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Karyology, phylogeny and biogeography of the Namaqua chamaeleon, *Chamaeleo namaquensis* Smith, 1831 (Chamaeleonidae, Reptilia)

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ABSTRACT

The karyotype of the Namaqua chamaeleon, *Chamaeleo namaquensis* Smith, 1831, has 24 chromosomes consisting of 12 macro- and 12 microchromosomes. This chromosome pattern is characteristic of the *C. chamaeleon* (Linnaeus, 1758) species group and indicates that *C. namaquensis* is a member of that taxon. It is hypothesized that *C. namaquensis* and *C. chamaeleon* are the most ecologically specialized and recently evolved taxa in the *chamaeleon* group.

INTRODUCTION

The systematic relationship of the Namaqua chamaeleon (*Chamaeleo namaquensis* Smith, 1831) was first discussed by Hillenius (1959, 1963), who suggested that on the basis of its external morphology *C. namaquensis* was probably related to the *C. chamaeleon* (Linnaeus, 1758) species group. Recently Klaver (1977) has shown that the lung anatomy of this species also places it with the *chamaeleon* group. Here I report that the chromosome number and morphology of the Namaqua chamaeleon is the same as the three other cytologically investigated species in this group.

MATERIALS AND METHODS

Chromosomes were prepared by a hypotonic citrate treatment of bone marrow tissue according to standard techniques for reptiles (Lowe, Wright, and Cole, 1966). Mitotic metaphases of five chamaeleons (3 ♂♂, 2 ♀♀), collected within 30 km of the Dessert Ecological Research Unit, Gobabeb, Namibia (23°33' S, 15°05' E), were examined, counted and photographed using a Zeiss research microscope. Chromosome terminology follows Bezy *et al.* (1977).

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RESULTS AND DISCUSSION

The diploid chromosome number of *C. namaquensis* is 24, consisting of 12 chromosome pairs arranged in two distinct size classes of 12 macrochromosomes and 12 microchromosomes (hereafter referred to as



Fig. 1. Karyotype of a female Namaqua chamaeleon (*Chamaeleo namaquensis*) from the Central Namib Desert, Namibia.

12M + 12m). The macrochromosome series has six pairs of metacentric and submetacentric "homologues" of decreasing size. In many cells a secondary constriction is evident on the end of the arms of the second largest pair. The microchromosomes are also a graded-size series, and several of the larger ones appear to be metacentric (Fig. 1).

Unlike most genera of lizards, considerable chromosomal evolution has occurred in *Chamaeleo* at the subgeneric level, and chromosomal data are highly concordant with an independently derived classification based on external morphology (Hillenius 1963) and lung anatomy (Klaver 1977). Of interest here are the species in Hillenius' *chamaeleon* group and their distinctive 12M + 12m chromosome pattern.

This karyotype, illustrated here for *C. namaquensis* (Fig. 1), strongly supports Hillenius' (1959, 1963) and Klaver's (1977) interpretations that the Namaqua chamaeleon is a part of the *chamaeleon* group. In view of such congruous results from these independent studies, it may now be concluded that *C. namaquensis* is a member of the *chamaeleon* species group.

Although placement of some species with the *chamaeleon* group is still

Although placement of some species with the *chamaeleon* group is still unsettled and the cytological survey incomplete (4 of 15 species are reported), sufficient data are available to discuss the phylogenetic and biogeographic relationships of *namaquensis*. Hillenius (1959) hypothesized that East Africa was the primary evolutionary centre of the genus, and that *C. chamaeleon* possessed the most primitive characters of the living species. The present distribution of *chamaeleon* is exclusive of East Africa, implying that it or a similar ancestor was eliminated from that region and replaced by a derived species such as *C. dilepis* Leach, 1890. An alternative hypothesis, and one I favour, suggests that *dilepis* represents a primitive species in the *chamaeleon* group, and from it the various taxa radiated to virtually all of continental Africa, eastward to Asia Minor and India, and as far south as Ceylon.

Like *dilepis*, all species except *namaquensis* and *chamaeleon* are arboreal and live in reasonably vegetated habitats. These latter chamaeleons are terrestrial, which is unique in the genus, and live in arid and semi-arid communities but at opposite ends of the continent, viz. northern Africa (*chamaeleon*) and southwestern Africa (*namaquensis*). Therefore, I view these two species as the most ecologically specialised and recently evolved taxa in the *chamaeleon* group. It seems reasonable then, that they represent the endpoints of a former widespread adaptive radiation that was centred in the forests of tropical East Africa.

This phylogenetic association and geographic distribution of *C. namaquensis* and *dilepis* repeats for reptiles the South West African-East African distributional pattern known for species pairs or conspecifics of mammals (Meester, 1965), birds (Winterbottom, 1967) and plants (Lind and Morrison, 1974) that inhabit the more xeric regions of these areas. Other lizards with similar distributions as these chamaeleons include *Agama planiceps* (SW Africa) and *A. agama* (E. Africa), and several taxa of skinks (e.g., *Mabuya variegata*, *M. striata*).

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