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Indian Ocean giant tortoises: their systematics and island adaptations

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Although wild populations are now confined to Aldabra, giant tortoises were originally present on many other Indian Ocean islands. All belong to the genus *Geochelone* but are referable to two distinct subgenera, *Cylindraspis* in the Mascarene islands and *Aldabrachelys* on Madagascar, Aldabra, the Seychelles and neighbouring islands. These are distinguishable by skull and nasal structure, degree of shell ankylosis and structure of the plastron. Neither group has obvious close relatives in other areas. Mascarene tortoises, which are completely extinct, comprised several species: *G. vosmaeri* and the smaller *G. peltastes* on Rodrigues, *G. inepta* and *G. triserrata* on Mauritius, and what should probably be called *G. indica* on Réunion. All the tortoises of Aldabra, the Seychelles and neighbouring islands seem to be referable to one species, *G. gigantea* which appears to have shown some geographical variation. Madagascar probably had two species, *G. grandidieri* and another usually named *G. abrupta* which may well be conspecific with *G. gigantea* and was possibly the source of the Aldabra populations.

Many of the distinctive features of Indian Ocean and Galápagos giant tortoises are interpretable as adaptations to the peculiar environment of ocean islands, particularly their lack of big predators and competing herbivores.

1. Introduction

When Europeans reached the various small islands of the west Indian Ocean, they encountered giant tortoises on many of them (Stoddart & Peake 1979, this volume). All of these populations, except that on Aldabra, became extinct in the wild by the early nineteenth century, largely as a result of human exploitation for food, but introduced mammals, such as dogs, rats and pigs, may also have played a part in at least some cases, particularly by destroying nests and young animals. Giant tortoises also existed on Madagascar but had apparently disappeared by the time Europeans arrived. Their remains are quite abundant, often looking very fresh, and radiocarbon dates suggest that some of them are only about two millenia old (see §5*b*). So it is not impossible that the species they represent overlapped with the first human colonists of Madagascar, who may have occupied the island not much more than 1100 years ago (Mahé & Sourdat 1973), and were exterminated by them.

Comprehensive systematic studies of the Indian Ocean giant tortoises were largely initiated by Albert Günther whose investigations culminated in the appearance of his monograph, *Gigantic tortoises (living and extinct) in the collection of the British Museum*, published just over a century ago. This stimulated a great deal of work over the next 30 or 40 years (see, for example, Boulenger 1889, 1891, 1894; Gadow 1894; Günther 1898; Rothschild 1906, 1915; Sauzier 1892, 1893; Vaillant 1885, 1893, 1898, 1899, 1900, 1903) but since then there has been relatively little interest in the relationship of these animals. It is therefore, perhaps appropriate to review their systematics here and at the same time speculate about their adaptations to island life.

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In the following account, *tortoise* is used for members of the family Testudinidae, *carapace* refers to the usually domed upper part of the shell of a tortoise, *plastron* to its lower section and *bridge* to the regions joining the two. Unless otherwise stated, shell lengths given are maximum straight-line lengths of carapaces. The following abbreviations are also used: B.M.(P), British Museum (Natural History), Department of Palaeontology; B.M.(Z), British Museum (Natural History), Department of Zoology; C.A.S. California Academy of Sciences, San Francisco; M.H.N.P.(P), Muséum Nationale d'Histoire Naturelle, Paris, Institut de Palaeontologie; M.H.N.P.(R), Muséum Nationale d'Histoire Naturelle, Paris, Reptiles et Poissons; U.M.C., University Museum of Zoology, Cambridge; unreg., unregistered.

2. Main groups of Indian Ocean giant tortoises

All of the Indian Ocean giant tortoises belong to a single genus, *Geochelone* Fitzinger 1835, which, until some 20 years ago was regarded as part of *Testudo* Linnaeus 1758, but appears to have had a long independent history (Loveridge & Williams 1957). *Geochelone* also includes the Galápagos giant tortoise, *G. elephantopus* (Harlan 1827), and about 13 smaller species found in the warmer parts of South America, Africa, Madagascar and southern Asia. It has a fossil record extending back to the Eocene (Auffenberg 1974) and its members are quite varied, being grouped into a number of subgenera, three of which are now restricted to the Indian Ocean. One, *Asterochelys* Gray 1873, is confined to Madagascar and contains relatively small tortoises, *G. radiata* (Shaw 1802) and the possibly conspecific *G. ynophora* (Vaillant 1885), while the others are made up of giant species. Of these *Cylindraspis* Fitzinger 1835 contains all the Mascarene forms and *Aldabrachelys* Loveridge & Williams 1957 those of Madagascar and the islands lying north of it. The moderately large tortoises of Africa, *G. pardalis* (Bell 1828) and *G. sulcata* (Miller 1779) belong to yet another subgenus, *Geochelone sensu stricto*. *Cylindraspis* and *Aldabrachelys* show several clear points of difference which are summarized below.

(*a*) *Skull and nasal passages*

The skull of *Cylindraspis* is essentially similar to those of other relatively large members of the genus *Geochelone*. It is not particularly elevated, the external nasal opening is about as high as wide and the supraoccipital crest is relatively long, laterally compressed and blade-like (figure 1). In *Aldabrachelys* the skull is high, especially in front, the external nasal opening vertically elongated and the supraoccipital crest quite short, and not usually compressed. This combination of specialized cranial structures is not known in any other recent tortoise and the elevated anterior region is correlated with a peculiar arrangement of nasal passages, at least in *G.* (*Aldabrachelys*) *gigantea*. No material exists of *Cylindraspis* in which the structure of the nasal chambers and their adnexae can be investigated but, from the formation of the anterior part of the skull, it is likely that it did not differ significantly from the basic arrangement found in nearly all modern species of *Geochelone*. In these, the passage from the nostril to the nasal chamber is short and not very inclined, the chamber itself is rounded in outline and its olfactory section is broadly open anteriorly (figure 2). In *G. gigantea*, on the other hand, the passage from the nostril is broad and long and ascends quite steeply. It is also singular in having a posteriorly directed diverticulum arising from its ventral wall. The olfactory part of the nasal chamber is elongate, extending further backwards than in other *Geochelone*, and anteriorly

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there is a flap-like ridge that contains cavernous tissue projecting from the medial wall. This may be capable of closing off the olfactory area in life.

It is not easy to envisage what selective pressures might have been responsible for the development of the specialized head structure found in *Aldabrachelys*. The deepening of the skull and shortening of the supraoccipital crest produce some alteration in the arrangement of the big adductor muscles running to the jaw but the functional consequences of this are not known. Observations by I. R. Swingland (personal communication) do, however, suggest a possible reason for some aspects of the peculiar nasal structure. He found that *G. gigantea* sometimes drinks by drawing water in through the nostrils instead of through the mouth. This ability would be beneficial to a tortoise living in arid habitats since water could be extracted from shallow puddles and cavities far too small to allow the mouth to be submerged below the surface for conventional drinking. The rather pointed snout of *G. gigantea* would also be advantageous in reaching the bottom of such hollows. In this context, the configuration of the olfactory section of the nasal chamber and the development of a possibly valvular structure

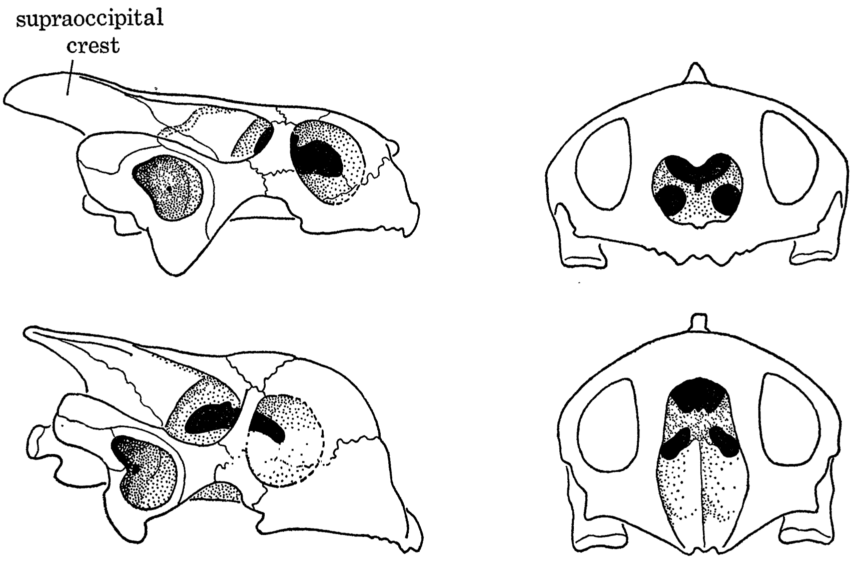

FIGURE 1. Skulls of Indian Ocean giant tortoises, lateral and anterior views. top, *G.* (*Cylindraspis*) *inepta* from Mauritius; bottom, *G.* (*Aldabrachelys*) *gigantea* from Aldabra.

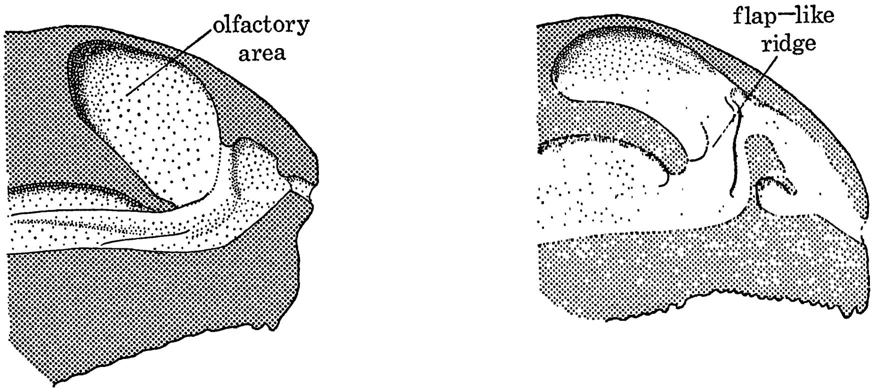

FIGURE 2. Right nasal passages of tortoises, lateral views: left, usual arrangement in *Geochelone* (based on *G. pardalis*, B.M.(Z) 1931.7.20.411); right, arrangement in *G.* (*Aldabrachelys*) *gigantea* based on B.M.(Z) 1978.772.

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at its entrance could be interpreted as devices that prevent its flooding, something that might be expected to happen in tortoises with more usual nasal structure (figure 3).

(*b*) *Shell thickness and ankylosis*

The species of *Aldabrachelys* have shells that are typically either moderately or very thick and, as in most other tortoises, the component bones usually remain separate although in a few (usually large and apparently old) animals there is at least some fusion. In *Cylindraspis*, shells are much thinner and in some cases even large shells may be only 1 or 2 mm thick in places. Also, nearly all of the available shells exhibit considerable ankylosis.

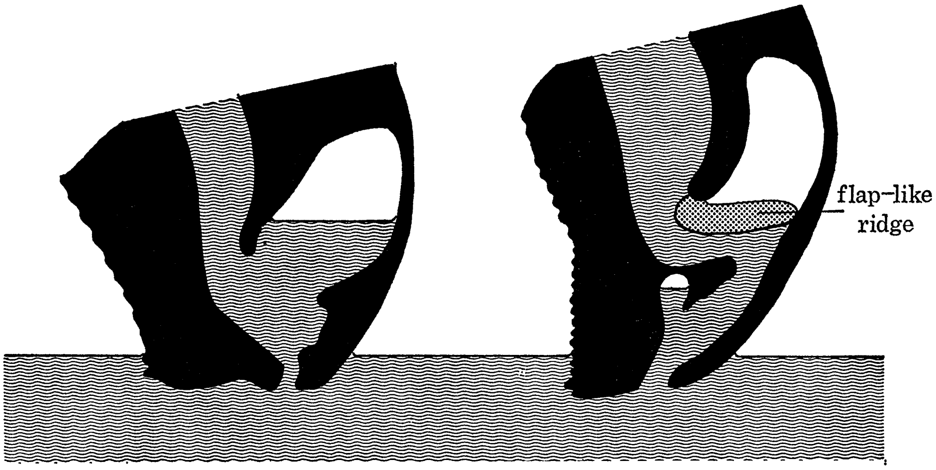

FIGURE 3. Hypothetical results of drinking water through nose: left, typical *Geochelone*, olfactory section partly flooded; right, *G. gigantea*, olfactory section free of water.

(*c*) *Size of front opening of shell*

In shells where it can be measured, the height of the front opening of the shell divided by its width gives about 0.28–0.43 for *Aldabrachelys* and about 0.45–0.9 for *Cylindraspis*.

(*d*) *Structure of the plastron*

Aldabrachelys is like most other *Geochelone* species in having a relatively large plastron, its length being about 73–95% of that of the carapace, and the front margin is thickened on its upper side to produce a distinct lip. The anterior tip is rounded and covered by a pair of scales, the gulars. The plastron of *Cylindraspis* is often smaller, its length frequently being only 66–77% of that of the carapace and the front margin is not clearly thickened although there is usually a T or + shaped swelling on the upper side. The anterior tip is either rounded and covered by a single gular, or forked and covered by two.

Proportions of the bones forming the anterior plastron also differ. In *Aldabrachelys*, the entoplastron is of moderate size and the epiplastra meet the hypoplastra broadly on each side of it. In *Cylindraspis* the entoplastron is relatively larger and the contacts between epiplastra and hypoplastra are restricted.

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3. Relationships and origins

Aldabrachelys and *Cylindraspis* each possess characters that are specialized (apomorphic in the terminology of Hennig (1966)) compared with equivalent conditions in the other and in *Geochelone* as a whole. *Aldabrachelys* has its peculiar skull and nasal structure and *Cylindraspis* is singular in the frequent ankylosis of its shell and in some features of its plastron. Given the marked nature of their differences, it seems likely that the two groups have had substantial separate histories and neither in its present form can be regarded as very close to the stock that gave rise to the other. Little can be said about the affinities of these subgenera to other tortoises. Mascarene examples with forked plastral tips, usually named *Geochelone gadowi* (Van Denburgh 1914) are often thought to be related to the Pleistocene *Geochelone* (*Megalochelys*) *atlas* (Falconer & Cautley 1837) of the Siwalik hills, north India, since it too shows this feature (Rothschild 1915). But some degree of plastral forking occurs in members of a number of disparate tortoise groups, so it is quite likely to have arisen independently, a hypothesis strengthened in the present case by the fact that, apart from their forked tips, the anterior plastra of *G. gadowi* and *G. atlas* are very different. In fact there may be a better case for associating *G. atlas* with *Aldabrachelys*, for a poorly preserved skull that may be attributable to this species (Lydekker 1885) appears to have a vertically elongated external nasal opening, approaching the specialized condition found in the Aldabran tortoises and their relatives. However, a great deal more would need to be known about *G. atlas* and allied forms before such a connection could be accepted. The Indian Ocean giant tortoises differ in the uncertainty of their origin from those of the Galápagos which have clear affinities to extant species in South America and are referred to the same subgenus, *Chelonoidis* Fitzinger 1835.

All three groups of insular tortoise seem likely to have reached their present ranges by transmarine migration. This is certainly true for Aldabra which has probably been submerged twice during quite recent times (Braithwaite, Taylor & Kennedy 1973) so that postulations about earlier land connections could not be used to explain the presence of tortoises. Floating or rafting seem feasible means of dispersal, for giant tortoises appear to tolerate contact with salt water quite well. The Galápagos *G. elephantopus* is known to float without injury for at least several days (Van Denburgh 1914) and Townsend (1936) records two that survived apparent transport across the sea by a hurricane for over 32 km (20 miles). *G. gigantea* is reputed to have made rather similar journeys (Vaillant 1899) and Grubb (1971) notes that it can swim reasonably well, unlike the Galápagos tortoise (Van Denburgh 1914), and has been seen floating well offshore. As it frequently forages on beaches, the chances of its being washed out to sea must be quite high.

4. Giant tortoises of the Mascarenes (subgenus *Cylindraspis*)

The tortoises of the Mascarenes are reviewed elsewhere (Arnold 1981), so only a brief account of them will be given here. They abounded on all three large islands but were exterminated by about the end of the eighteenth century. Because they disappeared so early, very few specimens were collected from living populations and knowledge of the group is based largely on fossils, in all samples of which the main elements of the skeleton are dissociated.

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(*a*) *Rodrigues*

Shells from Rodrigues show great variation in shape and, because of this, have been assigned to more than one species, Vaillant (1898) and Rothschild (1915) recognizing three and Auffenberg (1974) two. Examination of available material shows that shells and shell fragments certainly fall into two distinct classes. One, to which the name *G. peltastes* is given, consists of relatively small shells up to only 42 cm in length which are smooth, domed in outline and with unreflexed margins (figure 4*a*). The other, on which *G. vosmaeri* is based, contains shells reaching a maximum length of 85 cm with lumpy surfaces, strongly raised fronts and reflexed margins (figure 4*b*, *c*). Although some populations of the Galápagos tortoise (*G. elephantopus*) show ontogenetic change from rounded juveniles to adults with high-fronted shells (figure 4*d*–*f*), a single-species interpretation based on growth changes cannot be applied to the Rodrigues tortoises, for, while known *peltastes* and *vosmaeri* shells almost overlap in size, there are no specimens that could be regarded as intermediate in morphology. Furthermore, all the larger *peltastes* shells have their constituent bones completely fused together, a situation that would have made further growth impossible. Nor can the two shell types be regarded as sexual variants. The degree of dimorphism in size and form that would be involved is far greater than in any known tortoise species and there are strong indications that they both included animals of two sexes. Each contains some individuals with deeply concave plastra and others with relatively flat ones, in living tortoise populations typically characteristic of males and

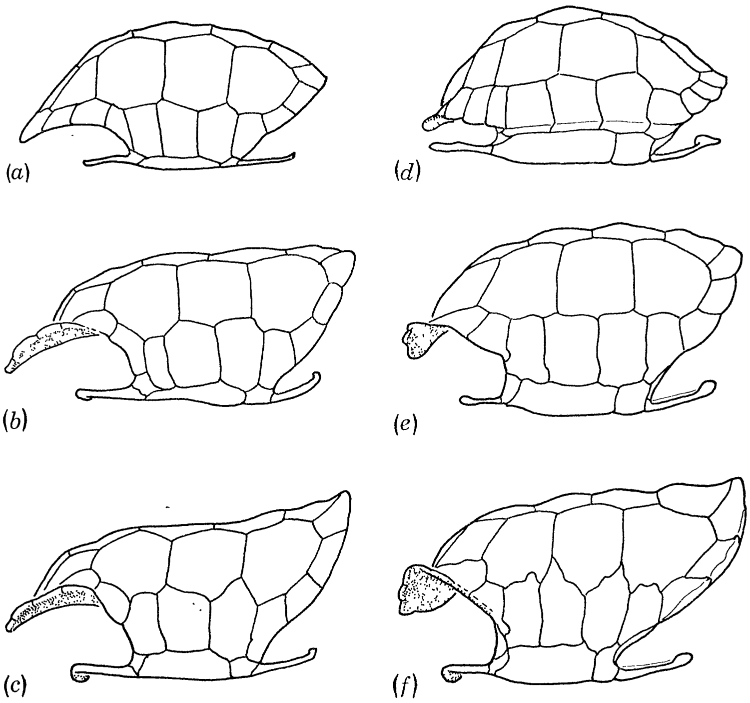

Figure 4. Tortoise shells from Rodrigues (left) and some Galápagos islands (right). (*a*) *G. peltastes*, male (40 cm); (*b*, *c*) *G. vosmaeri*, males (56 cm, 85 cm); (*d*) *G. elephantopus*, young animal (32 cm); (*e*) female from Pinzón (52 cm); (*f*) male from Fernandina (86 cm) ((*b*) based on Vaillant (1893); (*e*) and (*f*) on Van Denburgh (1914)).

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females respectively. It seems very probable therefore that there were two species of tortoise on Rodrigues. The third form described by Vaillant (1898) as *Testudo commersoni* is apparently synonymous with *G. vosmaeri*.

One problem with this interpretation is that no young *G. vosmaeri* shells are known but this may well be an artefact. Unlike similarly sized adult *G. peltastes*, their bony shells would not have been fused together, and being thin would have been very liable to fall apart after death. As the nineteenth century excavators who collected much of the known Rodrigues material consistently ignored small fragments, it is not surprising that no certain material of young *G. vosmaeri* is represented.

The two species of tortoise apparently present on Rodrigues must have been closely related for, although the shells are distinct, it does not seem possible to separate the other skeletal elements into two classes, except for the humeri. Such a degree of similarity is known in other sympatric tortoise species, for instance the Mediterranean members of *Testudo*, and *Geochelone denticulata* and *G. carbonaria* in South America. The two Rodrigues species seem to have been synchronous as shells of both are known in which the external keratinous scutes are present, suggesting recent origin, and both types appear to occur in the same cave deposits. The presence of two species of relatively large tortoise on such a small island is extraordinary. However, although Rodrigues is only about 118 km^2 now, it is very likely that it was considerably larger in the past (see, for example, Montaggioni 1970) and the two forms may even have speciated *in situ*.

The differences in adult size and shell shape in the two Rodrigues tortoise species may be functionally correlated with reducing direct competition by utilization of different food resources. Some support for this hypothesis is available from still surviving Galápagos tortoises. Here, where there were originally 14 separate tortoise populations, forms with high fronted ('saddle-backed') shells are largely associated with dry islands supporting only sparse vegetation and more rounded shells with lusher habitats. Mascarene tortoises show some tendency to follow this pattern, Rodrigues, the driest island, having the most saddle-backed animals. It is argued (Snow 1964; White & Epler 1972) that shell shape is related to differences in browsing opportunities. In rich habitats there is an abundance of food near the ground which can be reached easily and a smooth, rounded shell allows easy progress through dense vegetation. On dry islands where food is less easily available there is a premium on being able to browse over a more extensive vertical range, and a long neck is therefore advantageous. Its length may be as much as three-quarters that of the shell in some Galápagos saddle-backed males and *G. vosmaeri* must have at least approached this. The high shell front allows greater extension of the neck and raises its base, increasing the maximum upward reach; it also provides the necessary increased storage space when the head is withdrawn (the proximal part of the necks of tortoises forms a relatively rigid vertical arc when contracted that cannot be compressed easily). In the sparsely vegetated habitats usually occupied by saddle-backed tortoises, the unstreamlined shell is not a great disadvantage in locomotion. The sexual dimorphism in shell form and neck length found in saddle-backed Galápagos populations may increase the efficiency of exploiting the total feeding niche, but no observations on this point seem to have been reported.

The Galápagos situation suggests that on Rodrigues the large, high-fronted *G. vosmaeri* may have occupied more open habitats than *G. peltastes* and browsed higher. As might be expected where two species instead of one occupy roughly the same ecological space, the two Rodrigues forms show restricted variability in features that probably correlate with resource exploitation.

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Thus there appears to be less variation in shell shape than is encountered in some Galápagos populations and there is no indication of marked sexual dimorphism.

(*b*) *Mauritius*

At least nine names have been applied to the Mauritian tortoises. Most of these are synonyms, but it seems that, as on Rodrigues, two well defined species were present which should be called *Geochelone inepta* Günther 1873 and *G. triserrata* Günther 1873. The skulls of *G. inepta* have two ridges on each side of the palate, like nearly all other tortoises. These support the horny, blade-like structures with which food is bitten. *G. triserrata*, on the other hand, is unique in having three ridges on each side. This difference correlates with others, such as the relative width of the partition between the internal nasal openings and degree of bone fusion, and it is therefore impossible to regard it as attributable to variation within a single species. Two kinds of shell were found associated with the skulls, one of which (upper shell, figure 5) is essentially domed with a rounded plastral tip covered by a single gular scale and all the bones are completely ankylosed. The other, represented only by fragments, has a roughly horizontal anterior dorsal profile (rather like the lower shell in figure 5), a forked plastral tip covered by two gular scales (on which the name *G. gadowi* is based), and the bones of the shell are incompletely fused. It is not certain to which species they should be assigned but the degree of ankylosis suggests that domed shells may be *G. inepta*. The two forms were almost certainly synchronous for their remains appear to have been found promiscuously mixed at two sites (the marsh called Mare aux Songes in the southeast of the island and in caves near La Pouce in the northwest). They are less alike than the two Rodrigues tortoises but, as on that island, anatomical features suggest that they may have reduced direct competition by exploiting different ranges of resources. The palatal structure indicates that there could have been dietary specialization and shell shapes might be interpreted as adaptations to different habitats and different browsing ranges.

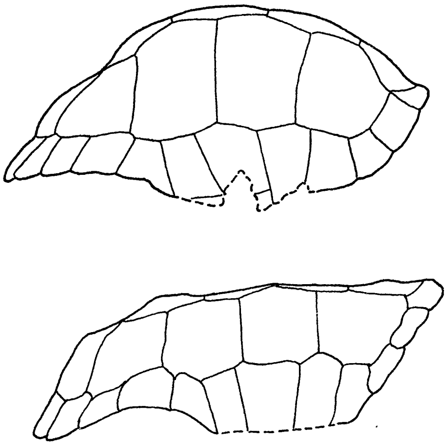

FIGURE 5. Top, domed shell from Mauritius, possibly of *Geochelone inepta* (based on U.M.C. R. 3846); bottom, carapace thought to be from Réunion (M.H.N.P.(R) 452), similar to high fronted Mauritius shells which may be attributable to *G. triserrata* (based on Vaillant 1900).

No evidence exists as to how the two species came to inhabit Mauritius. One possibility is that it resulted from a double invasion. The skull and presumed shell of *G. inepta* are quite

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similar to ones found on Rodrigues in several features and it may be that the ancestors of this species reached Mauritius from that island after *G. triserrata* was established. The direction of predominant currents and winds are appropriate for this. It might be thought that colonists landing on an island occupied by a similar species would be excluded but, while this may usually be so in stable conditions, it need not apply in periods of climatic change such as have frequently occurred in the Quaternary. For instance, in a period of increased aridity, the success of *G. triserrata* on Mauritius might have been reduced, perhaps resulting in its exclusion from some dry coastal areas. This could have allowed a more dry-adapted invader to survive the critical period of early colonization. Once coexistence had been established on the basis of differences in tolerance of aridity, other niche differences and their anatomical concomitants could have evolved.

(*c*) *Réunion*

Réunion tortoises are very poorly known, the only available material that certainly originated there being some bone fragments collected recently by G. S. Cowles. They show only that at least some animals had the ankylosis of shell bones frequent on the other Mascarene islands. Apart from these, there is a carapace without data in Paris (M.H.N.P.(R) 452; figure 5) that is the type of *Testudo indica* Schneider 1783 and may have come from Réunion. It is rather similar to the high-fronted shell type from Mauritius, possibly referable to *G. triserrata*, but differs in the shape of its anterior margin and greater thickness. If the supposition about its locality is correct, then the name *Geochelone indica* would apply to at least some Réunion tortoises. Petit (1737) investigated what he believed to be a Réunion tortoise and illustrated its palate which is very like that of *Geochelone triserrata*, but given the inaccuracy of many eighteenth century localities it is difficult to know what credence to give this report; the tortoise might after all have come from Mauritius. Taken at its face value, the little evidence available suggests that a tortoise similar to *G. triserrata* may have occurred on Réunion, which would not be entirely unexpected as this island is close to Mauritius and the two have some other reptile types in common. Whether Réunion was like Mauritius in having two species of tortoise is unknown.

5. Giant tortoises of Aldabra, the Seychelles and Madagascar (subgenus *Aldabrachelys*)

(*a*) *Aldabra, the Seychelles and nearby islands*

With the exception of Aldabra, wild tortoises disappeared from these islands by the early nineteenth century. Some continued to exist in captivity and semi-feral conditions but had often been transported from their natural localities to other places. With the rise in interest in giant tortoises, many of these animals found their way to museums and private collections to join the few earlier ones already there, but, as with these, any locality data attached to them were almost always suspect. It was on such material that a total of seven species was described between 1812 and 1906 (see §5*c*). Examination of the descriptions, and in most cases the types, of these forms, as well as of over 80 other specimens now in the British and Paris Museums, strongly suggests that all of them are assignable to a single species for which the applicable name is (fortunately) *Geochelone gigantea*. The total variation encountered is considerably less than that found in the Galápagos tortoises, which are all generally acknowledged to be assignable to one species. There is no evidence that more than one kind of tortoise existed

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at any locality and it does not seem possible to divide the available material into discrete groups on the basis of the differences encountered within it. Furthermore, as a proportion of the specimens have been in captivity, some of the variation present may be attributable to this, for tortoises are notorious for their tendency to develop odd shell shapes when subjected to unnatural conditions (see, for example, Schweizer 1965). Considerable emphasis has been placed on the presence or absence of the nuchal scale in classifying these animals and one supposed species, *G. sumeirei* was separated partly because the type lacks this scale. However, the condition may vary within an island population. This is true for the Aldabran tortoises where, although most have a nuchal, it is absent in a small minority (Gaymer 1968).

While only one species appears to have been present, this would be expected to have shown some geographical variation, since it extended over at least 1200 km of ocean, a far bigger range than any other insular tortoise. But the lack of specimens with good locality data, apart from Aldabra animals, makes it difficult to check this adequately and impossible to describe the pattern of regional variation formally in terms of subspecies. All that can be done is to compare known Aldabran material with the sample lacking reliable data, on the assumption that, although the latter certainly contains some tortoises from Aldabra, other populations will be represented. This seems likely, for some of the individuals included appear to have histories extending back to a time when the Seychelles still had tortoises and Aldabra was not often visited. When such a comparison is made, a clear difference in incidence of the nuchal scute is found. Of 236 Aldabran animals, the nuchal is absent in only three (most data from Gaymer 1968) but in the sample with poor data it is absent in 8 out of 77 (statistically significant: $p < 0.01$, χ^2 test). Shell shape is difficult to quantify but Aldabran adults more frequently have the anterior marginal scutes of the shell clearly reflexed upwards and the hind margin flared than those with poor data. It could be argued that the different pattern of variation in the sample with doubtful localities results from bias in its selection, managers of taxonomic collections tending to place a higher premium on specimens showing minority conditions. This factor undoubtedly exists but is probably insufficient to explain wholly the differences between the two samples. It might be minimized if Aldabra tortoises could be compared with the long established herds of *G. gigantea* on Mauritius which have probably not been subjected to such selection.

Although the sample with poor data suggests that non-Aldabran tortoises may in general have had less reflexion of the anterior edge of the shell, there was almost certainly considerable inter-populational variation in this and other features. In the British Museum, there are two recent fossil bony carapaces and some fragments (B.M.(P) R.4682, R.9373) which were received from the Cambridge Museum in 1919 and are attributable to *G. gigantea*. Unfortunately they lack firm data but correspondence related to their transfer suggests they may well have been collected by the Percy Sladen Trust Expedition to the Indian Ocean on one of the Seychelles or neighbouring islands (Gadow 1918, letter, British Museum, Palaeontology Department archives). In this material both the anterior and latero-posterior margins of the carapace are strongly reflexed and there is a distinct tendency for the fronts of the carapaces to be raised. So the latter modification has arisen independently in all three recent groups of insular giant tortoises (see § 6 *b*).

(*b*) *Madagascar*

Remains of giant tortoises are especially common in marshy areas in the west and southwest of Madagascar (Mahé 1972) but also occur in caves (Boulenger 1894). Much material is

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fragmentary and not many substantially whole shells are available for examination. The nine located and investigated in this study fall into two groups. Seven†, to which the name *Geochelone grandidieri* (Vaillant 1885) is applicable, are distinctly flattened and the carapace is very robust, sometimes being over 40 mm thick at the margins and from 18 to 30 mm in the thinner areas of the posterior dorsolateral region. It is usually very rugose and lumpy although smoother towards the periphery and the sutures marking the contiguous borders of the horny pleural and marginal suites are sinuous. The anterior and posterior margins of the carapace are often flared and a nuchal scute is usually present. A skull associated with B.M.(P) R. 1972 is clearly of the *Aldabrachelys* type but differs from that of *G. gigantea* in its flatter frontal region and more robust post-orbital bar; Mahé (1965*a*) describes a similar skull from Beloha, SW Madagascar. Boulenger (1894) provides good illustrations of this form, which attained a carapace length of at least 122 cm. Auffenberg (1966) suggests that the manus of *G. grandidieri* may differ from those of other *Geochelone* in having many elements fused, but I have not been able to confirm this.

The other two shells examined‡ include the type of *Geochelone abrupta* (Vaillant 1885) and differ from the *G. grandidieri* material in having a less flattened carapace with less bulging flanks which is also relatively thin, being 20–25 mm at the edges and 8–10 mm in the less robust parts of the posterior dorsolateral area. Also, the sutures between the costals and marginals tend to be straighter. In both specimens, the posterior margin of the carapace is slightly flared and in B.M.(P) R 5890 this is also true of the front edge, which lacks a nuchal scute, but this region is missing in the Paris individual. No skull has yet been firmly associated with *abrupta*-type shells (Mahé, personal communication) which attained a carapace length of at least 115 cm.

It is likely, in view of the degree of difference between their shells, that *G. grandidieri* and *G. abrupta* are not conspecific, although they appear to be closely related, but more material is needed to confirm this. On present evidence, *G. grandidieri* seems to be a good species but, so far as can be checked, *G. abrupta* is very similar to *G. gigantea* and may be referrable to the synonymy of this form. The two kinds of giant tortoise in Madagascar both seem to have occurred quite widely, at least in the west of the country and may well have been synchronous. The radiocarbon dates cited by Mahé & Sourdat (1973) as being based on tortoise bones were determined with shell fragments of *G. grandidieri* (Mahé 1977, personal communication). These are: Bemafandry, 2060 ± 150 B.P.; Behavoha, 2160 ± 110 B.P. and Taolambiby, 2290 ± 90 B.P. Ages of specifically identified fragments of *G. abrupta* are not available but Mahé & Sourdat do give dates for two sites from which remains of this form have been extracted: Amparihingidro, 2850 ± 200 B.P. and Ampoza, 1910 ± 120 B.P. These figures suggest that the two types of Madagascan tortoise overlapped in time, a conclusion supported by the fact that at Ampasambasimba shell fragments apparently attributable to both forms occur in the same deposit (Mahé 1977, personal communication). Although there is no indication of differences in browsing ranges or of food specialization in the known anatomy of the two tortoise types, dietary differences may have existed, as might differences in habitat.

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† M.H.N.P.(P) unreg.; Etséré (= Etsara), SW Madagascar; ♂ (holotype of *G. grandidieri*). M.H.N.P.(P) unreg., carapace only; Etséré; (paratype of *G. grandidieri*). B.M.(Z) 94.6.5.1; Ambatumifuku, 110 km (70 miles) north of Nossi Bé; ♂. B.M.(Z) 1978. 773, carapace only; near Nossi Bé. B.M.(P) R.1972; SW Madagascar; ♀. B.M.(P) R.1975; SW Madagascar; ♂. C.A.S. 39606; near Nossi Bé.

‡ M.H.N.P.(P) 1884–30; Amboulitsate (= Ambolisatra), SW Madagascar; ♂ (type of *Geochelone abrupta*). B.M.(P) R.5890; Ampoza, SW Madagascar; ♂.

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Remains assigned to *G. abrupta* occur near the northwest seaboard of Madagascar at Amparihingidro (Mahé 1965*b*) and, although known *abrupta* do not have the anterior margin of the shell so clearly reflexed upwards or the hind margin so flared as in typical Aldabran animals, such populations may perhaps have been the source of the tortoises of the atoll for the prevailing currents run towards it from this coast. Most of the extinct Pleistocene lizards of Aldabra have very close relatives in Madagascar and seem likely to have arrived from there by transmarine migration (Arnold 1976), so it is not improbable that the tortoises did likewise. Possibly the Seychelles also received their tortoises from this source.

(*c*) *Synonymy of* Geochelone gigantea (*Schweigger*)

Testudo gigantea Schweigger, 1812: 327. Type locality: 'Brasilien'.

Testudo indica (part): Gray, 1831: 9.

Testudo elephantina Duméril & Bibron, 1835: 110. Type locality: Islands in Mozambique Channel (Anjouan, Aldabra, Comores) where frequently taken to Bourbon (Réunion) and Maurice (Mauritius). Types from Bourbon, Anjouan and Île de France (Mauritius). Types: M.H.N.P.

Testudo daudinii Duméril & Bibron, 1835: 123. Type locality: 'Indes orientales'. Type M.H.N.P.

? *Testudo abrupta* Milne-Edwards, 1868: 1161 (*nomen nudum*).

Megalochelys indica: Gray, 1873: 724.

Testudo ponderosa Günther, 1877: 35. Type locality: unknown. Type: B.M.(Z) 64.12.20.27 (skeleton and shell with scutes).

Testudo hololissa Günther, 1877: 39. Type locality: Aldabra. Type: B.M.(Z) 88.3.20.1. (stuffed).

? *Testudo abrupta* Vaillant, 1885: 874. Type locality: Amboulitsate (= Ambolisatra, SW Madagascar). Types: M.H.N.P.(P) 1884–30 (a partial shell, shell fragments, pectoral girdles and vertebrae).

Testudo sumeirei Sauzier, 1892: 395. Type locality: 'Mauritius'. Type: B.M.(Z) 1929.12.27.1/1947.3.4.1. (stuffed).

Testudo gouffei Rothschild, 1906: 753. Type locality: Thérèse Island, Seychelles. Type: B.M.(Z) 1949.1.4.66. (skeleton and shell; scutes and skin mounted separately).

6. ISLAND ADAPTATIONS

(*a*) *Adaptive pressures in small island environments*

Three quite discrete groups of tortoises have reached isolated oceanic islands and survived there until historic times and it is of some interest to consider to what extent their distinctive common characters are results of adaptation to these environments. *A priori*, substantial modification of colonizing species would be expected since ecological conditions on small distant islands are very different from those of the continental or large-island areas where they presumably originated. Among the more obvious features of small islands inhabited by giant tortoises that seem relevant in this context are the following: (i) absence of large predators; (ii) absence of large competing herbivores; (iii) relative simplicity of community structure, (iv) climatic variability: all the tortoise islands show marked seasonal fluctuation in rainfall, and both the Indian Ocean (Stoddart & Walsh 1979, this volume) and the Galápagos area

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(Palmer & Pile 1966) are prone to longer term changes. A probable result of these factors would be a tendency for tortoise biomass to vary, possibly cyclically. Lack of predators and competitors might allow rapid increase of a colonizer to levels where vegetation resources were damaged, after which decline in density could result in recovery of the vegetation and possible repetition of the sequence. The relative simplicity of the ecosystem might reduce any possible buffering of this cycle and long-term weather changes would also be likely to change carrying capacity. No clear evidence of natural change in biomass is available for the Galápagos or the Mascarenes but Aldabra has shown a huge population increase in the last 70 years that appears to be having an adverse effect on the vegetation (see, for example Hnatiuk, Woodell & Bourn 1976).

The features of small-island environments outlined above might be expected to produce the following changes in continentally derived tortoises. (i) Loss or modification of antipredator devices. (ii) Increase in width of food niche exploited: continental tortoises are grazers and low browsers, being partly restricted to this spatial range by competition from mammalian herbivores and, in the absence of these, modifications to utilize a broader spectrum of food resources are likely. (iii) Increase in intensity of direct intraspecific competition especially for food as a result of at least intermittently severe conditions and high densities. (iv) An increased tendency to store resources in response to fluctuation in food supply.

Many aspects of the morphology of giant tortoises can be interpreted in terms of these factors, particularly reduction in antipredator devices which is important in allowing development of features related to the others.

(*b*) *Reduction of anti-predator mechanisms and its advantages*

In order to discuss the modifications to anti-predator devices that have taken place in island tortoises, it is first necessary to describe the protective strategy typical of continental species. These are potential prey for a wide range of medium sized and large carnivores and for some omnivores, as is apparent in the Galápagos where anti-predator mechanisms are poorly developed and introduced dogs and pigs kill many tortoises up to curved carapace lengths of at least 55 and 40 cm respectively (MacFarland, Villa & Toro 1974). Young tortoises are of course preyed on by a much wider variety of animals. Having little agility or speed and not being aggressive, tortoises are almost entirely dependent on their shell for protection and many of the distinctive features of this group, when compared with the primitive emydine terrapins (Emydidae) that are almost certainly ancestral to them, seem to be adaptations to increase its efficiency. While not always impenetrable, the shell makes feeding on mature tortoises expensive in terms of effort and, although continental species are attacked by a variety of animals, this is probably only when more easily processed prey is unavailable; no specialist tortoise predator seems to exist. Among the more obvious features increasing shell protection is the pronounced doming of the carapace. This reduces the range of predators that can take a tortoise of given volume in their jaws, and also ensures that others will have to open them very widely, a position where their crushing efficiency is relatively low. As well as this, doming produces a very strong configuration for resisting external pressures. Its development in land tortoises was presumably permitted by the lack of hydrodynamic constraints that act on aquatic chelonians and it is also important in providing additional space within the shell for housing the longer gut characteristic of these vegetarian animals. Shell strength is further enhanced by stout buttresses running from the carapace to the plastron on each side of the

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anterior and posterior openings which increase the rigidity of the bridge regions. The bones of the shell are thick and there is very extensive interdigitation at their sutures. The costal bones forming the dorsolateral areas are wedge-shaped, the members of the series becoming alternately broader and narrower ventrally (fig. 3 in Auffenberg 1974), an arrangement that reduces possible distortion.

Anterior and posterior openings are small so that easy access is prevented, the carapace arching downwards from above and the plastron being very large, often flexed upwards in front and terminating posteriorly in two points, each of which extends between the opening for the tail and that for one of the hind legs. Bridge regions tend to be long and a secondary effect of this is that the humerus is bowed anteriorly so that its distal section can project more easily outwards in front of the bridge. In times of danger, the shell openings are blocked by the limbs which fit them very closely and have heavily armoured exposed surfaces.

The shell pattern outlined above occurs in the vast majority of present continental tortoises, the only exception being the soft shelled *Malacochersus* which takes refuge in rock crevices, but all the insular species deviate from it to varying extents. This is most marked in the Mascarene forms. In these, the domed profile of the carapace may be extensively modified and the buttresses become very slender. The bones of the shell are often very thin (in Rodrigues tortoises, bony shells 50–60 cm in length may be only 1 mm thick in places). In such shells the efficacy of interdigitation in producing strong and rigid joints between the constituent bones is greatly reduced and it may be that the ankylosis frequent in Mascarene tortoises is a substitute means of strengthening the shell, which has important skeletal functions apart from protective ones. If this is so, it is at first sight curious that more tortoises elsewhere do not show ankylosis since some added strength against crushing might be obtained with little increase in mass. Such fusion does of course prevent further growth but many tortoises do not increase much in size over a substantial period of their adult lives, so this is not necessarily a drawback. However, lack of sutures may well have disadvantages, at least in some circumstances. An ankylosed tortoise shell is rather like a bird's egg. Here, external pressures are transmitted widely through the shell when intact keeping unit stress low, but if pierced (for instance by the teeth of a predator), stresses concentrate at the edges of the resultant small holes, leading to swift and extensive spread of cracks (Gans 1951). Such far-reaching fractures are sometimes visible in Mascarene shells although usually appearing to be *post mortem* in origin. In a typical continental tortoise, the deeply interdigitating nature of the sutures produces enough rigidity for the shell to transmit external pressures widely but the structural discontinuity between the constituent bones of the shell means that cracks are unlikely to spread beyond the one in which they were initiated. Only in extreme circumstances, such as where shells are very thin, and small puncture wounds rare, would the advantages of ankylosis in giving added general strength outweigh the risks of extensive failure if penetrated.

The free edges of the carapace are somewhat thickened in Mascarene tortoises (probably because these areas would be liable to damage by bumping against hard objects) but this is not so marked as in continental animals and the plastron has extremely thin margins. Posterior and especially anterior openings of the shell are very large (figure 6). The front of the carapace does not extend so far ventrally and its dorsal profile may be horizontal or even inclined upwards, and the plastron is reduced (figure 7) with small anterior and posterior lobes. Bridges tend to be rather short and the humerus consequently straighter. The shell openings are too large to have been blocked completely by the limbs, which, at least in *G. vosmaeri*, had very little armour.

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Many of the features typical of Mascarene shells contribute to making them lighter. Estimates suggest that Rodrigues shells of about 40 cm length would only have been about one-third the mass of that of an equivalent-sized African *Geochelone pardalis*. Such lightening may be beneficial in a number of ways. It would reduce the cost of building, maintaining and carrying the shell and allow its development in conditions where calcium was in short supply, which may be true of some of the volcanic areas of the Mascarenes. Reduction in mass should also increase agility, an advantage in exploiting a wider spatial range of food resources than continental tortoises, and in conditions of strong intraspecific competition. Enlargement of the front orifice of the shell also has clear benefits in increasing upper limit of browsing (§4*a*). The large shell openings and reduction of the plastron are important in permitting more extensive limb movements, again contributing to agility. Observations on living *G. elephantopus* and *G. gigantea*

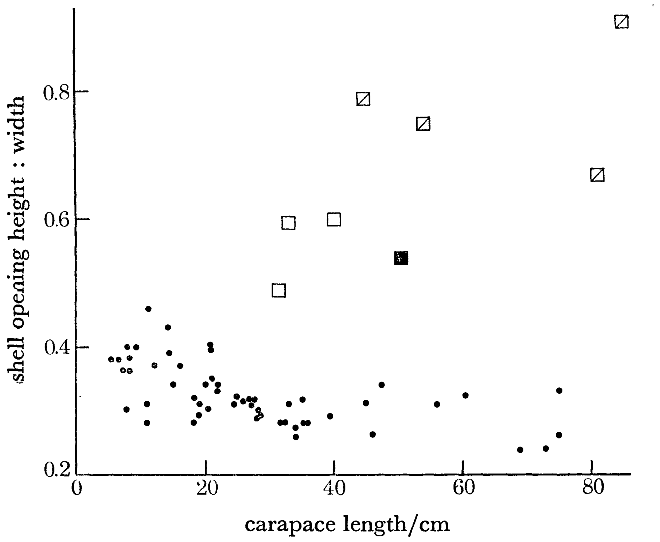

FIGURE 6. Proportions of anterior shell opening. □, Rodrigues shells, *G. peltastes*; ▨, Rodrigues shells, *G. vosmaeri*; ■, Mauritian shell, possibly of *G. inepta*; •, 12 species of continental and Madagascan *Geochelone*, namely *G. carbonaria*, *G. chilensis*, *G. denticulata*, *G. elegans*, *G. elongata*, *G. emys*, *G. forsteni*, *G. impressa*, *G. pardalis*, *G. platynota*, *G. radiata* and *G. sulcata*.

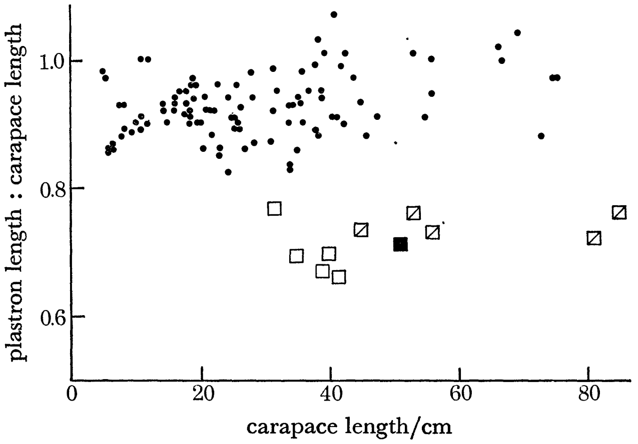

FIGURE 7. Relative length of plastron. □, Rodrigues shells, *G. peltastes*; ▨, Rodrigues shells, *G. vosmaeri*; ■, Mauritian shell, possibly of *G. inepta*; •, 12 species of continental and Madagascan *Geochelone* (see figure 6 for details).

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suggest that movement of the humerus in particular is considerably freer than in continental species and this, coupled with the relatively longer legs typical of the island forms, enables them to adopt a gait better adapted for coping with difficult terrain. In walking, the lower limbs appear to be held more vertically than in other tortoises, so that the shell is kept well clear of the ground and, although the humerus follows the edge of the plastron during the power stroke, it may be raised when returning forwards, so that the foot is more able to clear any irregularities in the substrate.

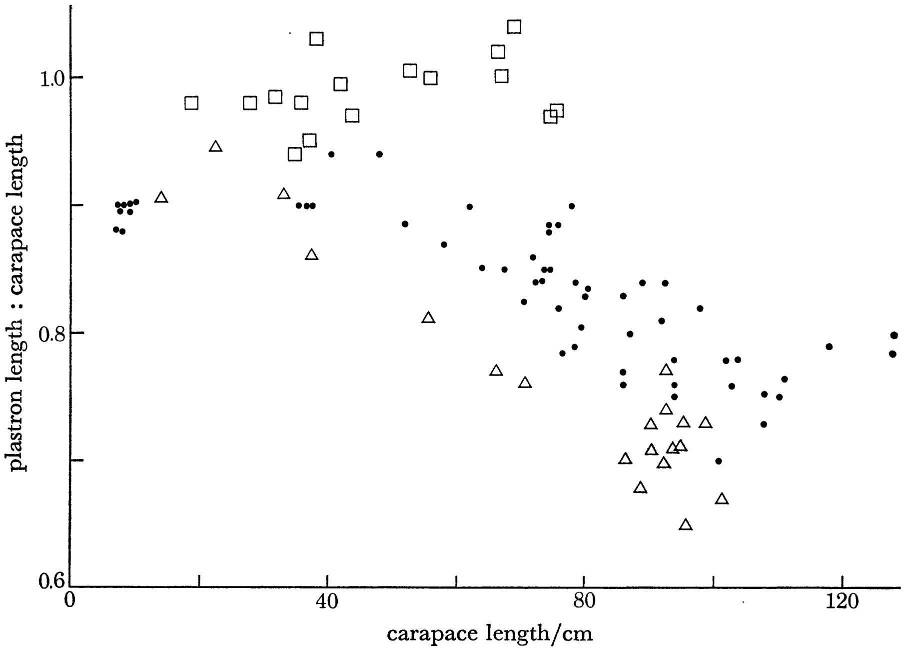

Figure 8. Change in relative length of plastron with growth. □, *G. sulcata*, continental Africa; •, *G. gigantea*, islands to the north of Madagascar; △, *G. elephantopus microphys*, Tagus Cove, Isabela island, Galápagos (data partly from Van Denburgh 1914).

As suggested previously, these tortoises may well have developed a tendency to store more resources than many continental species, in response to their markedly fluctuating food supply. This is difficult to confirm since relevant data for mainland species are lacking, but many authors comment on the very extensive fat deposits of giant tortoises, particularly the females, where it is used for egg production (see Vaillant (1893) and Froidevaux (1899) for the Mascarenes; and Van Denburgh (1914) for the Galápagos where an industry was based on collecting tortoise oil). Here again an open shell may be advantageous, for stored fat can easily be accommodated by the tortoise's bulging through the large shell orifices, avoiding displacement or compression of internal organs.

Galápagos tortoises show many of the presumed insular adaptations seen in Mascarene species but some are considerably less marked. Development is greatest in dry-island populations but even these are not so extreme in their general shell thinness, tendency to ankylosis, reduction of plastral lobes and thinness of plastral margins. Tortoises from moister, better vegetated habitats deviate even more but still show differences from continental tortoises in their often thinner shells and reduced plastra, bigger shell openings and relatively long necks and legs. Most Indian Ocean island *G. gigantea* are rather similar to these. They show comparatively little difference from their possible ancestral populations in Madagascar but this is

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not really unexpected, as here too predator pressure was probably not nearly as great as on the continental mainland.

At least some Galápagos and Indian Ocean populations show a tendency not discernible in available Mascarene material. This is for the plastron to decrease in relative size with growth (figure 8), which may be connected with the natural patterns of predation on these islands. In the Galápagos (MacFarland *et al.* 1974) and on Aldabra (Bourn & Coe 1979, this volume) large tortoises are immune to endemic predators but juveniles are not. In these circumstances, reduction of the plastron with growth means that young animals are well protected but adults gain the advantages of a less restricting shell. In all of the island tortoise species, there is an analogous trend in size of the anterior shell opening which increases with age. This is most obvious in saddleback populations but also occurs in the others.

Pigmentation may also have been modified in response to lack of predators. Nearly all continental species of tortoise appear to be cryptically coloured, and in many cases have disruptive markings, especially when young, but most island giants are almost entirely uniformly blackish which makes them conspicuous in some environments. Occasional *G. gigantea* (such as the type of *Testudo gouffei*) are paler and some of the few Mascarene shells with scutes are brownish but in the latter instance this is probably due to change *post mortem* in very old material. Sombre colouring may be important for thermal reasons since a dark surface will absorb a greater amount of solar radiation than a lighter one. This could be advantageous in cool conditions in allowing tortoises to approximate more closely to their optimum body temperature. But any such benefit would have to outweigh the increased risk of overheating at high temperatures, a common cause of death on Aldabra in areas where shade is unavailable (Bourn 1976).

If, as suggested here, development of many features typical of island tortoises was possible only in the absence of large predators and competing herbivores, it would be expected that exposure to these would be more harmful to the most strongly modified tortoise populations. A variety of mammals have been introduced to many islands but interpretation of any decline in tortoises is not easy as human exploitation has often apparently overshadowed the effects of other predators. However, it may be significant that the highly modified tortoises of the Mascarenes have disappeared completely with no survival in captivity even though the introduced *G. gigantea*, which shows less reduction in anti-predator mechanisms, has been kept on Mauritius for many years and breeds successfully there. Similarly in the Galápagos, figures quoted by MacFarland *et al.* (1974) suggest that on the whole the saddle-backed races have suffered more than those approaching closer to the continental type.

(*c*) *Large size*

Nearly all recent populations of oceanic island tortoise are characterized by large size. Usual maximum carapace lengths in historic times of the various populations range from about 75 to 130 cm, so that the largest are about 1.75 times the length of the smallest. This compares with a range of about 10–130 cm in all modern tortoises (largest 13 times length of smallest) and, if fossil forms such as *Geochelone atlas* are included, the maximum is extended to more than 180 cm (largest over 18 times length of smallest). So there may well be factors acting to restrict size in the island forms to a fairly limited range. Relatively large dimensions may be beneficial in increasing the vertical limit of browsing possible and big animals may be likely to survive longer in adverse conditions, an undoubted advantage on small islands. The

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only exception to large size in these insular tortoises is *G. peltastes* of Rodrigues which is only known to have reached a carapace length of 42 cm. However, this may be because the much bigger *G. vosmaeri* had pre-empted the niche-space where large size was an advantage.

Although the island tortoises are nearly all large compared with present continental species, it is not certain that any of them evolved great size in direct response to small-island conditions. In the past, very big tortoises were found in continental areas and on large islands and these forms may have been the source of some of the recent oceanic populations, as already suggested for Aldabra. This seems quite probable, for large tortoises are more likely to survive long spells of drifting than small ones since their dimensions and apparently greater buoyancy would enable them to keep their heads clear of the water and decrease the risk of drowning. Their survival time without food or fresh water would also probably be much greater. In the case of the Aldabran tortoises, the only instance where it is possible to make a relatively precise suggestion of the origin of an island population, there is no evidence of size increase. The supposed parent form in Madagascar, *G.* '*abrupta*', reached a carapace length of at least 115 cm (though admittedly the few remains are of a later date than that likely for the last colonization of the atoll by tortoises), whereas Grubb's (1971) biggest Aldabran specimen was 105 or 106 cm and the large fossil humerus mentioned by this author probably came from an animal with a carapace length of around 110–115 cm.

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