ON THE DISTRIBUTION OF THE GENUS XEROCERASTUS KOBELT & VON MÖLLENDORFF, 1902 (MOLLUSCA, GASTROPODA PULMONATA, SUBULINIDAE)

by

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Opgedragen aan Prof. Dr. H. Boschma ter gelegenheid van zijn 70ste verjaardag.

The subfamily Rumininae of the pulmonate gastropod family Subulinidae is represented in Southern Africa by the endemic genus *Xerocerastus* Kobelt & von Möllendorff, 1902. *Xerocerastus* has been divided into three subgenera, viz., *Xerocerastus* s.s., *Lubricetta* Haas, 1928 and *Namibiella* Zilch, 1954 [1]). About fourteen species with many varieties, of which most are probably only of ecological significance, are now generally recognized. The genus is not treated in Connolly's monograph (1939), but the group has been reported upon in detail by various authors, viz., Connolly (1930), Zilch (1939, 1954) and Van Bruggen (1963).

A number of years ago my attention was drawn to a sample of *Xerocerastus burchelli* (Gray) from the Northern Transvaal, preserved in the Rijksmuseum van Natuurlijke Historie, Leiden; this seemed outside the known range of both genus and species and the case was filed for further investigation. Only recently I have had opportunity to go into this matter and the results of this study are presented here.

Pilsbry (1919, pp. 309-310, fig. 158) was the first to discuss distribution and affinities of the genus *Xerocerastus*. Degner's (1923) studies of the anatomy showed that, contrary to general opinion, *Xerocerastus* does not belong to the Enidae, but must be referred to the family Subulinidae of the superfamily Achatinacea (c.q. Achatinidae s.l.). Consequently in showing the distribution of *Xerocerastus* as a subgenus of *Cerastus*, and in connection with the range of the latter, Pilsbry's map has to a certain extent lost its meaning. The genus *Xerocerastus* has to be considered an isolated element with no direct relatives in the fauna of the Ethiopian Region. The other genera of the subfamily Rumininae (*Rumina, Obeliscella* and *Zootecus*; Thiele (1931) still includes *Obeliscella* in *Xerocerastus*, which, however, does

1) The author prefers to consider *Namibiella* a subgenus of *Xerocerastus* instead of giving it full generic rank as done by Zilch (1960).

not seem permissible) occur around the Mediterranean, in Arabia and India, and on the Cape Verde Islands.

X. zuluensis (Melvill & Ponsonby) from Zululand does not belong to the genus under discussion, but has been referred to the Enidae by Connolly (1939). The nett result of all this is that *Xerocerastus* is restricted to a wide but to a certain degree well-delimited range in the southwestern parts of Africa.

In order to define the range more exactly all locality records have been extracted from Blume (1952), Van Bruggen (1963), Connolly (1912, 1930, 1941) and Zilch (1939, 1952, 1954); moreover all localities from material in the Natal Museum (Pietermaritzburg, NM) and Transvaal Museum (Pretoria, TM) have been taken into account in addition to some records in the South African Museum (Cape Town, SAM) and the above-mentioned record in the Leiden Museum (RMNH). The following seventeen unpublished localities are included here: Campbell (TM, NM), Herbert Division (SAM), Keimoes (SAM), Langklip (SAM), 42 miles N. of Springbok (SAM, NM), Still Bay (TM, NM) and Upington (NM) in the Cape of Good Hope; Khomas Highlands (TM, NM), Farm Schlesien (TM, NM), Swakop River valley (NM) and Windhoek (NM) in South West Africa; Boritse-Tsetseng (NM) in Bechuanaland Protectorate; Beit Bridge (NM), Makuleka (RMNH), Saltpan (TM, NM) and Shaluka (NM) in the Transvaal; Tuli (NM) in Southern Rhodesia.

The following localities are on record for the genus *Xerocerastus:*

Cape Province

(Cape of Good Hope)

Blaauwboschpoort, SW. of Prieska
Campbell
Cypher Krantz
Douglas
Griquatown
Herbert Division
Keimoes
Koegas
Kuruman (olim Latakoo)
Langklip
Prieska
Prieska, Olifantshoek
Newlands, N. of Delports Hope
Riverton
Springbok, 67 km N. of
Still Bay
Taku, Vryburg District
Upington

South West Africa

Great Namaqualand

Aroab
Bethanie
Bullspoort
Farm Friedland, Marienthal-Aus
Gokhas
Gokhas, farm Haruchas
Great Fish River
Keetmanshoop
Kuibis
Lidfontein
Nakob
Naukluft

Damaraland

Ameib-Usakos
Brandberg
Choarib
Choarib plains
Erongo plateau
Etosha Pan
Fransfontein
Gaub
Gobabis District
Gobabis, farm Breitenberg
Grootfontein
Heusis, Kuiseb River valley near Baumgartbrunn
Kaliombo
Karibib, Heliographenberg
Karibib, Marmorberge
Karibib-Usakos
Khan River N. of Tsoachaul
Khomas Highlands at Long. 16° 15′ E. Lat. 23° S.
junction of Kurikaub and Swakop Rivers
Namutoni
Neineis
Nuragas-Otjituo
Okambahe, Omaruru River
Okatjeru lime pan, 60 km N. of Gobabis
Okuntinto near Kaliombo
Omaruru
Omaruru, 50 km W. of
Onguati
Otavi Mt.
Otavifontein
Otjikoto
Otjikoto Lake
Otjiwarongo
Outjo
Rietfontein Mts., farm Auras
Rietfontein Mts., farm Horasib
Rietfontein Mts., farm Keilberg
Rietmont near Windhoek
Farm Schlesien, Long. 15° 50′ E. Lat. 23° 30′ S.
Swakopmund, 100 km E. of
Swakopmund, 140 km E. of
Swakopmund, 110 km N. of
Swakop River valley
Tsumeb
Uis
Ukuile near Karibib
Upingtonia, S. of Etosha Pan
Usakos
Voigtland's Farm, 26 km E. of Windhoek
Windhoek

Namib

Aschieb-Cape Cross
Foothills near Naukluft
Rössingberge
Swakopmund
Swakopmund-Cape Cross
Tecklenburg

Kaokoveld

Kamanyab
Kamanyab-Choabendus
Kaoko Otavi
Kowares, N. of Ohopoho
Ombombo
Otjikondo
Otjitundua
Zesfontein

Ovamboland

Epitonna, SE of Ondonga
Onolongo
Ovambonde

Bechuanaland Protectorate

Aha Mts.
Boritse-Tsetseng
Dekar
Kooa
Kooa-Sekuma
Lehututu

Kakia
Kang
Khuis
Kobis
Meno a kwena
Tsane Pan
Sekuma District

Transvaal

Beit Bridge
Makuleka, N. of Levubu River
Messina
Saltpan, Soutpansberg District
Shaluka, Pafuri, Kruger National Park

Southern Rhodesia

Tuli

The map (fig. 1) shows all records which could be located. Localities have been plotted in quarter-degree squares, which system is not always entirely satisfactory (e.g. in showing Beit Bridge in Rhodesia instead of in the Transvaal); however, for showing patterns of distribution only it has few serious drawbacks.

Apparently the genus *Xerocerastus* is distributed throughout the Northern Cape, South West Africa, Central and Western Bechuanaland, and in a narrow strip along the Limpopo River in the Northern Transvaal and Southern Rhodesia, plus one additional locality in the Southern Cape Province. There is only one record from Little Namaqualand and Bushmanland (67 km N. of Springbok). According to Connolly (1925) it does not occur in Portuguese East Africa, nor has it been reported from Angola, Northern Rhodesia and the Caprivi Strip. Certain of these regions are poorly known from the malacologist's point of view, but nevertheless it is unlikely that representatives of the genus will turn up in these areas, except probably in Portuguese East Africa. Negative evidence is available for the Mateke Hills, 50 km N. of the Limpopo River (Southern Rhodesia), from which the author has studied non-marine molluscs collected by Mr. W. D. Haacke of the Transvaal Museum, and most districts of the Kruger National Park except the extreme northern parts (Van Bruggen, unpublished data).

The species of *Xerocerastus* occur in deserts, semi-deserts and dry to very dry thorn and bushveld. However, the area which they inhabit is by no means uniform in vegetation, climate or altitude. Two permanent rivers roughly seem to form the northern and southern boundaries respectively, viz., the Cunene and Orange Rivers, although the latter is crossed in a number of places in the Cape Province. The Cunene River is generally accepted as the northwestern boundary of the South African zoogeographic province; indeed Connolly (1931) stresses this as follows: "... while the Kunene River, on the west, seems to form an inexplicable, but insuperable

barrier between the land shells of Angola to the north and S.W. Africa to the south, ...". This is not quite correct, because only the lower Cunene from Long. 15° E. westward, where it runs almost parallel to Lat. 17° S., is meant here (vide also Haas, 1936). In actual fact the Cunene River seems to be a boundary of convenience rather than one of major zoogeographical importance; one should draw the line further north in Angola where both rainfall and altitude increase considerably (see e.g. the thirty inches mean annual rainfall isohyet in fig. 1).

The various types of vegetation in the area inhabited by *Xerocerastus* species have been described as "Kalahari grassland or mixed open Acacia wooded steppe" with on the fringes "desert and near desert" (South West African coastal area), "Karoo shrub and mixed Karoo" (central Orange River basin and area east of coastal deserts in South West Africa) and "open woodland with Mopane and Baobab" (northwestern district of South West Africa and Limpopo Valley) (Keay, 1959). Moreau (1952) discusses "biotic divisions" and includes the whole area except the Limpopo Valley in his "South West Arid" region; Van Zinderen Bakker (1962) describes the area in his map I as "dry" bordering on "semi-arid warm-temperate" (central parts of Southern Africa), including the Limpopo Valley in his "semi-arid tropical" region, which embraces most of the East African lowlands.

The rainfall varies, but is always low; in fact most of the area inhabited by *Xerocerastus* is encompassed by the twenty inches mean annual rainfall isohyet. Most localities, however, actually have considerably less than twenty inches rainfall per annum. The exception here are localities in the north-eastern parts of South West Africa, which have a slightly higher rainfall, viz., from 20 to 24 inches per annum. Temperatures vary greatly; extremes are experienced between day and night, particularly in the dry season (April-October).

The altitudes vary from sea level to about 6000 feet (central highlands of South West Africa), although most localities are from between 1200 and 4500 feet.

The distribution of the subgenera considered individually does not show any noticeable patterns. *Xerocerastus* s.s. has a very wide distribution, which practically coincides with that of the genus as illustrated in fig. 1. Much the same can be said for the subgenus *Lubricetta,* although no species of this group have been found east of the borders of South West Africa, i.e. Lat. 21° E. The subgenus *Namibiella* has a more or less coastal distribution and does not seem to go beyond Lat. 18° E.; it may indeed be one of the endemic elements of the fauna of the Namib Desert.

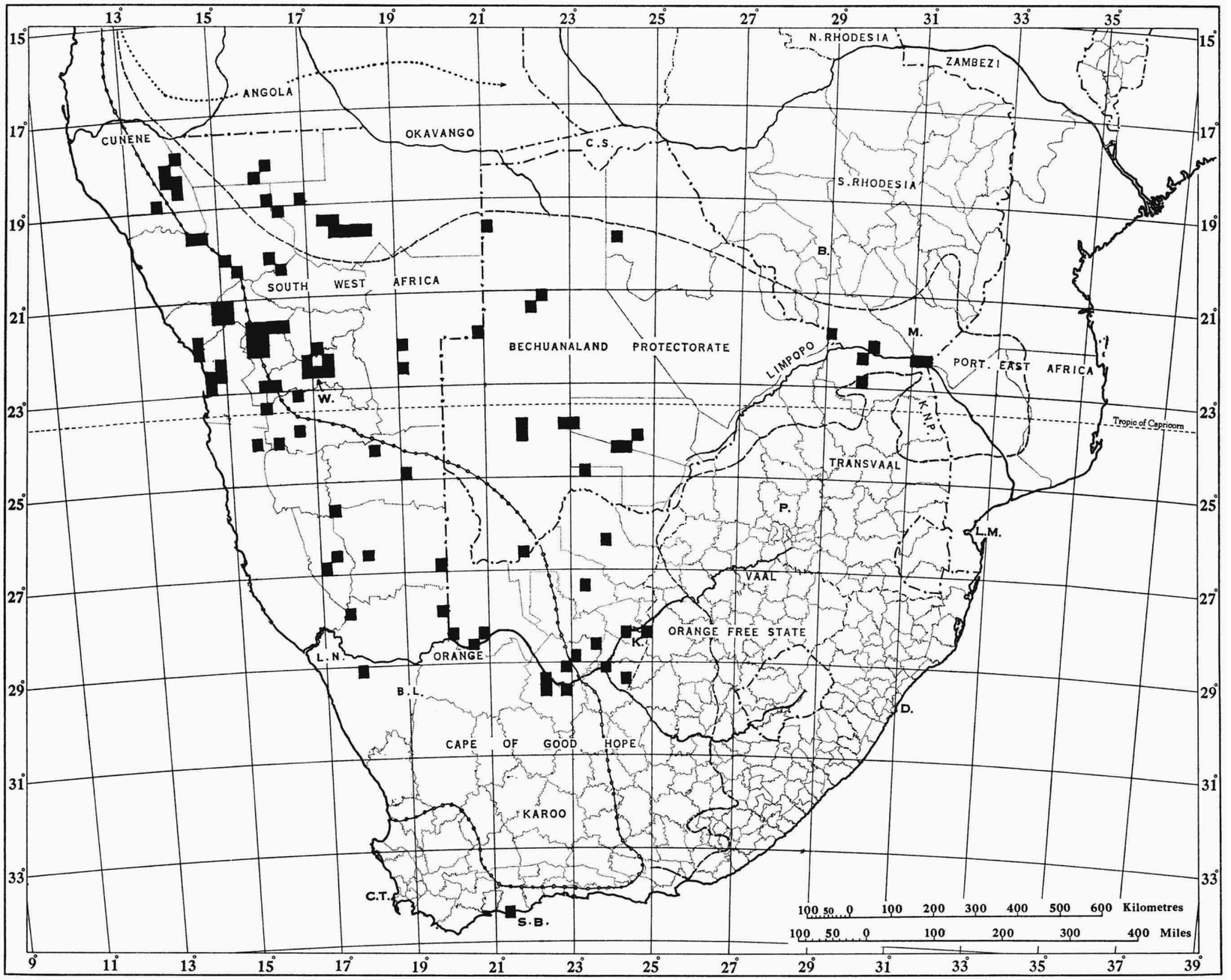

Fig. 1. Distribution of the genus *Xerocerastus* Kobelt & von Möllendorff in Southern Africa, based on a map of the Trigonometrical Survey (Government Printer, Pretoria). The following abbreviations have been used: B. - Bulawayo, B.L. - Bushman Land, C.S. - Caprivi Strip, C.T. - Cape Town, D. - Durban, K. - Kimberley, K.N.P. - Kruger National Park, L.M. - Lourenço Marques, L. N. - Little Namaqualand, M. - Mateke Hills, P. - Pretoria, S.B. - Still Bay, W. - Windhoek. The beaded line outlines the 10 inches, the broken line the 20 inches and the dotted line the 30 inches mean annual rainfall zone.

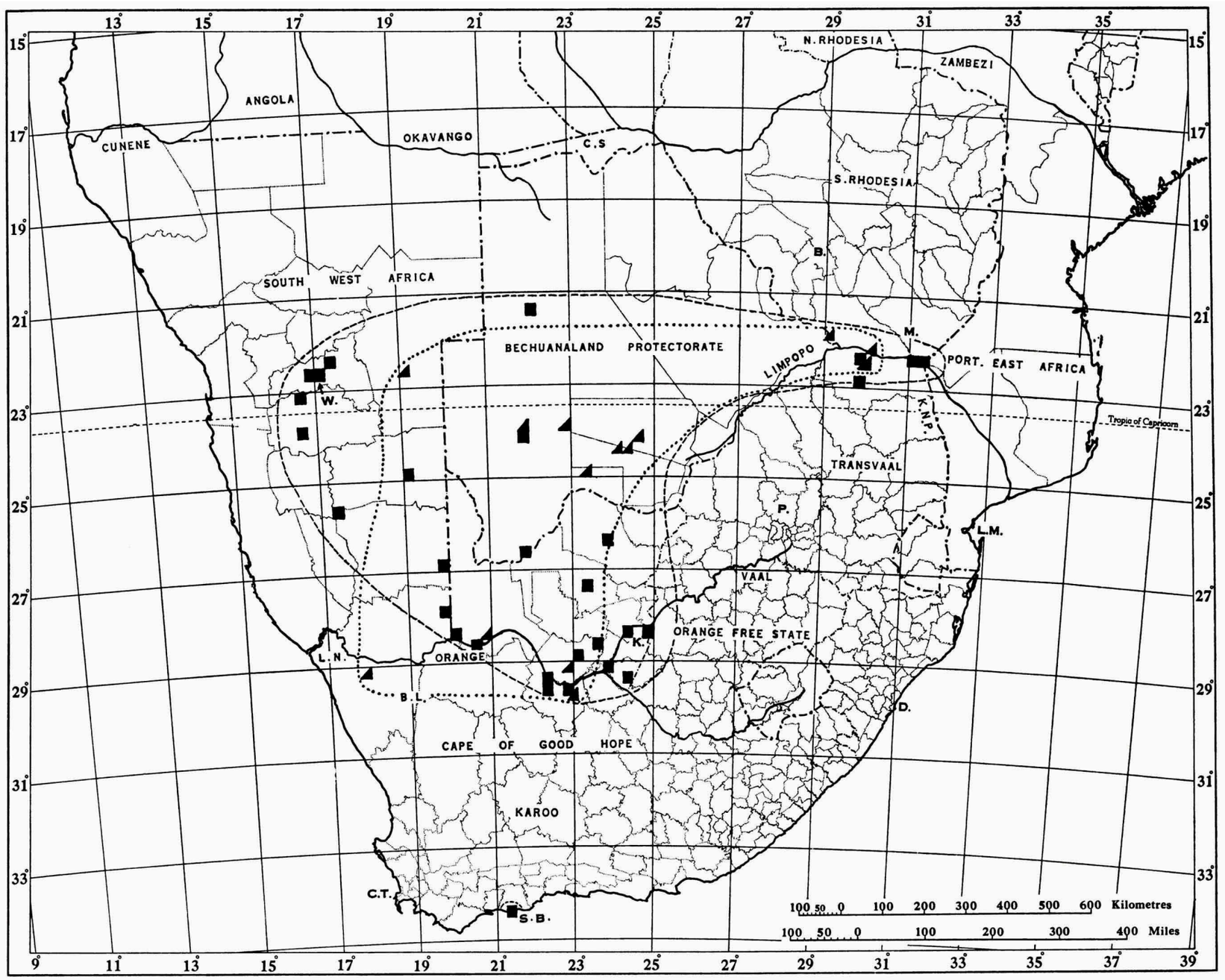

Fig. 2. Distribution of *Xerocerastus burchelli* (Gray) (squares within broken line) and *X. schultzei* (Boettger) (triangles within dotted line) in Southern Africa. Source and abbreviations as in fig. 1.

The distribution of the species is mainly centred in the west-central parts of South West Africa. Some species are only known from very few localities and may be insufficiently collected or localized endemic species. Most probably some of these have a restricted range, e.g. in the Namib Desert which is well-known for a high degree of endemism, particularly in various groups of invertebrates (e.g., Coleoptera: Tenebrionidae).

The most interesting facts which transpire from the first map (fig. 1), are the eastward extension of the range through the Limpopo River valley and the southward extension to the Indian Ocean. Only two species are involved here, viz., *Xerocerastus burchelli* (Gray) and *X. schultzei* (Boettger). The distribution of these species is as follows (see map fig. 2).

X. burchelli (squares) — Blaauwboschpoort, Campbell, Douglas, Griquatown, Herbert Division, Keimoes, Koegas, Kuruman, Langklip, Newlands, Prieska, Riverton, Still Bay, Taku (Cape of Good Hope); Aroab, Bullspoort, Choarib, Farm Friedland (Marienthal-Aus), Gokhas, Gokhas (farm Haruchas), Heusis (Kuiseb River valley near Baumgartbrunn), Nakob, Rietmont, Windhoek (South West Africa, Great Namaqualand and Damaraland only); Dekar, Khuis, Tsane Pan (Bechuanaland Protectorate); Makuleka, Messina, Saltpan, Shaluka (Transvaal).

X. schultzei (triangles) — Cypher Krantz, Prieska, 67 km N. of Springbok, Upington (Cape of Good Hope); Gobabis District (South West Africa); Kakia, Kang, Kooa, Kooa-Sekuma, Lehututu, Sekuma District (Bechuanaland Protectorate); Beit Bridge, Messina (Transvaal); Tuli (Southern Rhodesia).

X. burchelli is new to the fauna of the Transvaal and *X. schultzei* to that of Southern Rhodesia. Tuli is the only record of the genus north of the Limpopo River.

It will be seen that *X. burchelli* has generally a central distribution in Southern Africa, which, however, ranges from West (without occurring in the coastal deserts) to East; it does not seem to occur north of Lat. 21° S. nor west of Long. 16° E. *X. schultzei* is even more limited in its distribution, which is purely central; it does not occur north of Lat. 22° S. nor west of Long. 17° E. None of the other species occurs east of Long. 25° E. nor south of Lat. 28° S.

It is known from various vertebrates that the Limpopo Valley has a certain zoogeographic importance either as a major ecological barrier (see e.g. Benson, Stuart Irwin & White, 1962; Meester, 1962a-b) or as a fairly narrow corridor from the arid interior into the arid areas of the tropical lowlands of Portuguese East Africa (and also vice versa), which according to their fauna, are only an extension of those of East Africa. This is particularly evident in the northern districts of the Kruger National Park; how-

ever, the number of species which illustrate this phenomenon clearly is rather limited. For the first time it is demonstrated here for a group of invertebrates. 2)

Connolly's (1930, p. 304) suggestion that the shells of *Xerocerastus* have been carried to the Limpopo River valley by travelling Africans is obviously not very well founded. The distribution pattern seems perfectly natural; moreover, very few Africans seem to travel from the arid interior to Portuguese East Africa via the Limpopo. *Xerocerastus* does not occur in the main mining areas in the Transvaal, from which there is a considerable traffic to Portuguese East Africa (partly via the Limpopo Valley) and vice versa. The Limpopo Valley is in actual fact an extension of the arid interior of Southern Africa; the rainfall is very low and the vegetation accordingly xerophytic (see inter alia Stuart Irwin & Donnelly, 1962). This trough is an ancient interval in a pattern of Jurassic and Cretaceous faults which widely interrupts the Eastern Escarpment, resulting in discontinuous patterns of animal distribution to the north and south of this valley (see also Stuckenberg, 1962). For a considerable time it must have served as a pathway to the East for xerophilous fauna and flora, as it still does today. The geographic features are clearly reflected by the twenty inches mean annual rainfall isohyet in fig. 1.

The Saltpan in the Soutpansberg District (Northern Transvaal) is very much like the surroundings of pans in the Kalahari, with a typical Kalahari vegetation characterized by representatives of the family Bignoniaceae, such as the genera *Catophractes* and *Sesamothamnus* (Dr. G. van Son, in litt.).

The locality Still Bay in the Southern Cape Province (abbreviated S.B. in figs. 1 and 2) is rather puzzling and does not seem to fit into the general distribution pattern. There is, however, no doubt about the authenticity of the sample in question; in November 1940, Dr. V. Fitzsimons collected, among other shells, a number of *X. burchelli* at Still Bay on dunes lying along the seashore and a little inland. Only recently the author opened the sealed and properly labelled box in the Transvaal Museum; consequently this record cannot be rejected. The map shows Still Bay to be well outside the known continuous range of the genus, for which fact two explanations may be offered. The first reasonable explanation is, that the species occurs throughout the Karoo continuous with the range in the central Orange River basin, but that so far it has escaped the attention of field collectors. There has certainly been a dearth of mollusc collectors in the Karoo — on the

2) The arachnologist of the Natal Museum, Dr. R. F. Lawrence, has also encountered examples of this phenomenon in collections from the Kruger National Park (personal communication).

other hand *Xerocerastus* usually occurs in large quantities and in most if not all localities the conspicuously white shells are found lying around everywhere in the open. This is one of the reasons for representatives of the genus being abundant in collections, because they are very likely to be picked up by non-specialists.

The other possibility is one of relict occurrence, in which case one should assume that the species has become extinct in the intervening area. However, no apparent reason for this phenomenon can be found. Still Bay is ecologically rather different from most of the other mentioned localities; the climate is of a mediterranean character (Winter Rainfall area, 15 to 20 inches mean annual rainfall) and the vegetation is a typical coastal Cape macchia. In the absence of further data this question is best left in abeyance for the time being (see also below).

As far as is known at present one genus of the subfamily Rumininae occurred already in the Tertiary (*Rumina:* middle Miocene of Europe and N. Africa) and another in the Quaternary (*Zootecus*: Pleistocene of Egypt and S. Arabia). It is perhaps reasonable to assume that the hypothetical ancestor of *Xerocerastus* evolved somewhere in the central district of South West Africa, derived from ancient Achatinoid stock which probably had its origin further north. This could have happened during the Pleistocene or late Tertiary, particularly so because the few distinctions between the various species are still of a very indecisive nature. In the absence of competitors in the dry areas forms of *Xerocerastus* adapted themselves to a variety of dry environments throughout their modern range and even penetrated the inhospitable desert on the shores of the Atlantic Ocean. Apparently *X. burchelli* and *X. schultzei* have an even wider range of ecological tolerance than the other species and consequently they were able to colonize areas such as the Orange River basin and the Limpopo Valley, the former even as far south as Still Bay on the shores of the Indian Ocean.

In this respect it is interesting to notice that Van Zinderen Bakker (1962) mentioned that during the "hypothermal phase" in the late Upper Pleistocene temperatures were lower and humidity higher — factors which may well have accounted for the disappearance of *X. burchelli* from the intervening areas. On the other hand one has to realize that during the Pleistocene the Cape coast was exposed as far as the Agulhas Bank; these low-lying areas were probably also suitable for *X. burchelli.* These speculations lead to the assumption that the occurrence of *Xerocerastus* in the Southern Cape is of a relict nature.

The malacofauna of South West Africa and adjoining areas is rich in endemic forms such as *Succinea badia* Morelet, *Subulina vitrea* (Mousson).

various species of *Achatina* (*A. ampullacea* Boettger, *A. dammarensis* Pfeiffer, *A. passargei* von Martens, *A. schinziana* Mousson and *A. tracheia* Connolly), the tribe Dorcasieae (only representatives of the family Acavidae in the Ethiopian Region) and the genus *Sculptaria* (only representative of the family Corillidae in the Ethiopian Region); however, none of these has an eastern extension of the range into the Limpopo Valley. Indeed, except *Xerocerastus,* not a single other species or genus of terrestrial gastropods is at present known to do this. [3])

The deserts and semi-deserts of S.W. and N.E. Africa are known to have closely allied faunas. In many cases allied species replace each other; it is an undoubted fact that once these two regions were joined by means of an arid corridor through Central and East Africa. The relationships vary in different groups of animals, but have been quite clearly established in certain families of mammals and beetles.

A search for relatives of *Xerocerastus* in the north-eastern parts of the African continent reveals the following. According to Bacci (1951) *Zootecus insularis* (Ehrenb.) is the only representative of the subfamily Ruminae in Somalia; Verdcourt (1960), adding some new localities from N.E. Africa, quotes Bequaert as having written to him that this species occurs in "India, Arabia, Egypt, Eritrea, Sudan, Senegal and Cape Verde Islands" adding that its present distribution is partly due to human activity, thus obscuring the picture considerably. There is always the possibility that *Zootecus insularis* replaces the genus *Xerocerastus* in the arid regions of N.E. Africa; it is interesting to note, however, that the available ecological niches in the southwestern arid regions of the African continent have been occupied by Subulinidae, while the family Enidae (subfam. Cerastuinae, olim Pachnodinae) has occupied those in the corresponding region further north.

In conclusion one may say that rainfall appears to be one of the main factors controlling the distribution of the genus *Xerocerastus* in Southern Africa; with few exceptions all known localities have a rainfall of usually considerably less than twenty inches per annum. *X. burchelli* and *X. schultzei* seem to have the widest ecological tolerance and have penetrated the Limpopo River valley in the East and the Orange River basin in the South. The former species has even been reported from one locality on the shores of the Indian

3) The genus *Pupoides* (fam. Pupillidae) shows a tendency to do this; however, the range of this genus is entirely different from that of *Xerocerastus. Pupoides* occurs in S. and E. Africa (also in localities in the Transvaal and Natal well outside the range of the southwestern endemic species) and S.W. Asia.

Ocean, which, however, makes the distribution pattern discontinuous. The significance of the Limpopo Valley as a corridor from the arid interior into the dry areas of the lowlands of Mozambique has been demonstrated here for the first time for a group of invertebrates.

Acknowledgements are due to Dr. K. H. Barnard, Mr. W. D. Haacke, Dr. J. C. Poynton, Mr. B. R. Stuckenberg and various other colleagues, who supplied data and/or assisted materially in many other ways.

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