

West Indies, and the Galapagos Islands. Although never native to Australia or Melanesia, waif dispersal across marine barriers is common (Williams 1950a, 1952; Simpson 1942, 1943).

The living tortoises are for the most part subtropical to tropical in distribution, being most common in subhumid to arid grasslands and savanna habitats, though there are a few mesic tropical forest forms.¹ During the Tertiary their ranges extended throughout what are now temperate latitudes (Brattstrom 1961; Hibbard 1960; Auffenberg and Milstead 1965) (Fig. 1). This is believed due to a high degree of climatic equability, enabling tropical and temperate biotas to intermingle (Axelrod 1967). As the climate became cooler, the distribution of tortoises was obviously affected (Hibbard 1960; Brattstrom 1961). Quaternary tortoises in the middle and northern latitudes were subjected to at least four major periods of colder climate, often more moist. Drier, warmer climates characterized parts of the three interglacial ages. Each of the glacial and interglacial periods may have been cooler than the preceding corresponding periods. Though the evidence is meager, tortoises seem to have expanded northward during each interglacial. More important, the northern range limit of tortoises with each successive interglacial was farther southward. Though the range was smaller during glacial periods, it seems to have become more restricted with each succeeding advance, but none of these changes were severe enough to bring about major tortoise extinctions. During and after the last glacial, severe drought and cold in the northern latitudes played important complementary roles in extinction of large tortoises. Unlike their large contemporaries, smaller species of tortoises survived these major temperature changes by retreating into a burrow. It is inconceivable on mechanical grounds alone that the extinct giant tortoises of the Pleistocene tunneled. Few living testudinids of any size burrow in the earth. Those that are known to do so (*Gopherus* and some species of *Testudo*) continue to inhabit the higher latitudes.

Not all tortoise extinction can be explained solely on late Quaternary climatic changes. For example it does not fully explain the extinction of truly gigantic land species in tropical continental areas. Within historic times such giant species have lived only on islands without large predators. This has led some workers to suggest that gigantism in tortoises occurs only in the absence of predation, but this is not so. Each of the

¹ Few really complete ecological studies of tortoises are available. The more important ones are: Beck 1908; Fryer 1911; Miller 1932, 1955; Hediger 1935; Bogert and Cowles 1947; Woodbury and Hardy 1946; Guibe 1950, 1954; Cherchi *et al.* 1958; Cernov 1959; Eibel-Eibesfeldt 1959; Khozatsky 1959; Medem 1960, 1962; Honegger 1964; Obst and Meusel 1965; Carpenter 1966; Hutchison *et al.* 1966; Schmidt-Nielsen and Bentley 1966; Grubb 1967; Stoddart and Wright 1967; Frazier 1968; Auffenberg 1969; Auffenberg and Weaver 1969.