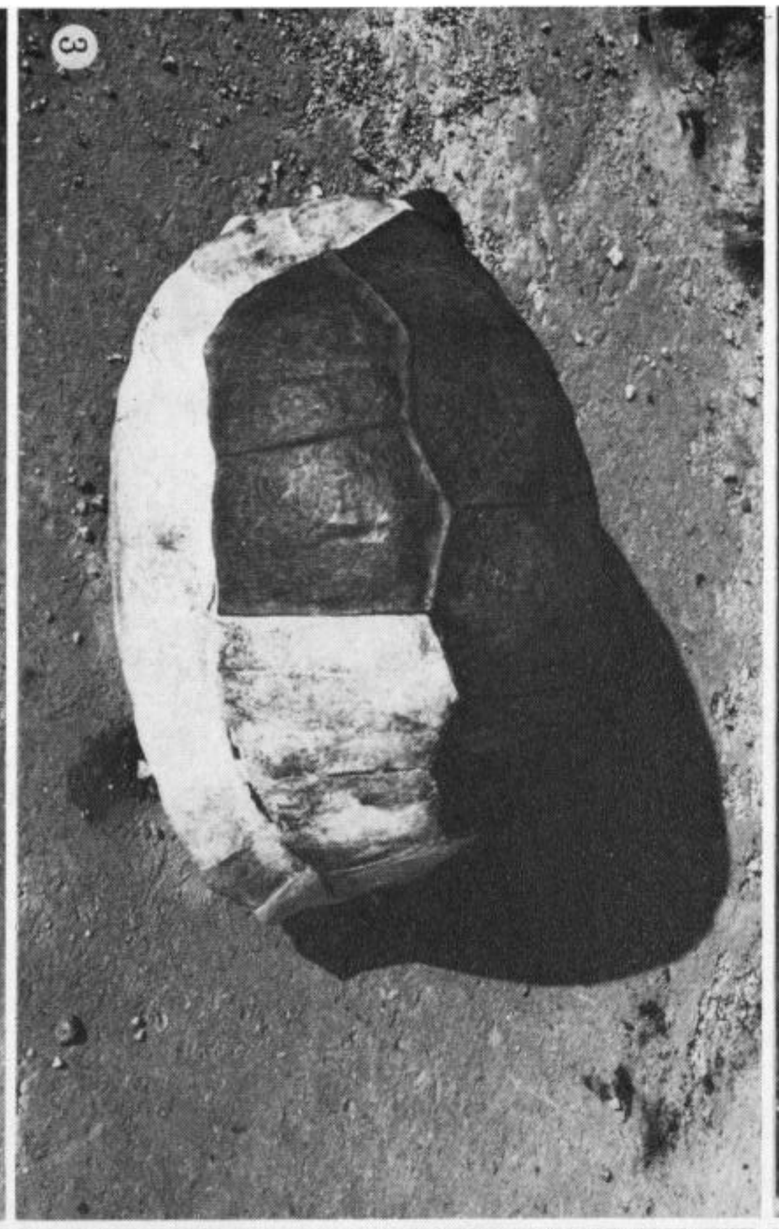

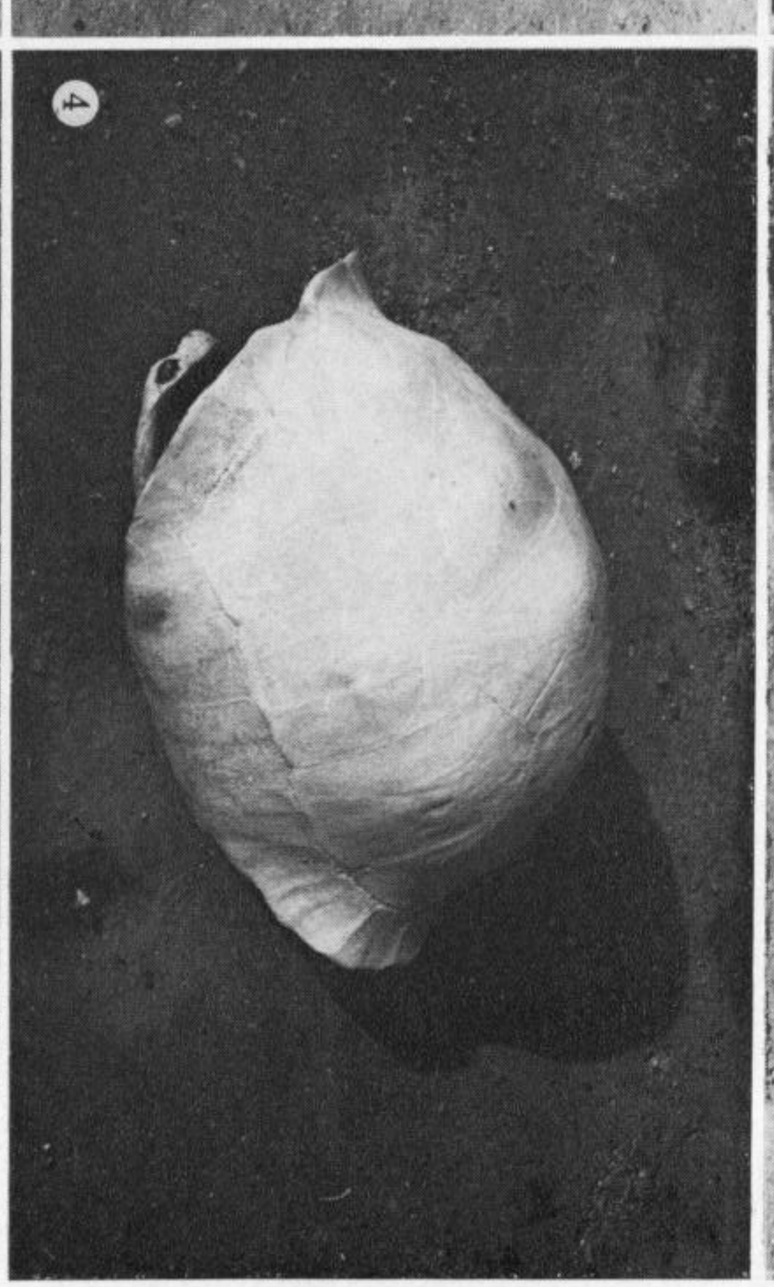

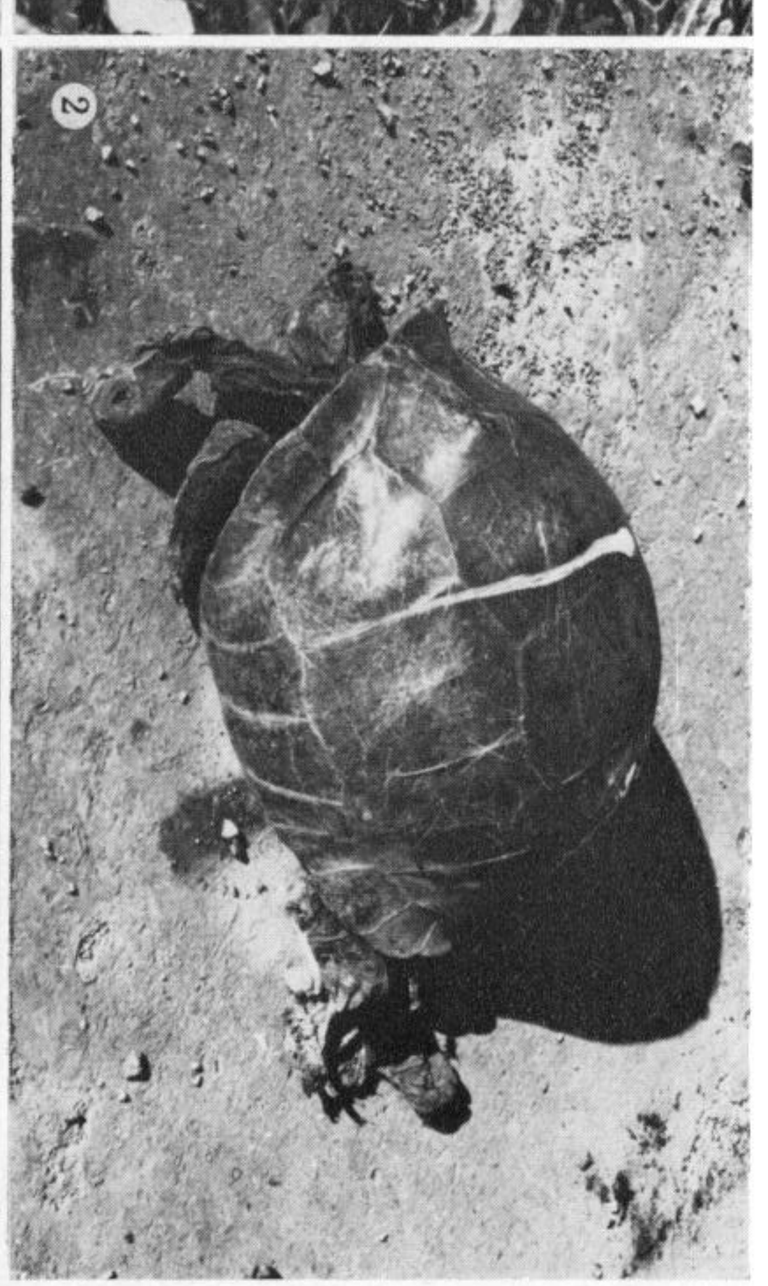

FIGURES 1–8. For description see opposite.