SHORT NOTES

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A HYPOTHESIS EXPLAINING THE ENIGMATIC DISTRIBUTION OF THE GEOMETRIC TORTOISE, *PSAMMOBATES GEOMETRICUS*, IN SOUTH AFRICA

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The genus *Psammobates* Fitzinger, 1835 comprises three species, namely *Psammobates geometricus*, *P. oculifer* and *P. tentorius* (Loveridge & Williams, 1957; Boycott & Bourquin, 1988; Branch, 1988). *P. geometricus* and *P. oculifer* are monotypic species, while *P. tentorius* is divided into three subspecies, namely *P. t. tentorius*, *P. t. trimeni* and *P. t. verroxii* (Loveridge & Williams, 1957; Greig & Burdett, 1976; Pritchard, 1979; Boycott & Bourquin, 1988). Previously the *P. tentorius* complex was subdivided into as many as 28 different species and subspecies (Hewitt, 1933).

It was suggested by Siebenrock (1904), Duerden (1907), Müller (1939) and Greig & Burdett (1976) that the *Psammobates* taxa fall into two groups, *geometricus* and *oculifer* constituting the one and the *tentorius* complex the other. The proposed sister group relationship between *geometricus* and *oculifer* is, however, based mainly on phenetic principles and does not necessarily reflect the true phylogeny. For phylogeny reconstruction, a cladistic analysis, based on the search for synapomorphies, is called for (Wiley, 1981). A preliminary analysis of phylogenetic affinities within *Psammobates*, forming part of a study on the biology and conservation status of *P. geometricus* (Baard, 1990), corroborated the above grouping.

The present distribution of the three species of *Psammobates* (Boycott & Bourquin, 1988; Branch, 1988), however, seems to contradict this grouping since the two sister species (*P. geometricus* and *P. oculifer*) are geographically separated by *P. tentorius*. Bearing in mind, however, that allopatric speciation is in all probability the most common mode of speciation (Wiley, 1981), it is to be expected that sister species initially will have allopatric distributions. Furthermore, it is not difficult to perceive that *P. tentorius*, through range expansion, could have penetrated into areas left void by a contracting *geometricus-oculifer* ancestral species.

As far as the herpetofauna of southern Africa is concerned, the southwestern Cape is considered the richest centre of endemism (Hewitt, 1910; Poynton, 1964; Poynton & Broadley, 1978). Restricted distribution ranges are characteristic of forms from the southwest, while forms in the northeast tend to have more extensive distributions. The genus *Psammobates* appears to conform to this general pattern in that the species with the smallest range, *P. geometricus*, is a southwestern Cape endemic. Poynton (1989: p.2) describes two contrasting faunas in the southern subcontinent, "the one being more cool-adapted and presently showing relict patterning in areas of high altitude and latitude, the other being warm-adapted with continuous ranges brought about by recent range expansion". He goes on to point out that this led to a "dynamic model involving reciprocal spreading and withdrawing of the interlocking cool- and warm-adapted groups following the cyclic changes in Quaternary climate". Mouton & Oelofsen (1988) discuss the importance of the Cape Fold Mountains, the coastal lowlands and the cold Benguela sea current in speciation events among cordylid lizards in the southwestern Cape. During changing climates these mountains become effective barriers trapping warm-adapted populations along the western coastal lowlands. Due to a supposedly increased influence of the Cold Benguela current on coastal climates during glacial periods, populations along the coastal lowlands become subjected to more adverse climatic conditions than inland sister populations. These coastal populations may become adapted to local conditions, and may eventually speciate.

It is not difficult to picture *P. geometricus* to have originated through a very similar series of events as that proposed for the *Cordylus cordylus* complex by Mouton & Oelofsen (1988). During a warmer interglacial period a warm-adapted ancestral species could have had an extensive range which also included the southwestern coastal lowlands. With the advance of a subsequent glacial period, range contraction and fragmentation could have taken place leaving behind an isolated population along the southwestern coastal lowlands. Due to differential environmental pressures west and east of the Cape Fold Mountains, the western population could eventually have diverged from the original eastern stock in becoming more cool-adapted.

Psammobates geometricus today occurs in three areas which are more or less geographically isolated from one another (Fig. 1). These are the southwestern coastal lowlands (the area from Gordon's Bay in the south to Piketberg in the north), the Worcester-Tulbagh valley and the Ceres valley. These three areas are separated from one another by mountain ranges. Presently *P. geometricus* occurs nowhere on mountainous terrain and it is therefore believed that such areas serve as physical barriers restricting movement of these tortoises and consequently gene flow among the populations. The question to be addressed therefore, is how these isolated populations originated or, in other words, how the populations were formerly geographically linked.

The answer to this depends on knowing the genealogical relationships among the extant populations. Because such information is not available at present, it would be impossible to arrive at any firm conclusions in this regard. It is, however, still possible to discuss the various ways in which the present populations could have been linked in the past.

During periods of lowered sea-levels (Deacon, Hendey & Lambrechts, 1983), the western coastal lowlands and the Worcester-Tulbagh valley could have been linked via the southern coastal forelands of the present day Hangklip area (Fig. 1). For example, Tankard's (1976) time-depth plot of

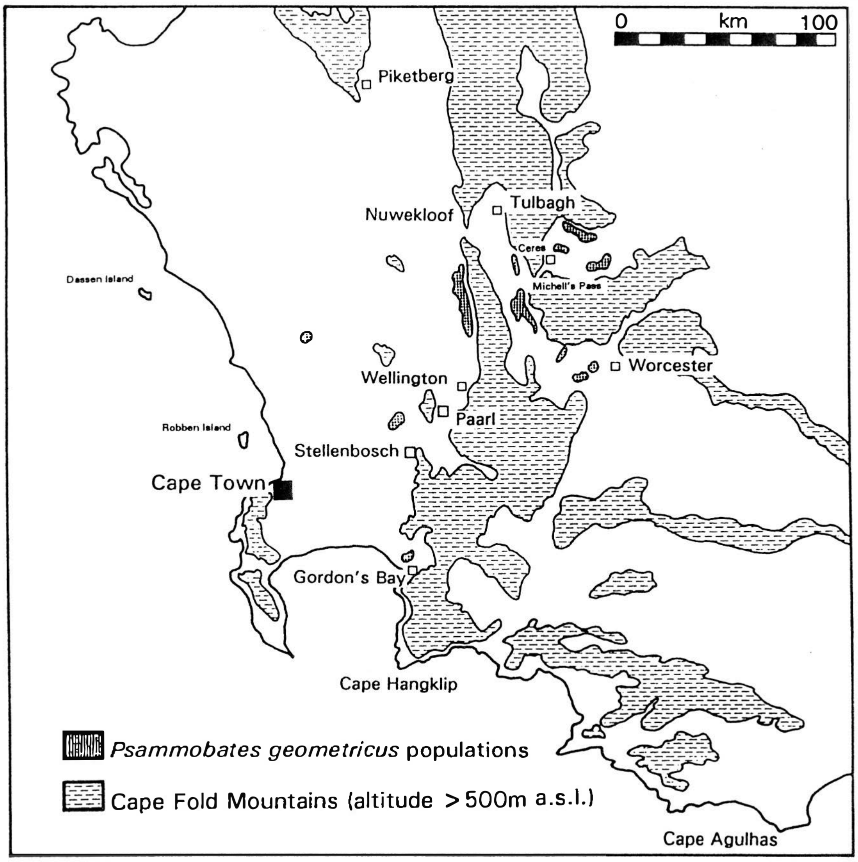

Fig. 1 Map of the southwestern Cape Province, indicating the present location of *Psammobates geometricus* populations, as well as possible communication routes and routes of genetic exchange between populations.

sea-levels for South Africa over the past 47 000 years suggests a rapid fall in sea-level with the advance of the final Wurm glaciation, with a minimum sea-level of -130 m reached at 17 000 to 18 000 years B.P. This implies that a considerable portion of the continental shelf would have been exposed during such times allowing communication between the western coastal lowland and Worcester-Tulbagh valley populations of *P. geometricus.*

Another possible communication route between the coastal and Worcester-Tulbagh valley populations might have been the gap in the Fold Mountains through the present-day Nuwekloof Pass (Fig. 1). At present *P. geometricus* is absent from this ravine and, the terrain being very rugged, it is unlikely that it ever functioned as a link between the two populations.

As regards the Ceres valley population, there are also two possibilities of how this population and the Worcester population could have been linked in the past. A link was possible through the Dwars River ravine (the present-day Michell's Pass) (Fig. 1). At present, this route appears to be impassable for terrestrial tortoises, particularly with the Dwars River and its steep embankments limiting access. However, geological information from this region (Visser, De Villiers, Theron & Hill, 1980; Söhnge & Hälbich, 1983; A. P. G. Söhnge, pers. comm.) suggests that the present drainage patterns in the Ceres and Worcester-Tulbagh valleys differ considerably from those approximately 10 million years B.P. (i.e. during the formation of the gorge, temporary flat areas could possibly have facilitated a link). A more likely communication route between the Ceres and Worcester-Tulbagh populations would have been via a northeastern, inland route (Fig. 1). The historical inland extension of, firstly, climates favourable to *P. geometricus* and, secondly, its favoured habitat, renosterveld, might possibly have facilitated this inland link via the present-day Karoo.

The natural occurrence of *P. geometricus* in the Ceres valley was questioned by Juvik (1971), who suggested that the population there might have originated from pet tortoises brought in from elsewhere. However, since there are at least six natural populations in the valley, as well as a strong presence of renosterveld habitat, and considering that *P. geometricus* appears to be closely associated with this habitat (Greig, 1984; Boycott & Bourquin, 1988; Branch, 1988; Baard, 1990), we regard it highly unlikely that a fairly large population in the wild could have originated from a few escaped or released individuals.

In conclusion, it is clear that there are various ways in which the three populations could have been linked geographically in the past. More definite conclusions in this regard, however, would only be possible once the relationships among the populations are known. A study to determine these relationships by means of electrophoresis or DNA-analysis is therefore highly recommended.

Unravelling the genealogical relationships between members of *Psammobates* presents an exciting challenge to future workers in this field. A cladistic study of the family Testudinidae, additional to that of Crumly (1984) and

Gaffney & Meylan (1988) is, however, fundamental to this. An analysis of the biogeography of this genus and possibly other genera as well, may contribute significantly to our understanding of the biogeographical patterns already observed in other animal groups in southern Africa.

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