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GEOCHELONE ROBUSTA (ADAMS 1877): AN INSULAR GIANT?

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ABSTRACT

Giant size is probably plesiomorphic among insular giant tortoises, that is they are probably descended from a giant tortoise ancestor that reached the island overland or by making a sea-crossing. *Geochelone robusta* is unlikely to have evolved giant size in Malta as most of the known fossil European species of *Geochelone* were giant tortoises and the ancestor of *G. robusta* is thus likely to have been a giant tortoise. This species was a palaeotropical relict, that is a survival from the time, earlier on during the Tertiary, when the climate of the region was warmer. *Geochelone robusta* survived the cold stages of the pleistocene and Quaternary because the climate in Malta during the very coldest stages did not include prolonged, severe frosts.

INTRODUCTION

Adams (1877) described two species of large tortoise from Zebbug cave, Malta, and Tagliaferro (1913) described yet another from Kordin (Corradino). Nevertheless, it seems likely that these specimens were different-sized individuals of the same species (Savona Ventura, 1984).

A *Geochelone* of large size has also been reported from Sicily (Burgio & Fiore, 1988; Burgio & Cani 1988). It is not known whether the Sicilian and Maltese *Geochelone* were conspecific or even closely related. *Geochelone (G.) robusta* (Adams, 1877) from Zebbug Cave, Malta, Middle Pleistocene) is believed to have exceeded one meter in length, and thus ranks among the giant tortoises of the fossil record. This paper examines the hypothesis that giant size evolved on the Maltese Islands.

DISCUSSION

The Island Rule. Vertebrate biologists have long shown an interest in insular giants and dwarfs that differ markedly in size from their relatives on the mainland. Van Valen (1973) summarised the information available by proposing a rule, known as Van Valen's rule or the Island rule. This states that small species of vertebrate evolve larger size on islands, whereas large species become smaller. Lomolino (1985) provided convincing evidence in favour of the Island rule, showing that the rule holds good for mammals. Numerous examples of insular gigantism and dwarfism have been reported in the literature (see Azzaroli, 1982; Adler & Levine, 1994; Case, 1978; Sondaar, 1977, 1991; Thaler, 1973; and references therein). Exceptions to the rule are, however, numerous, even among mammals, and the data available on insular birds and reptiles are by no means conclusive (Lundelius, 1990). Brown & Lomolino summarise modern research on the evolution of body size among vertebrates living on islands (Brown & Lomolino, 1998, pp 434—444).

Giant tortoises. As Auffenberg (1974) has pointed out, giant tortoises living on islands are not examples of insular gigantism. Giant tortoises have roamed all the continents except Australia and Antarctica since the Eocene, and they appear to have become extinct everywhere except on a few oceanic islands.

Fig. 1 documents the shrinkage of the range occupied by species of *Geochelone* in the Western Palaearctic. Most of the species included in the figure were giant tortoises, approaching or surpassing one metre in length of carapace. The maximum carapace length of living species in the genus varies from 26 to 125 cm (Ernst & Barbour, 1989). Small species of *Geochelone* also exist. However there are very few smaller species in the Tertiary fossil record of the Western Palaearctic, most of the *Geochelone* species being large or giant tortoises.

Thus it is likely that Malta was colonised by a species of *Geochelone* that was already very large, and it is unlikely that giant size evolved in the Maltese Islands.

Evidence from other insular giant tortoises. As Whittaker (1998) has pointed out, the issue is whether a particular species of giant tortoise on an island evolved large size on that island or whether it was already a giant when it reached the island. Arnold (1979) was the first to point out that giant species of *Geochelone* can make sea crossings and colonise islands and appear to have done so with higher frequency than small species of tortoise.

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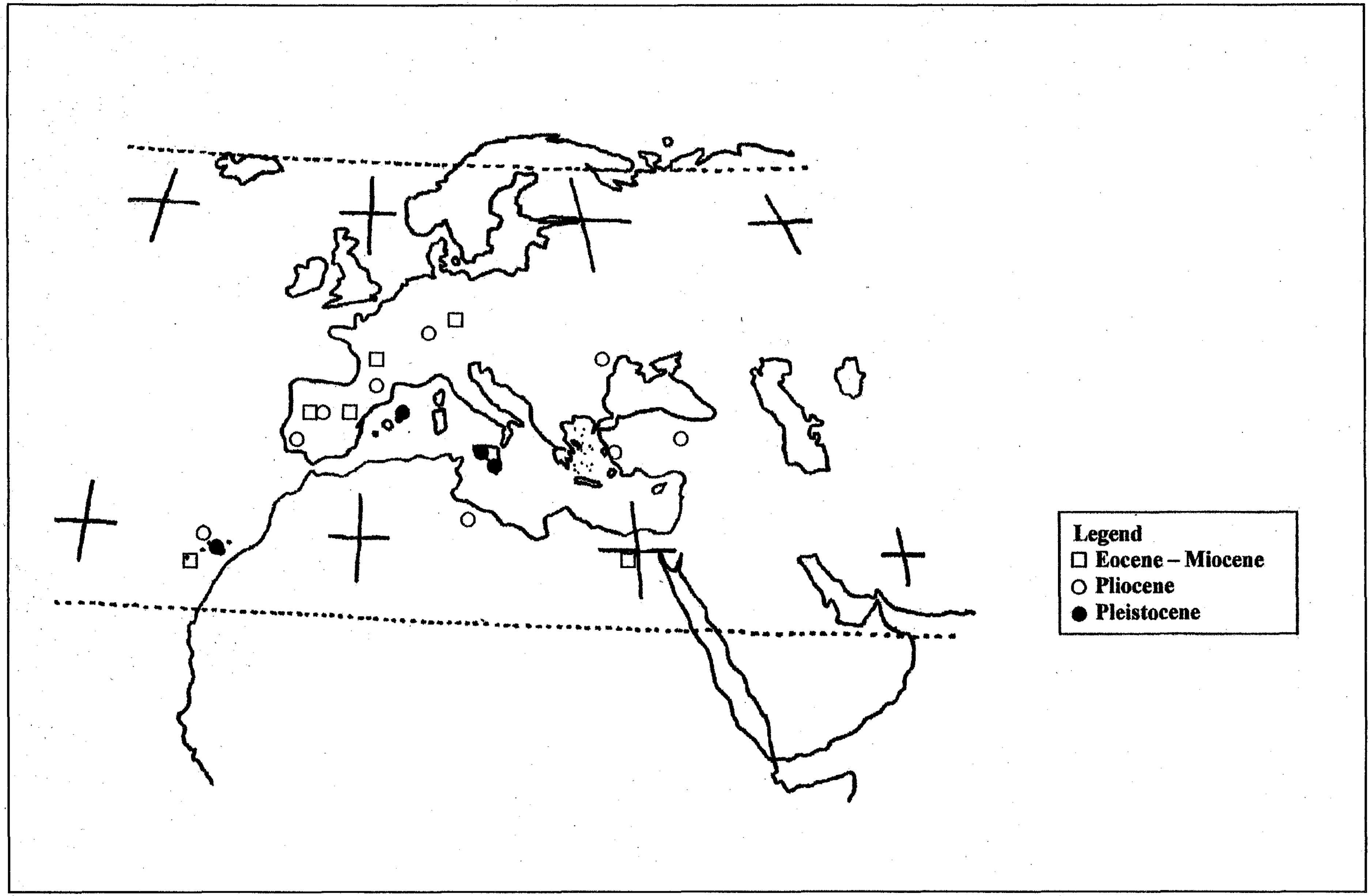

Fig. 1 The distribution of Western Palaearcic fossil species of *Geochelone*. Some of the symbols represent two or three species at approximately the same locality. Most of the species referred to in the figure were giant tortoises. The symbol on the Libyan coast refers to unnamed remains of a small *Geochelone* species.

Arnold refers to anecdotes in the literature well as modern observations to show that giant tortoises float well, with their heads well out of the water. Grubb (1971) saw an indidual *Geochelone (Aldabrachelys) gigantea* (Schweigger, 1812) floating in the sea 0.5 km from land in the marine lagoon inside Aldabra, Indian Ocean. Gaymer (1968) reported that this species has some control over its position and direction of movement while floating in sea-water. Giant tortoises are also more likely to survive prolonged immersion in sea-water and starvation than small species (Arnold, 1979). These facts mean that giant tortoises are better at colonising oceanic islands.

There is plenty of evidence to support these ideas. The Indian Ocean and Galapagos giant tortoises have clearly made sea crossings within the Mascarene, Seychelles and Galapagos archipelagoes. It is quite evident that the giant tortoises moved between the islands of each archipelago, making long sea crossings in the process.

Further support for this hypothesis comes from the subgenus *Aldabrachelys* of the genus *Geochelone*. Table 1 lists the distribution of the various species in this subgenus and gives their maximum size, showing that there are no small members of the subgenus *Aldabrachelys*. It seems likely that all *Aldabrachelys* species evolved from an ancestor that was very large, and that giant size is a plesiomorphy in this subgenus.

Further evidence comes from biochemical studies of the Galapagos tortoises [*Geochelone (Chelonoidis) elephantopus* (Harlan 1827) complex] (Marlow & Patton, 1981). These tortoises are not particularly closely related to any of the South American *Geochelone* species in the same subgenus. The mainland ancestor of the Galapagos tortoises is certainly extinct. Several extinct species of giant tortoise are known from South America, but no attempt has been made to identify a possible ancestor. As has happened elsewhere only small to large tortoises have survived in South America, all giant tortoises being extinct.

Hutterer *et al.* (1997) present information that could be interpreted to mean that *Geochelone* species increased in size in the Canary Islands. However the authors consider that more evidence is required before a definite conclusion can be reached.

In summary there is no clear evidence to suggest that insular giant tortoises have evolved giant size after colonising an island. It appears, rather, that giant size is plesiomorphic among such tortoises.

A Palaeotropical relict. Examination of figure 1 shows that during the Pleistocene, giant species of *Geochelone* are known only from Malta, Sicily, Minorca and the Canary Islands. Auffenberg (1974) argued that giant tortoises became extinct on mainland Europe and north America during the late Tertiary because they were unable to escape the cold by digging a burrow or taking refuge in

Table 1. The subgenus *Aldabrachelys* (genus *Geochelone*) on islands in the Indian Ocean.

Species	Locality	Age	Maximum size (cm)
G. (A) laetoliensis Meylan & Auffenberg 1987	Laetoli, Tanzania	Late Pliocene	114
G. (A) abrupta (Grandidier 1868)	Madagascar	Quaternary	125
G. (A) grandidieri (Vaillant 1885)	Madagascar	Quaternary	140
G. (A) daudinii (Dumeril & Bivron 1835)	Seychelles (granitic islands)	Recent (extinct)	80
G. (A) arnoldi (Bour 1987)	Seychelles (granitic islands)	Recent (living)	90
G. (A) gigantea (Schweigger 1812)	Aldabra	Quaternary to Recent (living)	106

Note. Data are from Bour (1987) and Meylan & Auffenberg (1987). The estimate for *G. laetoliensis* was made by the present author, using data in Meylan and Auffenberg (1987). The remains of *G. laetoliensis* are fragmentary but this species may have been ancestral to the Indian Ocean species.

a natural cavity, as the genera *Testudo* and *Gopherus* can do. If this argument is correct, the survival of *Geochelone robusta* in Malta until the arrival of humans in the Late Pliocene demonstrates that prolonged severe frosts did not occur in Malta, even during the coldest stages of the Pleistocene.

The earth's climate has cooled steadily since the end of the Cretaceous, 65 million years ago. By 12 - 14 Ma, mountain glaciers had begun to appear on high mountains in the higher latitudes of the northern hemisphere, and there was a permanent ice-sheet on Antarctica. Further sharp cooling took place around 6 - 5 Ma, with an ice-sheet appearing over the North Pole. During the Late Pliocene, around 2.5 Ma, a very sharp cooling took place and the earth's climate began to alternate by 4 to 10°C globally during climatic cycles. There is some evidence that large continental glaciers appeared in the northern hemisphere at this time and continued to appear during cold stages. Around 0.9 Ma, during the Pleistocene, temperature fluctuations increased markedly, and cold stages became colder. Most of the Pleistocene was colder than the present climate. Climates as warm as the Holocene have prevailed for only 10% of the time during the last 250,000 years (Bryant, 1997; Burrows, 2001; Prentice & Denton, 1988).

It seems likely that the appearance of continental ice-sheets in Northern Europe around 2.5 Ma, or shortly afterwards during the Late Pliocene, brought cold winters to most of the northern half of Europe, with frequent severe frosts. It is tempting to speculate that the continental European giant tortoises became extinct at some time during the Late Pliocene, but the fossil record of the genus *Geochelone* is far too meagre and the dating too imprecise to allow this hypothesis to be tested using the data in the literature.

Extinction. The extinction of *Geochelone robusta* in Malta appears to have occurred after the arrival of modern Man. Adams (1977) lists the contents of Zebbug cave, where giant tortoise bones were found. The remains of *Equus, Hippopotamus, Cervus, Elephas, Leithia, Cygnus* and *Anas* suggest that the cave was used as a larder by primitive humans. Caves remain cool in summer, virtually free from flies and the contents are safe from scavenging carnivores. Unfortunately the contents of Zebbug cave have not been dated reliably using modern methods. It seems reasonable to suppose that extinction was brought about by humans hunting the giant tortoises for food.

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