Reprinted from
*South African Journal of Science* Vol. 75 July 1979

# Ecology of a Living Desert: Twenty Years of Research in the Namib

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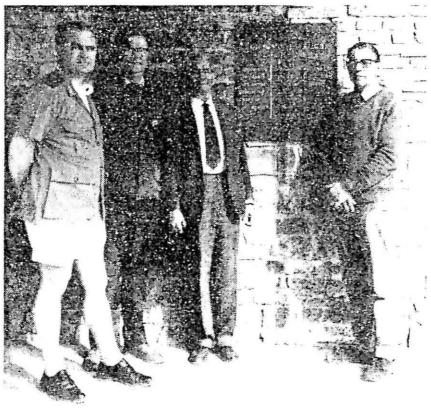
The Namib Desert, located on the south-western coast of Africa, is unique in the world of dune deserts for it is only in the Namib that a fauna thrives in the vegetationless parts of the dune ecosystem. Wind-blown seeds and other plant detritus that collect at the base of the slipfaces are the trophic base for this fauna composed mainly of tenebrionid beetles, arachnids and several reptile species.[1–4] As an ecological and evolutionary laboratory, the Namib dunes are paralleled only by such unique areas as the Galapagos Islands. Why has such a fauna developed only in these dunes?

It was to investigate this question that the Desert Ecological Research Unit (DERU) was established by the CSIR at the Transvaal Museum's Namib Desert Research Station at Gobabeb in 1966. This station was originally built in 1962/63 by Dr Charles Koch, entomologist of the Transvaal Museum, with the encouragement of Dr V. Fitz-Simons, then director of the museum. Dr Koch had been the first to recognize and then publicize the distinctive nature of the Namib desert fauna and was a strong advocate of establishing a desert station to facilitate further field research. Today scientists at Gobabeb are continuing the work on aspects of the ecology of the Namib dune fauna with funds from the University Research Division of the CSIR. The facilities, now called the Namib Research Institute, have been enlarged and are now maintained by the Division of Nature Conservation and Tourism of South West Africa. In addition, many visiting scientists from all over the world contribute expertise and back-up facilities to enhance the overall programme.

The selection of the site followed much deliberation on possible alternatives and reflects Dr Koch's deep understanding of the ecology of the central Namib. Gobabeb is located on the ephemeral Kuiseb River, an ecosystem in itself, which sharply separates the dune ecosystem to the south from the gravel plains to the north, thus providing easy access to all three ecosystems.

In a desert water is often the most important limiting factor. In the central Namib, summer rain dominates in the east and fog in the west along the coast. The occurrence of these two water sources is reflected in the distribution of the vegetation on an east-west gradient. Gobabeb, situated 56 km inland from the coast, is located in the area where perennial rain-induced plant life and fog-influenced vegetation are both at a minimum. Measurements of rain and fog-water precipitation, although available for only 14 years, confirm that Gobabeb receives a minimal amount of precipitation in comparison with other sites studied in the central Namib. This location, within the transition zone between the two moisture sources, has provided excellent opportunities for the study of the effect of both fog and rain on an ecosystem.[5–8]



*Unveiling of a plaque at the Namib Research Institute at Gobabeb, to commemorate the late Dr Charles Koch, founder of the station. Left to right: Mr B. de la Bat, Director of Nature Conservation and Tourism, S.W.A., Dr C. v. d. M. Brink, President of the CSIR, Professor C. A. du Toit, former Chairman of the DERU steering committee, and Professor F. C. Eloff, Chairman of the Board of Trustees of the Transvaal Museum. [Photo: C. K. Brain]*

The central Namib also offers the opportunity for the study of relatively simple ecosystems. For example, the Kuiseb River with its underground water is a linear oasis extending from the interior highlands to the sea. Along its usually dry course many non-desertic elements enter this desert region, although the number of species and individuals involved is much less than that of wetter neighbouring areas. For some animals sufficient food and water are available only along this oasis, thus resulting in a linear distribution of territories for these river-restricted animals such as the baboon, steenbok and klipspringer.[9–12] Other conditions peculiar to the Kuiseb lead to special study situations such as the possibility of observing the behaviour of hyena and jackal in the absence of other large predators.[13] Similarly, limited and only partially overlapping food and water supplies have led to a study of differential mortality of gemsbok at water holes, some which they themselves excavate.[14]

On the dunes and plains vegetation is limited to only a few species, although concentrations of plants occur where water is more readily available, for example on the isolated rocky hills. The fauna, because of its use of detritus as well as living plants for food, is less limited. The nature of the lightly vegetated substrate allows for ease of observation and capture of the many elements of this fauna. The laboratory facilities of the Namib Research Institute, although not extensive, are well situated to provide the necessary services to amplify and supplement the field studies in these three relatively simple ecosystems.

Research in the central Namib is a cooperative effort between resident researchers employed by the DERU and visiting scientists from far afield. To publicize this research, Dr Koch initiated the *Scientific Papers of the Namib Desert Research Station*. Some of the early reports were reprinted from the *Annals of the Transvaal Museum*, *Cimbebasia* and the *Journal of the South West Africa Scientific Society*, while the later papers were original publications of current research. When the Division of Nature Conservation and Tourism assumed responsibility for the facilities of Gobabeb in 1970, they took over the Scientific Papers and incorporated this series into the journal *Madoqua*. As a result of the Division's policy of encouraging publication in *Madoqua*, many of the current research papers from the DERU appear in that journal. More recently, the DERU has initiated the *Namib Bulletin* as a supplement to the *Transvaal Museum Bulletin*. This publication, which appears irregularly, was designed as an aid to coordination of research and thus provides summaries of current projects and bibliographies listing recent Namib-related research publications. In addition to publication of scientific material, information is made available to the public, a tradition Dr Koch established. Hence several films have been made with the assistance of the DERU and a number of popular articles have appeared in various magazines and books.

Orientated towards the special op-

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portunities afforded by the Namib, the central aim of the DERU is to accomplish an understanding of the geomorphological and climatological environment and to relate these physical factors to an understanding of the biological relationships.[15] Strictly biological interactions are less significant in extreme desert environments but are investigated when relevant. In addition, basic information is also being generated for use by the Division of Nature Conservation and Tourism in managing the Namib-Naukluft Park.[16] As a result of the nature of the Namib ecosystems and particular components therein, several major research themes, within the context of the main objectives, have been more thoroughly investigated than others. The following is an outline of several of these themes; it is not a complete listing of all research carried out through the DERU, nor does it refer to all the scientists who have been associated with the unit through the years.

## Geomorphology and climatology

Geomorphological studies provide clues to the distribution of present and past environments and hence indicate possible directions of evolutionary pathways of the contemporary life systems of the Namib. In an extreme environment, as is experienced by the Namib, climate is a controlling factor of both landscape formations and life systems Of particular significance and interest, but difficult to interpret, is the role of long-return events, especially rainfall. Because of its relevance to the region, research by visiting scientists working in such fields is encouraged and assistance is given when possible, although, as yet, a DERU staff member has not been found to work in this important area. What the DERU does do, with the assistance of Nature Conservation staff at Gobabeb, is maintain a series of meteorological stations across the Namib. These data are made available both in their raw form and as basic compilations,[17–19] and have been used in many of the following studies.

The very arid state of the Namib is generated, in part, by the presence of the cold Benguela Current along the western shoreline and recent evidence suggests that the current developed only in the Late Miocene. Subsequently the climate of the Namib has fluctuated, although always remaining arid. Evidence of these previous climatic differences is very obvious in the Namib and is the subject of many studies. Wieneke and Rust, working on the coast and central Namib plains, have recognized three phases: arid activity, arid stability and humid activity and have published their conclusions in a series of papers.[20–24] They have recently included the northern Namib in their endeavours. Others have recognized specific pieces of evidence in the dune environment[25–28] and Selby has presented support for palaeowind directions on the plains.[29] General geomorphic histories have been synthesized by Ollier[30] and Hövermann.[31]

Other studies have been of a more local or descriptive nature, for example Goudie[32] on geomorphology and Scholz[33] on soils near Gobabeb. Specific events, such as the only recorded flowing of a desert river,[34] and descriptions of specific phenomena, for example the occurrence of patterned ground,[32,35,36] and the characteristics of an ephemeral desert lake,[37] have received attention. Of particular use to the ecologist is Besler's synthesis of climate and geomorphology on a transect across the central Namib from the coast to the eastern border.[38]

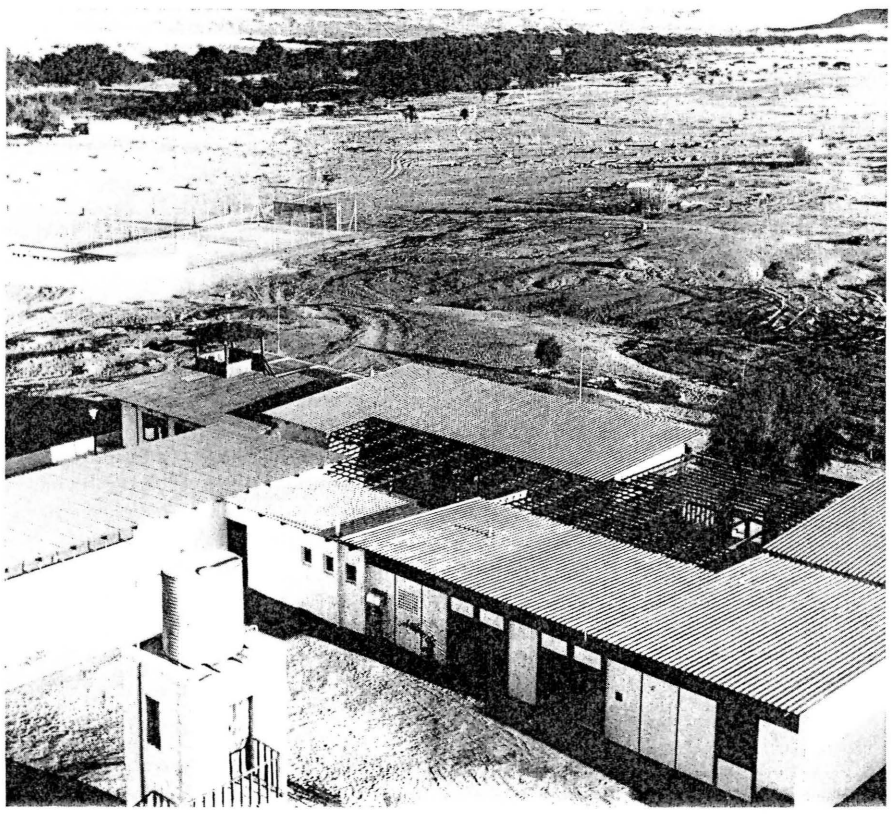
Although the geomorphology of the dunes and plains is not entirely distinctive they are often treated as separate units. The varying dune patterns and their relationship to present and past wind regimes have called for explanation,[39–41] as have the underlying structure and the movement of the dunes.[42–44] Besler has recently carried out extensive studies in this environment.[45] The Kuiseb River, with headwaters several hundred kilometres away from the Namib, has a history only distantly related to that of the desert itself but is, nevertheless, of interest to desert geomorphologists. This interest may be generated in part because of the very obvious evidence for past climatic changes. Several people have worked on aspects of its past history and present geomorphology.[43,46–48]

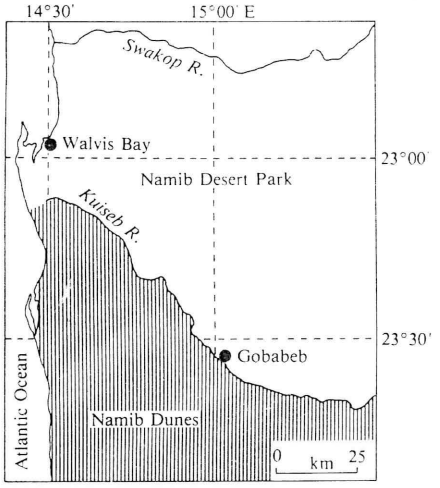
Comparison of similar processes and/or formations occurring in vastly different areas has formed a part of several of the papers listed and is the main subject of several studies.[49–53] Because a thorough understanding of the environment and its history is essential to understanding the present biological relationships of the Namib, further studies of the climatology and geomorphology of the region are encouraged and several important aspects are currently under investigation.

## Biology

Classical desert biology usually concerns itself with adaptations of plants and animals and is orientated around the major themes of thermal relationships and water loss and gain. This is because of the conditions prevailing in continental deserts where most research has been carried out. There extreme temperatures and low relative humidities, intense solar radiation and dry winds prevail and little rainfall occurs. In contrast and because of its coastal situation, the Namib, although it experiences little rain, enjoys frequent fog, and other climatic conditions are much less extreme. Hence research in the Namib has not been as sharply focused on the classical themes and, in fact, several Namib 'desert' organisms have been found to exhibit apparently 'non-desertic' characteristics.[54–56]

*A view of the Namib Research Institute at Gobabeb, looking towards the bed of the Kuiseb River and to the dunes beyond. [Photo: C. K. Brain]*






*Location of the research station at Gobabeb in the Namib Desert Park.*

*Age as an explanation for faunal richness.* The first papers written by people associated with the DERU concerned the richness and unusual nature of the Namib dune fauna.[1–4] One explanation, first conceived by Dr Koch, was that of the great age of the Namib ecosystem. Since this idea was first proposed, further information has become available from a variety of disciplines, estimates of the age of the Namib have been revised and its importance as the sole reason for the richness of the Namib fauna has been rejected.[57] This intriguing subject remains a topic of discussion.[58]

*Opportunism.* Opportunistic behaviour is characteristic of desert organisms living in an extreme environment but here the discussion will be restricted to those organisms found outside the desert and entering it only because of particular circumstances and using special adaptations to cope. Willoughby studied larks (Alaudidae) which enter the desert after rain has fallen.[59] He suggests that the basis for their success in arid regions is their ability to tolerate rapidly and severely changing environmental conditions by virtue of their lack of rigid specialization. This applies to many other animals and plants as well. In the Namib plasticity of feeding habits has been described for the jackal,[60] hyena,[61] starlings[62] and baboons.[12] Behavioural opportunism has been found in baboons as displayed by defensive stoning.[63]

*Water balance.* Edney, in perhaps the only study carried out on classical lines, measured water loss in several Namib beetles and concluded that they have among the lowest rates recorded for any arthropod.[64] In contrast, because of the character of the cuticle and stomata, water loss may be higher than expected in the 'non-xeromorphic' plant, *Welwitschia mirabilis,*[55] and the dune succulent *Trianthema hereroensis.*[56]

Koch[2] was the first to suggest that fog may possibly have an effect on the Namib ecosystem, and Louw and co-workers[65–68] were the first to demonstrate the use of fog-water by an assortment of Namib animals. Tschinkel[69] measured the sorption of fog-water by wind-blown plant detritus and its consequent availability to the dune fauna that consume this material as their primary food source. Bornman[70] demonstrated uptake of fog-water through the leaves of *Welwitschia mirabilis,* a plant living on the Namib plains, and later the same was shown for *Trianthema hereroensis*[56] in the dunes. Recently, three student projects were concerned with water balance of dune tenebrionids[71–74] and Kuiseb vegetation.[75]

Further work has been carried out describing the unusual behaviour associated with fog-use and quantifying fog-water uptake by individuals of several tribes of tenebrionid beetles.[76–79] These studies involve a new approach to the investigation of the water relations of desert arthropods and are pursued effectively because of the accessibility and abundant insect fauna of the Namib. The conclusion has been drawn that the adaptations for uptake of fog-water by tenebrionids are predominantly behavioural in nature and do not involve obvious physiological or morphological changes. Because of the extensive contribution DERU scientists have made in this field, a review of the ecology of fog in the Namib is to be included in a new book entitled *The Role of Fog in Ecosystems,* edited by J. O. Juvik.

*Temperature adaptation.* Studies of temperature regulation have emphasized the range of temperature available to the smaller desert organisms, either above and below the sand surface in the dune ecosystem or in the shade and open sun of the dry riverine habitat. Therefore, in these desert habitats the animals need move only between surface and subsurface or between sun and shade to find suitable temperatures at any time of the day or night. Edney[80] noted that for Namib beetles the upper lethal limits of temperature are remarkably higher than for non-desertic species. Hamilton,[81–83] as a result of extensive observations on many tenebrionid species in many parts of the Namib, developed the concept of 'maxithermy.' That is, these beetles have a high preferred temperature range between 38–40°C which they maintain by behavioural means. This elevated temperature places them at a competitive advantage because of the increased energy flow. Study of the unique 'white' tenebrionids, which occur only in the northern Namib desert, also contributed towards the formulation of this hypothesis. Henwood[84,85] has provided further evidence in support of the 'maxithermy' concept, working on two black beetle species common in the vicinity of Gobabeb. His experimental field work was backed up by simulation studies in the laboratory.

*Survival strategies.* The aim of most studies undertaken by the DERU staff and visitors is to explain how organisms survive in the desert environment. The use of opportunistic behaviour, maintenance of water balance and use of thermoregulatory behaviour are just three of the more readily defined categories of strategies used. As stated by Noy-Meir[86] at the most recent International Congress of Ecology, species in deserts operate as separate systems with minimal links and feedbacks. Survival strategies are instead closely related to the periodic pulses of food availability which in turn are dependent on occasional rainfall. In the Namib dunes dependence on these periodic pulses of food is modified by the continual presence of wind-blown plant detritus and fog as a source of food and water for elements of the dune fauna.[8] Behavioural and physiological adaptations to some climatic factors have already been mentioned but many other studies have touched upon these aspects in the course of pursuing broader objectives.

Holm[87,88] conducted the first extensive study of this nature, which involved pit-trapping every possible dune invertebrate during one year. Activity of the invertebrates, mainly tenebrionid beetles and silverfish, was correlated with daily and annual climatic characteristics and with distribution within the dune habitat. Studies already mentioned by Hamilton

*White tenebrionid beetles are unique to the Namib Desert and study of these species has led to a greater understanding of this ecosystem.*

and Louw approach the survival of these organisms from a broad point of view, namely physiological, morphological and behavioural. Other studies have either dealt with the integrated strategies employed by single organisms, for example the chameleon,[89,90] the side-winding adder,[91] bats,[92] tenebrionid beetles,[93–96] anurans,[97,98] *Welwitschia mirabilis*[54,55,70,99,100] or groups of organisms such as the gekkonid lizards.[101] Metabolic adaptations have been studied in tenebrionid beetles[102,103] and plants.[100,104] Reproduction[105,106] and diet[107] of several dune animals have also been investigated.

The remarkable set of circumstances prevailing in the central Namib have led to some unexpected scientific insights. While setting up an experiment to determine the rate of weathering of bones in an arid environment, Brain[108–111] made a study of goat bones which had been discarded by Hottentots in their villages along the Kuiseb River banks. The composition of this sample, in terms of skeletal parts, has proved to be of great significance. Only the most robust parts of the goat skeletons survived the feeding action of the Hottentots and their dogs, and Brain's studies of these bones have elucidated the reasons for the remarkable skeletal disproportions found in the australopithecine fossil assemblages of the Transvaal.

## General and future

In addition to specific research projects the DERU supplies material for taxonomic[112–114] and other studies.[72–74] As the DERU has developed, the taxonomic papers, which numerically used to dominate the *Scientific Papers of the Namib Desert Research Station*, are now being outnumbered by those dealing more directly with ecological topics.

This trend continues as the post-doctoral research associates of the DERU carry out in-depth projects of one or two years' duration. Recently studies of Namib vegetation,[115,116] reptile ecology,[90,91,106,107,117] and Kuiseb Canyon ecology[62,118–120] and solifuge biology have yielded and are yielding interesting results. Similar types of projects for higher degrees[48,71,72,75,84,85,87,89,97,116] are also included in the overall programme and are actively encouraged.

As the Namib is one of the least known of the world's deserts, baseline data are relatively scarce. Thus supporting data necessary for theoretical work are being generated by the DERU support staff in collaboration with other groups and individuals. These data include, but are not limited to, climatological and microclimatological analyses, long-term measures of vegetation and invertebrate populations, information on the breeding biology of characteristic species especially as reproduction relates to the environment, and observations of changes in the very nature of the soil substrate, past and present.

*A sun-spider,* Metasolpuga *sp., thermoregulating on a hot day in the Namib near Gobabeb. After running for a brief period on the hot gravel surface, the sun-spider cools off on the top of a grass tuft. [Photo: C. K. Brain]*

Future objectives include further elucidation of behavioural and physiological adaptations of plants and animals to the desert environment, the respective roles of irregular rainfall and more regular advective fogs in the structure and functioning of the dune and plains ecosystems, and the possible processes leading to the evolution of these ecosystems. Needless to say, the contribution of collaborating scientists will be essential to carry out these objectives.

The programme of the DERU is thus a varied one, partly by design and partly because of the large input from visiting scientists of many disciplines. To date, particular disciplines have been underrepresented but, where possible, steps are being taken to remedy these deficiencies. Rather than being an unwieldy situation, the combination of the DERU staff carrying out long-term projects, visiting scientists studying particular aspects on a shorter-term basis, and the two groups cooperating on many projects has turned into a most productive arrangement. By studying one geographical area intensively, supplemented by comparative work in other areas, a body of basic knowledge is beginning to accumulate which greatly facilitates further research both basic and theoretical. But the opportunities are so vast that it will be many decades before scientists can even begin to comprehend all the ramifications of the fluctuating ecosystem that is the Namib.

The CSIR and Transvaal Museum are thanked for financial support and the Division of Nature Conservation and Tourism for facilities at Gobabeb; the Director of the Transvaal Museum, Dr C. K. Brain, is thanked for contributing a section to the manuscript and for his continued support of the Unit over the years.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