THE INFLUENCE OF CLIMATE ON THE ACTIVITY PATTERNS AND ABUNDANCE OF XEROPHILOUS NAMIB DESERT DUNE INSECTS

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S U M M A R Y

The basis of this thesis is a trapping experiment conducted over one year (1969). Unbaited pit traps were placed in the most important habitats of a Namib Desert dune system and were checked and emptied daily.

The traps were spread over the area in such a way as to ensure that total number of catches was representative of the total area, i.e. number of traps in a specific habitat was proportional to the relative surface area of this habitat within the total area.

While other animals were also trapped, this study is restricted to wingless terrestrial insects. A total of 47 species of terrestrial insects was recorded in the area, of which more than half belong to the family Tenebrionidae. At least five new taxa of the Arthropoda were discovered in this area in the course of the survey.

Daily catches of the 47 species dealt with, were studied in relation to daily measurements of wind, maximum and minimum temperature, and precipitation in order to discover possible correlations.

The total catches of every species in the various habitats were used for constructing distribution histograms of these species within the experimental area.

The technique of trapping developed for this survey provides comparable data on time of day, time of year, and place of activity of the various terrestrial species. A trap developed for this purpose is described.

An integrated picture of the ecology of the Namib Desert dune area, which is unique in the world for its rich variety of desert-adapted species, is constructed on the basis of the data collected during this survey.

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OPSOMMING

Die basis van hierdie verhandeling is ŉ eksperiment wat oor een jaar (1969) strek. Put-valle sonder ŉ lokaas is in die belangrikste mikrohabitatte in ŉ duinesisteem in die Namib Woestyn geplaas, en daagliks nagesien.

Daar is gesorg dat die aantal valle per mikrohabitat, proporsioneel was aan die verhouding van die oppervlakte van daardie mikrohabitat tot die sisteem as geheel, sodat die totale vangste van al die valle saam verteenwoordigend was vir die hele gebied.

Terwyl ander dieregroepe ook in die vangste verteenwoordig was, word die aandag in hierdie verhandeling toegespits op ongevleuelde grondlewende insekte. Agt-en-veertig spesies van grondlewende insekte is in die eksperimentele gebied aangetref, waarvan meer as die helfte aan die familie Tenebrionidae behoort.

Ten minste vyf nuwe taksa van Arthropoda is gedurende die opname ontdek. Daaglikse vangste van die 47 spesies van grondlewende insekte, is vergelyk met daaglikse lesings van wind, maksimum en minimum tempteratuur, en neerslag met die doel om moontlike korrelasies te bepaal.

Die totale vangste van elk van die spesies in die verskeie habitatte is verder ook gebruik om verspreidingshistogramme van die spesies binne die eksperimentele gebied op te stel.

Die tegniek wat gebruik is om die insekte mee te vang, maak dit moontlik om gegewens oor die tyd van die dag, tyd van die jaar, en plek van aktiwiteit van die gevangde diere te verkry. ŉ Val wat vir dié doeleindes ontwikkel is word beskryf.

Aan hand van die data wat gedurende die opname versamel is, word ŉ geïntegreerde beeld van die ekologie van hierdie sisteem, wat uniek in die wêreld is, vanweë sy rykdom aan gespesialiseerde woestynlewe, saamgestel.

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C O N T E N T S

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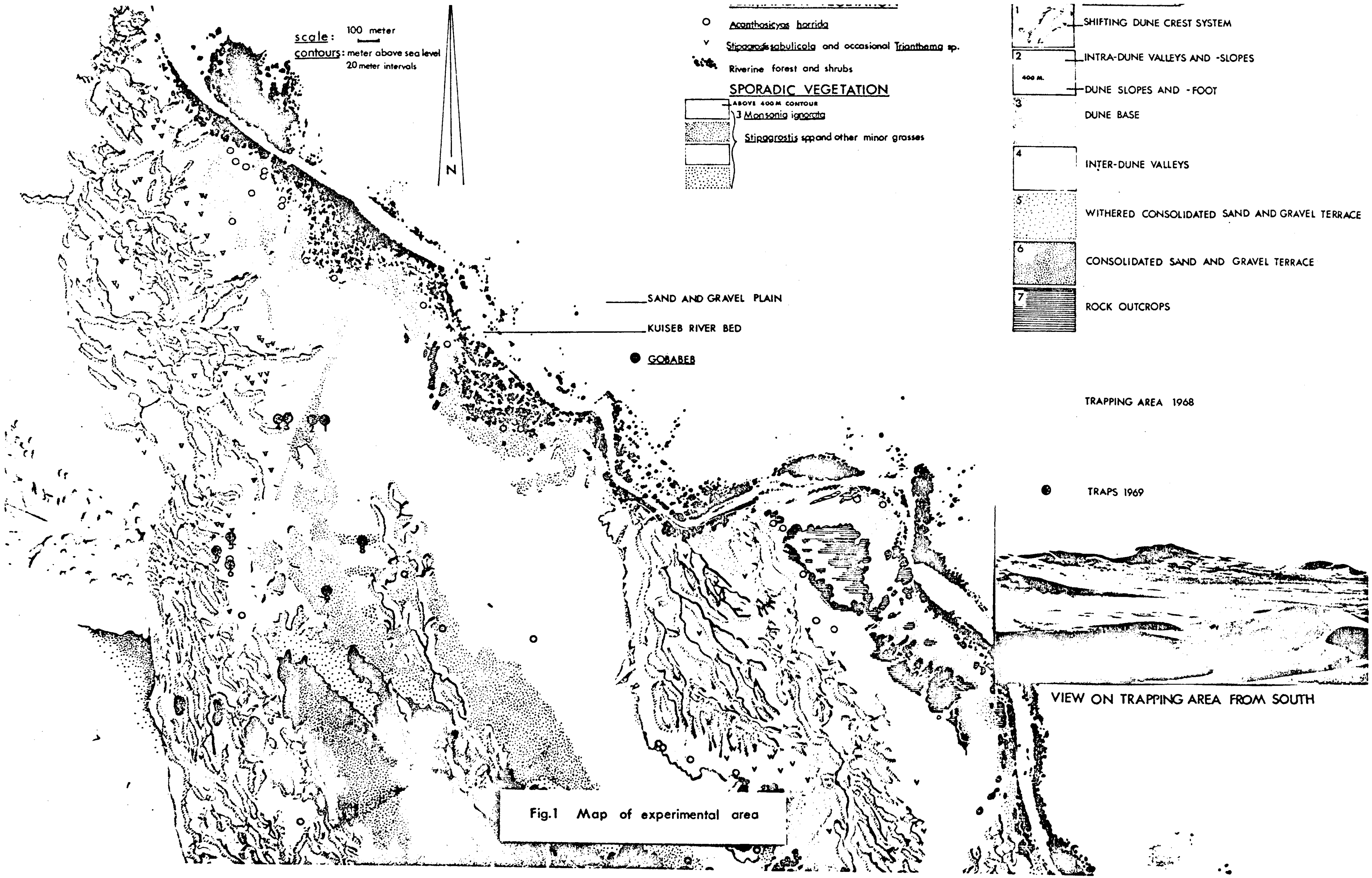

Fig.1 Map of experimental area

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I. INTRODUCTION

BIOLOGICAL RESEARCH IN DESERTS.

It is hardly necessary to point out the value of desert research in our time, although it was regarded as a purely academic proposition only a few decades ago. It is obvious that the ever dwindling exploitable surface area of the earth in relation to the ever increasing world population, makes it imperative to accumulate basic and applied knowledge of the desert biome as intensively as possible. The first dividends on this investment are already showing, for example, in the Negev Desert where spectacular developments in agriculture followed the basic and applied research executed there.

However great the ultimate economical advantages of any research project may be, economic considerations need not and should not be the only acceptable motivation for research. The curiosity of man and his endeavours to satisfy it, are vital components of all cultures, and it would indeed be a great loss if this purely inquisitive attitude towards nature were to vanish from the natural sciences.

Desert research, then, is seen by the author as an effort to illuminate part of man's environment which he is about to enter, for which purpose he needs both a detailed technical knowledge and a general understanding of this environment.

BIOLOGICAL RESEARCH IN THE NAMIB DESERT.

The Namib Desert has been described as a "workshop" of evolution (Koch, 1961) with good reason. Contrary to the usual decline in diversity and biomass of ecosystems from humid to arid regions, this desert sustains a surprisingly rich fauna. This highly diversified fauna has been noted and described only very recently. While the origin of the rich fauna of the Namib Desert lies in the history of the area and ajoining areas (Koch, 1961) a study of the present ecological situation could not only provide clues to the reason for the evolution and survival of this unique fauna, but may also prove a valuable opportunity for testing and re-evaluating ecological and evolutionary concepts, both because of the relatively simple structure of the ecosystem, and its uninterrupted unspoiled state.

This research potential of the Namib Desert has been appreciated at an early stage by leading South African scientific bodies, mainly through the insight of Dr. Charles Koch, the prominent champion of Namib Desert

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Research. Since the Namib Desert Research Station at Gobabeb was founded through this co-operation in 1962, much basic work has been done on the natural history of this desert, both by local scientists and guest scientists from abroad. The fauna and flora of the area is taxonomically relatively well-known at this stage, and some detailed work on aspects of physiology, ethology and ecology of the various inhabitants of the desert have been studied. The weakest link in the knowledge of the area at this stage lies in the lack of detailed quantitative data collected over long periods of time. Climatological data are accumulated continuously on a large and detailed scale at Gobabeb itself and at a series of satellite stations, and will be of great biological significance once they are analysed in more detail. However, long term quantitative biological data are not available for the same period of time.

It was therefore felt that a quantitative analysis of a Namib Desert ecosystem, concurrent and correlated with the climate project would fill a significant void in the knowledge of the unique ecology of this area.

CLIMATE AS AN ECOLOGICAL FACTOR.

The primary aim in correlating climate with populations and population activities in this paper, is not to prove or disprove a theory on the primary or secondary role of climate in regulating population numbers in general, although climate could be expected to be a key factor in most life systems within the ecosystems of this particular area. In causal relationships with two or more contributing and interacting factors it is often merely a matter of opinion which of the factors is primary. More important to both the quantitative ecologist and economic entomologist is a knowledge of the key factors in the life system under study, and their quantitative effect on the population (Clark, L.R. et al. 1967).

Since climate is relatively easily measured and the method well standardised, it appears worthwile to investigate it prior to or parallel with any other factors in the search for key factors in any unknown life system or ecosystem. Strong correlation between population phenomena and climate will point to the critical factors in the climate of that system, but, equally important, poor correlation will point to other key factors in the system.

With regard to the role of climate, the ecosystems of the Namib Desert may definitely not be taken as typical for arthropod populations, just as any isolated life or ecosystem may not be regarded as representative, vide the life system of <u>Austroicetes</u> (Clark, L.R. et al. 1967), but any system studied in detail may serve a useful comparative purpose for similar systems.

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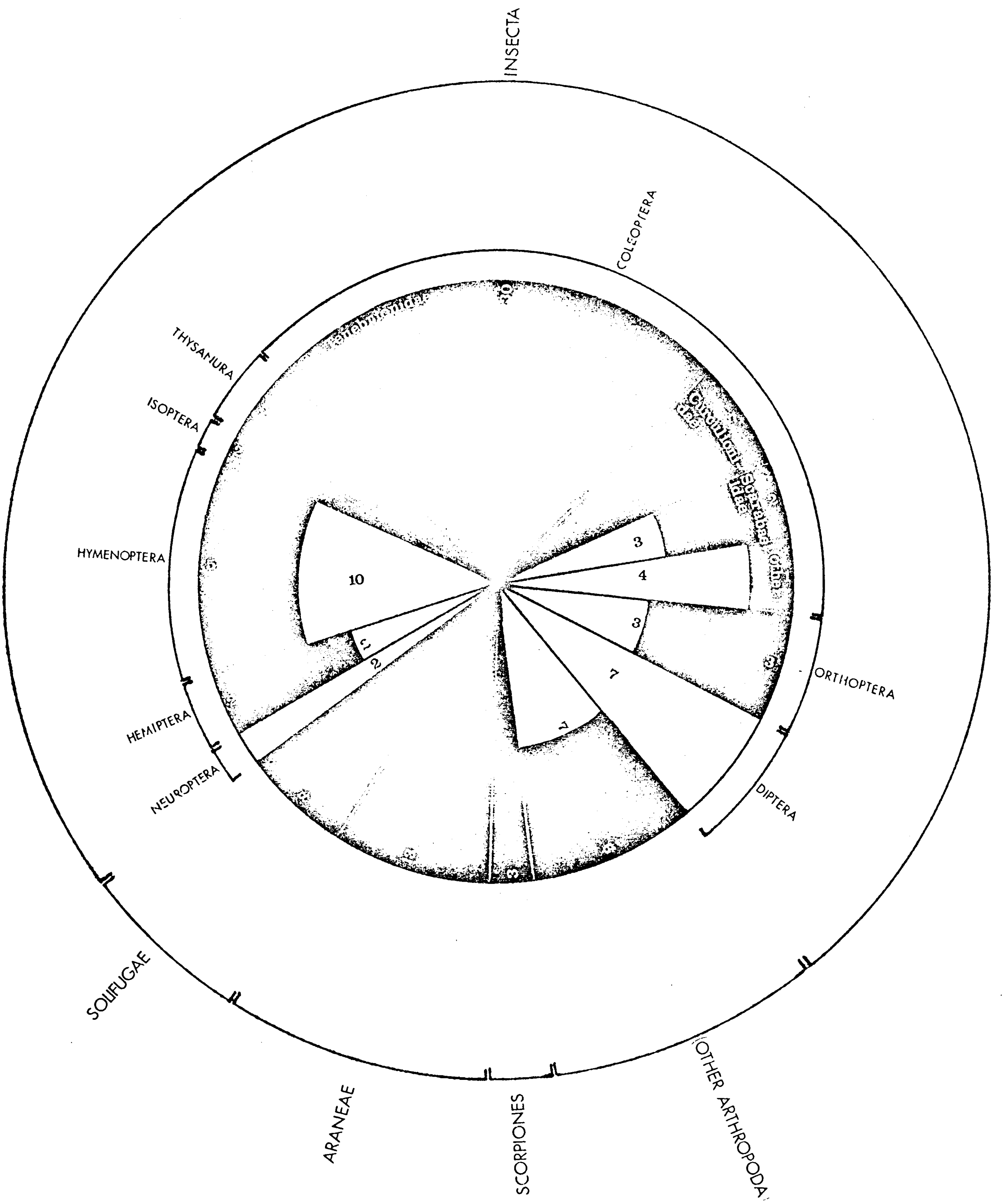

Fig. 2 Numbers of species of the main arthropod groups trapped and observed in the experimental area during 1969.
(Black indicates apterous species, termites, ants and aphids included)

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THE ECOSYSTEM AND THE FAUNA.

The Namib Desert can be divided into three major biotopes, viz. the riverbeds, the plains and the dune areas. Various subdivisions are made by authors according to their particular field of interest.

The dune area can be divided geographically into a northerly and southerly dune region, separated by the central plains. The southerly region, extending from Swakopmund southward, is the largest, and while the northerly region is more or less a coastal belt of dunes, the southerly region may be subdivided into a coastal belt, a central dune area and a marginal inland dune area. For this study, a small area in the northern part of the southern dune region was investigated. This area is situated about halfway between the coast and inland, i.e. in the central region of the southern dune region.

Of the three major biotopes of this desert mentioned above, the choice fell on the dune biotope because the greatest variety of endemic species, and the most extreme morphological adaptations in the fauna were known to occur in this biotope. The actual choice of the experimental site was made mainly because of its proximity to the facilities and weather station of the research station at Gobabeb. This happened to be a suitable site for the purpose of this study, since it included marginal populations of adjoining systems. The experimental area is mapped in fig. 1.

To record all populations in this desert ecosystem at once, was impractical for a one man team. The apterous insect groups were therefore concentrated on in this study. This choice was made because the arthropoda are the furthest adapted to this desert evolutionarily, and because the apterous insects dominate the local arthropod fauna (fig. 2.) A second consideration was sampling technique. The apterous insect fauna lent itself well to a standardized sampling technique (see Chapter II)

AIMS OF THIS STUDY.

The main aim of this study may be summarized as follows:-

(i) To map population activity of apterous insects in a Namib Desert dune system in time and place, correlated with macro climate, over a one year cycle.

(ii) To determine the ecological niches and habitat preferences of the subject species, and construct a quantitative and qualitative model of the ecosystem.

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(iii) To contribute to the knowledge of ecology and more specifically the ecology of the Namib Desert by indicating relationships between the abiotic environment and the fauna in this relatively unknown ecosystem.

As by-products of this study a sampling technique for this particular problem situation was developed, which proved to contain useful ideas for similar investigations,* and the taxonomical knowledge of the fauna of the area was augmented by the discovery of several new taxa in the course of the investigations.

* Studies presently under way under Prof. E. Edney, Berkeley, California.

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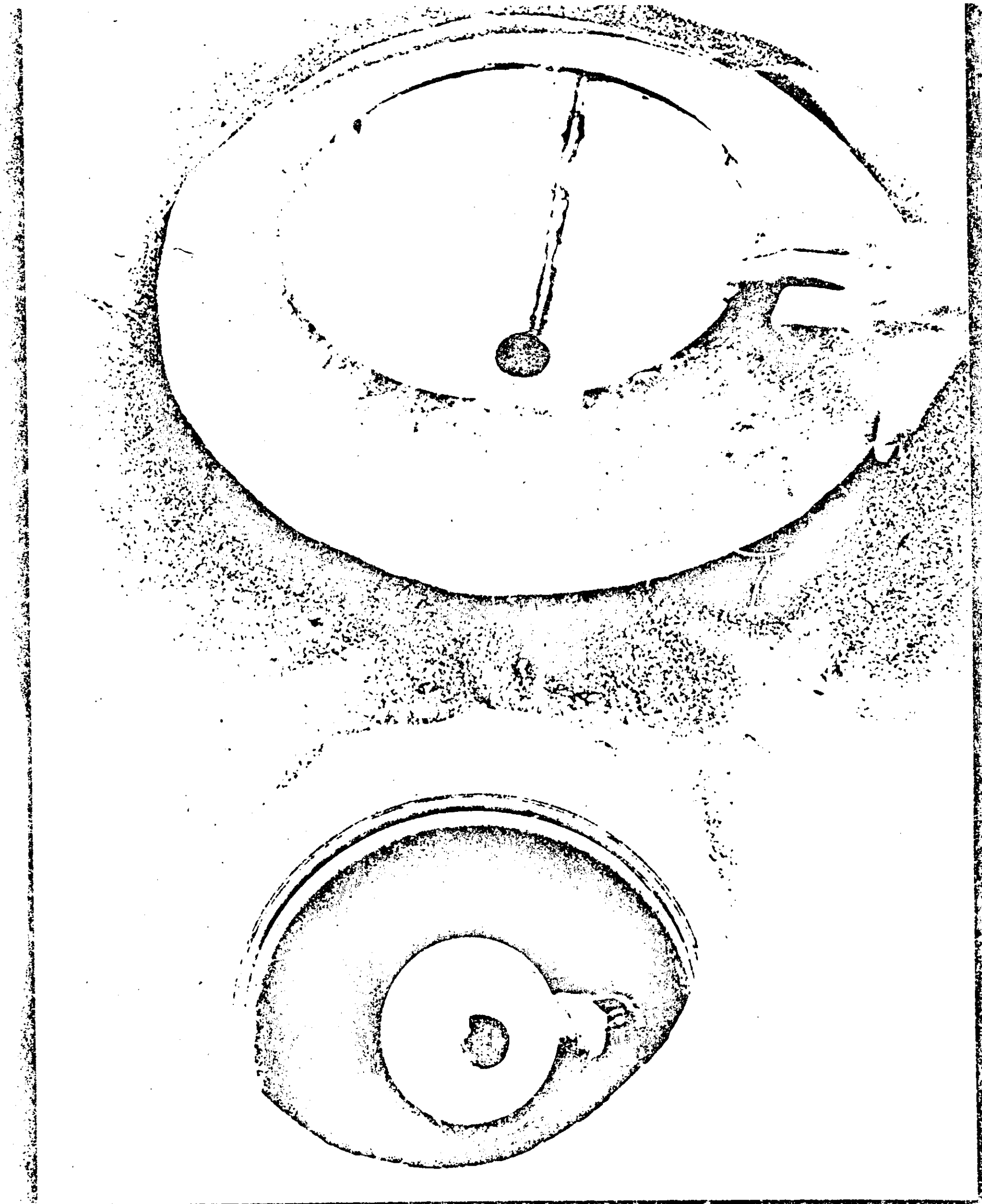

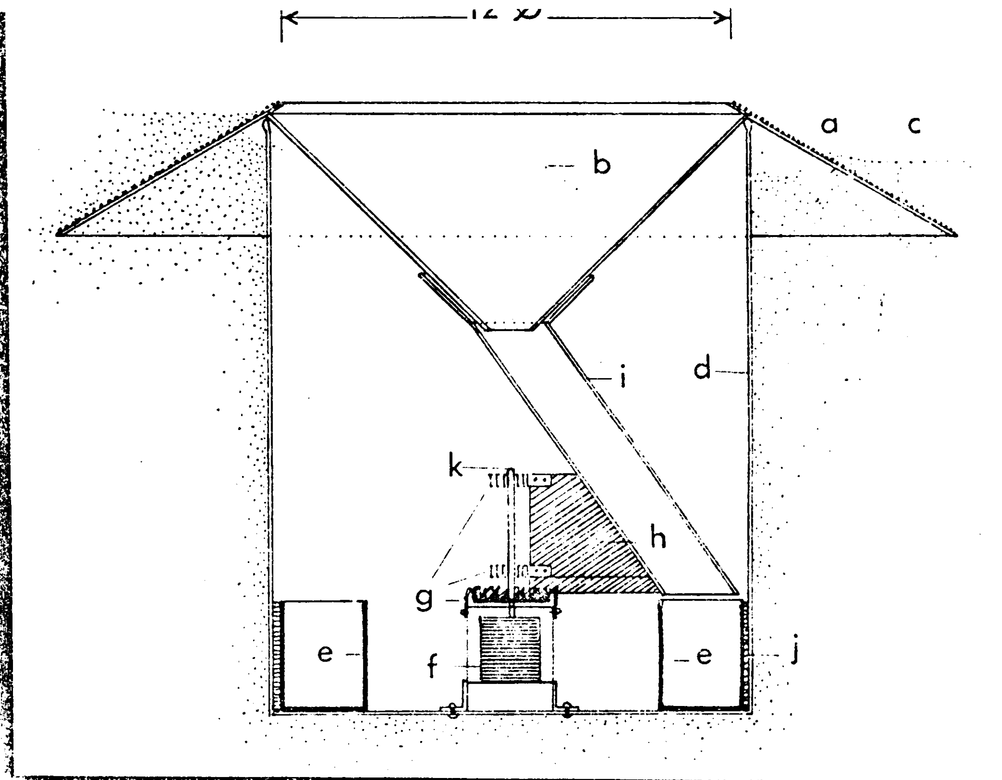

a — Sand-coated overhanging collar

b — Smooth 45° funnel

c — Sand surface

d — 4 Gall. mantle tin

e — Ring of containers for 2hourly catches

f — "LAMPRECHT" meteorological clock

g — 2Hourly shift-and-stop mechanism for distributor

h — Suspension plate of distributor

i — Distributor

j — Foam rubber

k — Clock axle

Fig. 3 Pit trap for separated two-hourly catches over a twentyfour-hourly cycle. Left: View into opened trap. Right: Cross section.

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II. TECHNIQUES

TRAPPING.

To determine surface activity of xerophilous insects in the experimental area in time and place, a grid of pit traps was installed permanently in the area. These traps consisted basically of cylindrical tins, sunk into the sand, with the opening on the level of the sand surface. This type of trap had been used extensively in the past in the Namib Desert for collecting specimens of xerophilous arthropod species of taxonomical interest, and was known to give satisfactory results.

Avoidance of traps was no problem, since the dune dwelling species move about without fear of precipices, which are non-existent in the dunes under natural conditions, and are therefore excluded from the "experience" of these species. This lack of "vertigo" seems more pronounced in dune dwelling species than in closely related rock dwellers, at least among the tenebrionid beetles.* Furthermore all diurnal poikilotherms move about at great speed in the dunes, and cannot change course suddenly. In this respect nocturnal animals could be expected to have a better chance of avoiding a trap, but relative counts of nocturnal animals trapped and counted on strip count censuses, were fairly consistent with the same counts of diurnal animals, indicating little difference in ratio of animals active and animals trapped for diurnal and nocturnal animals respectively.

Care had to be taken to avoid any attraction to traps, since an unbiased trapping sample was aimed at. During a preliminary trapping experiment in 1967, it was found that certain diurnal tenebrionid species at least (Stenocara phalangium, Cerosis hereroensis, Onymacris plana), were strongly attracted to shade, or indeed even black objects. To conceal the dark hole of the trap, the rim was therefore raised by an inch or two above the sand surface, with an incline around the trap from all sides towards the trap opening. With this arrangement. the dark opening of the trap became visible only to animals already on the incline around the trap, within centrimeters of the opening. Olfactory and sound attraction between sexes of the same species, and towards prey, could not be avoided altogether, but since traps were emptied out daily, this was restricted to a minimum.

Despite these limitations, the system of pit-trapping was felt to give reliable and fairly unbiased data on surface activity at the individual trapping sites. To obtain a representative sample of the whole area, as reflected by the total catch from all traps, the choice of

* "Vertigo" was tested by placing the animals on an elevated surface such as a table top, and observing their behaviour when they reach the edge.

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sites for the traps was vital. On the basis of trapping experiments in 1967 and 1968,, as well as many observation and census outings in the area, representative habitats could be discerned and defined (see Chapter VI). Nine traps in all were then placed in all these most important habitats, on a pro rata basis to the surface area which the respective habitats cover in the whole area. The total surface area of the nine trap openings was one meter square, and the total catches of any species per day, were roughly interpreted as average activity of that species per square meter of the whole area. Trapped animals were released directly after recording and marking in the immediate vicinity of the trap.

The main problems encountered with the conventional pit trap used previously in this area, (a one gallon tin sunk into the sand to surface level), were: firstly, the rapid filling of traps with wind-blown sand, or the dropping of the sand level around the trap through wind action, rendering it ineffective, secondly, difficulties experienced in extracting all sand and trapped animals from the trap without removing and re-burying the trap with a great expenditure time and energy. Thirdly, data were affected by predation by birds and mammals on trapped arthropods.

A modification in design was therefore necessary, and instead of the above-mentioned one gallon tins, two types of pit traps were ultimately used, after several trials with various prototypes. The first trap type used was a cylindrical four gallon tin, of the type in which lubricating oils are sold, fitted with a snugly fitting but removable plastic container inside. On account of its depth, this trap eliminated most predation and the overflowing with sand. Trapped animals and sand in the traps could be removed by taking out the inner plastic container and pouring the contents through a one mm grid sieve, which would pass the sand, but retain all animals. The remaining problem with these traps was fluctuations in sand level around the traps, and consequently these traps were used only in localities where the surface remained relatively stable (Fig. 1: trap nos. 5, 6, 8 and 9).

The second type of pit trap used consisted of a four gallon mantle tin similar to the trap described above, which was covered with a collar and funnel which could cope with daily fluctuations in sand surface level around the trap. Since the collar was coated with a layer of sand glued to the metal surface, it provided access to the trap for terrestrial animals at varying sand surface levels, while the funnel was steep and smooth, causing the animals to fall through the hole in the centre. The proportions of the trap were the same as for the pit traps without funnel and collar. In this trap all important technical problems were eliminated, since pre-

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dation by birds and mammals was also completely prohibited by the funnel.

The second type of trap was furthermore fitted with a clockwork, which rotated a distributor pipe below the funnel opening, to distribute the 2-hourly segments of the 24-hourly cycle. These containers could be removed and inspected separately. For comparison with the data from traps without this timing mechanism, the two-hourly catches were simply added up to a 24-hourly total. Information on circadian activity of species trapped could be derived from catches collected by these timed traps.* (Fig. 3).

* "Circadian activity of Namib Desert dune arthropods" in prep.

MARKING AND RECAPTURE.

All Coleoptera were marked with dabs of water resistant "Embroidery paint", which is available in a great variety of shades in tubes with nozzles. A different colour code was used for each two-weekly period of the year, and the paint was applied in a code on different positions of the thorax and elytra of the beetles for the nine different traps. Since more than 50,000 individual specimens were marked in this way, a complete analysis of recapture data is beyond the scope of this study, although relevant information will be referred to.

RECORDING OF DATA.

All traps were emptied daily at 1000 hours, and catches were then recorded in the field on record sheets, using a set of abbreviations for the different species and colour codes. All material which could not be readily identified, was preserved and sent to specialist taxonomists for identification or description, while a preliminary code was used on the record sheets for such species.

RECORDING OF CLIMATE.

Data recorded at the S.A. Weather Bureau first order weather station, Gobabeb, about 2.4 Km. North-East of the experimental area, were used. No additional recordings of macro-climate were done. Wind data were evaluated from charts of a "Lamprecht" autographic wind recorder, and fog data from charts of a "Lamprecht" autographic fog recorder. All other data are from standard S.A. Weather Bureau equipment.

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III. THE EXPERIMENTAL AREA

A. THE CLIMATE.

A preliminary analysis of the weather data of the weather station Gobabeb from 1962 to 1967 (B.R. Schulze, S.A. Weather Bureau, 1969) has recently been published. While drawing heavily on this paper for climatic data no attempt to present climate in any such detail will be made here, and only factors of primary importance to the fauna will be discussed.

Wind:

Wind is the crucial factor in the climate of this desert from the point of view of the arthropod population, because not only temperatures and humidity, but also food supply are directly linked with wind. The main characteristics of the wind regime at Gobabeb are the predominance of easterly or land winds in winter, and the predominance of westerly or sea winds in summer. The first group (i.e. easterly or winter winds) consists of the true dry and often hot mountain winds from the south-east, east and north-east as well as colder and humid southerly winds. The latter group (i.e. westerly or summer winds) consists of the remaining wind directions, which all bear cool and moist sea air, with the exception of the North wind, which may have a hot and dry character. The highest incidence of calms occurs in spring and autumn. This is, of course, a very generalized description of the average wind pattern, but it will be adequate for the purpose of this paper. The actual occurrence and amount of wind during 1969 corresponds well with the average description presented above (Fig. 5).

The true easterly winds, (south-east, east and north-east) are correlated with high fog precipitation, higher air humidities and the lowest temperatures of the summer months. Average maximum and minimum temperatures are both only about 5°C lower in the winter than in the summer. These seasonal temperature differences would presumably be much more pronounced without the balancing effect of the wind.

The easterly winds, notably south-east and east, reach high velocities and originate inland. They bear a large amount of dust and organic particles from the interior of South-West Africa, part of which is deposited on the Namib dunes as aerial fall-out or detritus. As a food source, this detritus plays a key role in the ecosystems of the Namib Desert.

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The fog from the Atlantic ocean, brought into the dune area by low velocity westerly winds, is the main source of free water in the dune system, and plays an equally important role in the ecology.

Temperature:

As mentioned above, maximum and minimum temperatures are on average about 5°C higher in summer than in winter, with an average maximum of about 32°C in summer, and 27°C in winter. The average minimum is 15°C in summer and 10°C in winter. Highest maxima in the summer months are in the vicinity of 40°C, with an absolute recorded maximum temperature of 42.3°C. The highest maxima in the winter months are between 33°C and 37°C. Lowest monthly minima range from about 9°C in summer to about 4°C in winter, with an absolute recorded minimum of 2.1°C.

These figures present a picture of a rather moderate temperature range for a desert. While these temperatures were all measured in the Stevenson screen and do therefore not represent the environmental temperatures for the terrestrial fauna, (surface temperatures range from about 0°C to over 70°C), temperatures on the lower as well as on the upper end of the scale are hardly extreme, compared to conditions in inland semi-desert areas.

A property of the temperature conditions at Gobabeb, which might have an important bearing on the activity of poikilotherms, is the sudden changes in temperature which frequently occur. Changes in maximum and/or minimum temperatures of 10°C to 15°C within one to three days are by no means uncommon, both in summer and in winter. These changes are mostly associated with changes in wind direction and velocity. The mechanisms by which the poikilotherms cope with these fluctuations, will be discussed in Chapter VIII.

Precipitation:

Fog precipitation has the highest incidence in early summer, while rain is recorded most frequently in late summer. Fog, rain and dew, however, can all be expected throughout the year, and a period of more than three weeks without one or the other of these forms of precipitation, rarely occurs.

Fog precipitation can be expected from midnight to about eight o' clock in the morning, on rare occasions early in the evening and/ or up to about eleven o' clock in the morning. Rain may fall at any time of the 24-hourly cycle, and is mostly in the form of isolated

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showers.

For the purpose of direct consumption, the amount of water precipitated is of little importance to the small dune animals, since even a minimal dew provides more free water than they require. The frequency of precipitation, however, is highly important to these animals, since it marks the intervals the animals have to go without free water. In an indirect sense, however, the amount of precipitation is as important, since the permanent vegetation depends on an adequate precipitation of fog and/or rain, and the "rain flora" only grows after an adequate shower of rain (see "Vegetation" below). The average annual rainfall at Gobabeb was 24 mm for the years 1962 to 1967, ranging roughly between 15 and 35 mm per year, while fog precipitation is of the order of 30 mm per year.

It has been pointed out (Cloudsley-Thompson, 1954) that the distribution of precipitation in time is as important as the amount of precipitation in desert ecology, since both the effect of heavy precipitation on rocky areas and light and scattered precipitation on sandy areas is minimal because of the run-off and rapid evaporation of the available water respectively. On the strength of the data available, it seems that amount and frequency of precipitation is correlated in the Namib Desert, both in the case of rain and fog. The highest averagemonthly rain precipitation is in March and the highest monthly fog precipitation in October.

Humidity of the air and other climatic factors:

As a rule, air humidity is negatively correlated with air temperature in the daily cycle. Apart from the occurrence of fog, air humidity is low, varying from daily averages of 60% RH in summer to 36% RH in winter. As pointed out above, air humidity and temperature are largely dependent on wind direction and velocity, and the lowest humidities (between 0% RH and 5% RH) are recorded during the easterly desert storms. During the daylight hours, air humidity is rarely above 50% RH throughout the year. The humidity of the air may be of great importance for some species in the dune ecosystem. Prof. E. Edney (University of California, Davis) informed the author that certain Thysanura of this area were found to absorb water from the atmosphere above 40% RH, but since no humidity data on the various micro-habitats are available, this aspect can not be enlarged upon in this discussion.

Apart from evaporation, which is about 3,500 mm p.a. from an open

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water surface, (about the same as recorded inland at Windhoek but with the difference that at Gobabeb the evaporation in winter is relatively higher) there are no measured factors of the macro climate that merit discussion, either because of rare occurrence or because of presumed minimal or extremely indirect effect on insect populations.

B. GEOLOGY AND GEOMORPHOLOGY.

A number of papers referring to the geology and geomorphology of the Namib Desert dune area have been published, both from the descriptive viewpoint (Koch, 1961, Giess, 1962, Coetzee, 1969 and others) and the more exact approach (Goudie in prep., Besler in prep. and others). This description will therefore be confined to features most relevant to the ecology of the apterous dune insects.

The hostile or beneficial properties of dunes as environment for fauna are inseparably linked with climate, and furthermore dependent on the specific requirements of the subject species. In view of all these variables involved in assessing the significance of the dune substratum in the life systems of the inhabitants it will be necessary to discuss the dune substratum in some detail. Firstly, therefore, the general situation and formation of the dune area will be discussed briefly. Then the three main types of substrate within the dune area will be discussed separately, with reference to ecological characteristics.

The role of the substrate in the various life systems of individual species will be enlarged upon in Chapter VII.

Situation and general description of the experimental area:

The area under discussion is situated about 60 kilometers inland from the South West African coast, and south of the Kuiseb river bed, at Gobabeb. (Fig. 1). The major dune ranges are orientated roughly North-South in this area and extend from the Kuiseb in the North to about 25 kilometers South of the Kuiseb, where they are separated from the main body of the Southern N·mib dunes by a gravelly plain, ten to twenty kilometers across. These two dune areas, are however, connected both in the West at Tsondabvlei, and in the East, where a belt of coastal dunes 30 kilometers wide connects the two areas. The dune ranges are between fifty and one hundred metres high, and one to two kilometers apart, with sandy and gravelly plains be-

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tween. These plains are ecologically an integral part of the dune system in this area, differing from the plains North of the Kuiseb in fauna, and provide a habitat both to an endemic fauna and to dune-living animals under certain conditions. The two major sub-divisions of the dune biosphere (Koch, 1961) will, therefore, be extended to include three macro-habitats, viz.:

(i) The inter-dune valleys;
(ii) The semi-stable and vegetated dune areas;
(iii) The vegetationless dune crest system.

The inter-dune valleys:

This area represents about one third of the surface area of the experimental site, and consists of a fairly solid and stable substratum of sand and rounded pebbles. The surface is covered with coarse whitish sand, alternating with rocky or gravelly outcrops and patches of dune sand. A powdery mixture of sand and gypsum dust is found below the surface, and in the South of the experimental site a solid bank of sandstone underlies this layer. This sandstone bank surfaces further south to form a sandstone terrace strewn with rounded pebbles. The presence of pebbles and a relatively stable substrate, provides a favourable habitat for a number of animals. The pebbles provide shade for small diurnal arthropods and serve as physical obstacles which deposit wind-blown detritus on a small scale. The stable substratum on the other hand provides a suitable medium for fossorial life. Relatively few species, however, inhabit this area permanently, mainly on account of scarcity of food. This becomes apparent after heavy rain when these valleys become covered with minor grasses. Under these circumstances some species from surrounding areas shift their activities to the plains, and about half a dozen species endemic to the plains suddenly appear.

Some vertebrates, ants and termites inter alia use the plains exclusively for their fossorial activities, while other species of these same groups tunnel into the semi-stable dune slopes only.

The semi-stable and vegetated dune areas:

These areas constitute about half of the surface of the experimental area and can be sub-divided into the dune foot area, the vegetated slopes and the intra-dune valleys. The dune foot collects the largest sand particles, which are lighter in colour than the remainder

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of the dune sand, which is reddish. For most species it is a transitional area between the plains and dunes, and harbours a small characteristic fauna. The semi-stable dune slopes are marked by the presence of vegetation, forming isolated hummocks of perennial plants (see "vegetation" below). These slopes are semi-stable because of a number of factors, inter alia the grain size of the sand, the humidity of the sand, the aerodynamics of wind on the dune and the binding and wind-breaking action of the vegetation. The third area, or intra-dune valleys, is similar to the semi-stable dune slopes but for the texture of the sand, which is loose and fine. The sand in this area is stable and supports vegetation mainly on account of the sheltered position of these valleys, which lie between the dune crests within one dune range. The fauna of the last two areas mentioned, is qualitatively similar. Since the texture of the sand is more suitable, sand-diving animals prefer the intra-dune valleys to the semi-stable slopes. Also detritus feeders prefer the intra-dune valley area because more wind-blown detritus collects in these pockets than on the exposed hard dune slope.

The above three areas all have fairly compacted or level sand which makes tunneling possible, if only during the night. The writer found it most surprising that the sand surface is stable enough at night for tunneling, although air moisture may not be above 50% RH, while it is unsuitable for tunneling during the day. The complex hygroscopic qualities of dune sand under different temperature and moisture conditions are probably responsible for this phenomenon (Orlov, B.P., 1928). The fact is that in these areas the sand is largely unsuitable for tunneling by day, which can be demonstrated by releasing a nocturnal fossorial animal by day on this sub-stratum. All attempts at tunneling are thwarted by the caving-in of the sand.

All tunnel entrances also collapse in the morning making the tunnels invisible by day, while at night the same, but now stable dune areas are studded with tunnels of all sizes.

Shade in these areas is restricted to the permanent vegetation and this vegetation also provides the physical obstacles necessary for precipitation of wind-blown detritus. Small waves or ripples in the sand, transverse to the direction of the wind, which mainly form on the dune foot, also collect wind-blown detritus on a small scale.

The vegetationless dune crest system:

This is the smallest part of the total area of the experimental

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site, (about one sixth), but from an ecological point of view the most interesting, since the highest specializations in morphology, behaviour and metabolism are required of the inhabitants of this part of the dunes. The most important properties of this area are the absence of vegetation, the presence of steep dune slip-faces of very fine, dry and wind-deposited sand and the high concentration of food in the form of wind-blown detritus. The latter is deposited on the slip-faces by the same aerodynamic principle by which the wind-blown sand is deposited on the leeward side of these barchan type dunes. The dune crest system is therefore highly dependant on wind, both for the formation of the slip-faces themselves, and for the deposition of detritus. Another feature of the slip-faces is that they provide shade for an hour or two in the morning or afternoon, since these slip-faces face east or west predominantly. During the hottest time of day they are, however, without any shade, and animals lacking the ability to dive into the sand for protection against the heat cannot survive.

This environment excludes all tunneling activity, since the very powdery and steep sand slopes will never compact sufficiently. For the animals in this area, sand diving is the only escape from adverse climate or enemies.

The instability of the slip-faces poses a problem to the inhabitants. With a change in wind direction, slip-faces are transformed temporarily to bare dune slopes without detritus, and the inhabitants must either find their way to a newly formed slip face or remain dormant until the wind pattern changes or reverses. This would presuppose a sensing mechanism by which the animals could detect favourable conditions from below the sand.

The advantages of the dune crest system for an animal possessing sand-diving ability are, however, manifold: it is a medium in which a wide range of environmental temperatures is available in the different depth strata (Hamilton and Coetzee 1969), while the corresponding moisture gradients enable the animal to select ideal environmental conditions by merely shifting its position vertically. Furthermore, food is relatively abundant in the form of deposits or "cushions" of wind-blown detritus, both on the surface of the slip-face or covered with sand.

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C. VEGETATION.

The vegetation of the dune area can be divided into two groups, viz. perennial vegetation and "rain" vegetation. The first group consists of larger plants, which grow in isolated hummocks. Species in the experimental area are, in sequence of abundance, Stipagrostis sabulicola (Pilger) de Winter (a tall hard and spiny dune grass), Trianthema hereroensis Schinz (a non-spiny succulent shrub), and Acanthosicyos horrida Welw. (The Narra, a flowering shrub with spiny modified leaves). All these plants grow on the semi-stable dune areas, (with A. horrida near the dune foot only), and form vegetated sand mounds by precipitating wind-blown sand.

The second group of plants, or the rain flora, consists of various minor grasses, mainly of the genus Stipagrostis, as well as some lilies and one Monsonia sp., Monsonia ignorata Merxm & Schreiber. Because of their small size, these plants only grow in the areas where the sand surface is more stable, viz in the inter-dune plains and in the most stable part of the dune foot. All these plants perish within weeks after sprouting, the lilies and M. ignorata lasting longest. While the perennial flora must be able to subsist on fog precipitation to a large extent, the rain flora is dependent on a fair precipitation of rain. A shower of between 15 and 20 mm rain seems necessary to bring out a cover of rain flora. This flora was present in 1967 and 1969 when more than 20 mm of rain was recorded, while it was absent in 1966 and 1968 when less than 10 mm of rain occurred.

The role of the flora in the life systems of the insect species dealt with in this paper, will be described in more detail in Chapters V and VII. The importance of the two mentioned plant groups in the system as a whole will only be outlined here.

The importance of the vegetation in the ecology of the dune system:

The perennial vegetation is of minor importance as a food source in the system as a whole, although there are a number of phytophagous species depending on them. Their main importance to the apterous insect fauna lies in secondary aspects such as provision of shade, precipitation of detritus, and, perhaps most important of all, precipitation of fog. It is well-known that fog precipitates most effectively on protruding objects and sharp points, with the result that the precipitated moisture flows down the stems or leaves of the plants and moistens the sand directly underneath the plant. This humid substratum, combined with

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a food supply in the roots of the plant or the layers of precipitated detritus, creates a favourable environment, especially for the larvae of many insects.

As a food source, the "rain" flora is much more important, and when present, produces the most phenomenal explosions of arthropod populations. Since showers in the Namib Desert are invariably localized, and rain falls on any particular area only once in two or three years in sufficient quantity, this food source is available only to insects exhibiting a quiescence, or to generally adapted insects that are present and can switch from other food sources to green vegetation. Both these groups are well represented, but since the "rain" flora is succulent for only a short period, the insect populations cannot overtake the food supply. The result is that a large proportion of this vegetation goes unconsumed, dries up, and is distributed by the wind throughout the area as wind-blown detritus. This detritus, together with vegetable matter that is imported into the system from adjoining territory by the wind is then distributed in place and in time to the detritus feeders in the system.

For months after the rain, until the small dry grass-clumps are uprooted and blown away by the wind, the "rain" vegetation also acts as detritus "traps" and provides shade for the small arthropods of the plains, in much the same way as the pebbles on the surface.

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IV. THE FAUNISTIC COMPONENTS OF THE ECOSYSTEM

A. PRIMARY FEEDERS.

The primary feeders of this system can be classified into the same categories as the flora, viz. primary feeders of the perennial flora and primary feeders of the rain flora.

Herbivorous mammals recorded in or near the experimental area are the Namib hare, the Oryx, the one or more species of *Gerbillus*. The only other vertebrate that may be classified as herbivorous is the dune lizard, *Aporosaura anchietae* Bocage which feeds on grass seed (Louw and Holm, in press) but since it feeds on the seed lying on the sand and not whilst on the plant, and furthermore also feeds on small arthropods, this animal could better be described as omnivorous.

The phytophagous insects on the perennial vegetation are, like the mammals, species or genera which also occur in the interior of the subcontinent. They are less highly adapted morphologically and in their biology to a desert environment than the other ecological groups, such as the detritus feeders. Their micro environment which is essentially the same as for their counterparts in semi-arid regions does not call for major changes. In general terms this group forms a more or less isolated sub-system in the dune ecology, and owing to their sporadic presence, plays a minor role in the energy flow of the whole system over long periods of time, although they become dominant in the system when present in great numbers after good rain. The families concerned, viz. Pseudococcidae, Meloidae, Chrysomelidae, Curculionidae, Pentatomidae, Acrididae and Gryllacridae are represented, mostly by single species. Some Tenebrionidae larvae may feed on roots of permanent vegetation (see "detritus feeders" below). A few species of the Curculionidae and Acrididae are also found on the perennial vegetation seasonally or only after good rain, when this vegetation is in best condition.

The second group of phytophagous insects, viz. the rain dependent group, are ecologically and morphologically much further specialized than the first group mentioned above. The sporadic and isolated occurrence of rain necessitates a quiescence in one of the stages of metamorphosis if the rain flora is to be effectively utilized.

It seems that the quiescence would be mostly in the egg stage, since the time lapse after rain and before imagos appear (in the

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Coleoptera groups), is proportional to the size of the species and therefore with the expected duration of development, while in the case of the Acrididae the first instar nymphs appear immediately after the rain.

It must be realized that, while the groups mentioned above are strictly primary feeders, the majority of insects in this system belong to the more or less omnivorous group described as detritus feeders and scavangers. These insects subsist mainly on vegetable detritus and dead animal matter, but most of these species, excluding the dune crest fauna, will feed opportunistically on rain vegetation, resulting in a considerable increase in their populations (vid. Onymacris rugatipennis, Haag No. 15.) Permanent vegetation is rarely consumed by this group (vid. Onymacris plana (Peringuey) and O. laeviceps (Gebien) Chapter V).

B. PREDATORS.

Adequate predation records are notoriously difficult to secure in any ecosystem. Stomach content and faeces analysis of predators is one way around the problem, but this requires a full scale research project on its own if statistically significant data are to be obtained. In this line valuable work has been done on the prey of owls in the Namib Desert (Niethammer, 1968, Nel, 1969) but reliable records on predators of the Arthropod fauna are scarce. The predator prey relationships discussed below are derived from the various sources of the literature on this area as mentioned from case to case as well as observations and stomach content analyses by the writer. Fragmentary though this information may be, it is mentioned to give more insight into the nature of the ecosystem.

Predatory mammals in the central dune area are the saddle-backed jackal and the brown hyena. The first occurs in the experimental area, and, judging from droppings, feeds extensively on dune Coleoptera, and most likely also on the various dune reptiles. Gerbillus spp. is known to feed on tenebrionid beetles readily in captivity, and burrows in the dunes are often found with remains of beetles strewn about. The Namib Desert golden mole is a voracious eater, and probably accounts for much of the nocturnal predation on arthropods. This animal does not seem to be fastidious as to what it takes, as long as the size is manageable. (Holm, 1969).

Very little is known about predation by birds on dune arthropods.

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Although the arthropod content of owl pellets is mentioned, it has unfortunately not been analysed (Niethammer, 1968). The desert chat has been observed by the writer to feed on termites and dune ants, and crows feed extensively on especially the "rain" arthropod fauna, as observed directly and in droppings. The birds of prey which enter the dune area will most probably prey on reptiles mainly. Furthermore the most unlikely birds will feed on the "rain" arthropod fauna when it reaches high population densities a few weeks after the rain. At such times even herons and wild geese have been noticed on the inter-dune plains.

Among the reptiles, Meroles spp. and the Namib chameleon are diurnal predators of arthropods. The former concentrates on small beetles and other arthropods, while the chameleon can manage the largest dune arthropods (Burrage, in prep.). The blind snake, Leptotyphlops, favours the plant-grown dune slopes, and most probably feeds on ants, termites and tenebrionid larvae (Fitzsimons, 1962). The barking geckos in this area occur mainly in the inter-dune plains, where they also feed on ants, termites and other small and soft-bodied arthropods. Bitis peringuey (Boulenger) the side winding adder of the dunes lives mainly on the nocturnal Palmatogecko rangei (Anderson), although B. peringuey is not strictly nocturnal, and may take Aporosaura, (a diurnal lizard), too. The main reptile predator of Meroles is the grass snake, Psammophis nostostictus (Peters) which shares the same habitat, viz. the vegetation hummocks. Palmatogecko, the web-footed dune gecko, is strictly nocturnal, and seems to feed on all nocturnal arthropods except the larger Tenebrionidae like the Onymacris species. A scorpion (Protophthalmus holmi, Lawrence) and a whole Lepidochora beetle were found in the stomach of one specimen of Palmatogecko by the writer.

The main predators of arthropods in this ecosystem, however, are the many species of spiders and solpugids. Spiders of the larger sized genera have been observed repeatedly by the writer taking nocturnal tenebrionids, while the small species of spiders and solpugids seem to subsist mainly on small soft-bodied arthropods, such as the termites and Thysanoptera. Different species of spiders and solpugids occur in all parts of the area and during all segments of the daily cycle. Their average activity decreased sharply during the winter months, however, in spite of a greater abundance of prey in winter. Opposed to this, the only truly endemic scorpion of this dune area, Protophthalmus holmi, (Lawrence) was recorded during 1968 and 1969

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only in the winter months. In specialized morphology and ethology the arachnoidea of the area are second only to the Tenebrionidae, and most species are completely endemic to the Namib Desert (Lawrence 1962, 1966, 1969). Among the insects, there are several important predatory species among the Hymenoptera, Diptera and Neuroptera. Most of these are summer forms again, and with few exceptions do not differ much from their close relatives in the inland. Most predatory insects are alate in this area, with the exception of the Mutillidae, the Myrmeleonidae larvae and the partially predatory Gryllacridae.

Again the group of detritus feeders and scavengers cannot be strictly separated from the specialized predators mentioned above, since some species will prey opportunistically. Mostly disabled animals fall prey to this group, but on rare occasions true predation by tenebrionids on smaller tenebrionids and Thysanoptera has been observed. Since it is the exception rather than the rule, this predation is presumably of little importance in the general ecology of the area.

C. DETRITUS FEEDERS AND SCAVENGERS.

The mechanism of detritus precipitation in the dune area is discussed in Chapter III above. Various physical obstacles do precipitate detritus in the various habitats of the dune area, and specialisation among the detritus feeders is often only on the micro habitat. It is possible, however, that where more than one species of detritus feeders live sympatrically in one habitat, the species may specialize in feeding on different components of the detritus, which is very heterogeneous, consisting of grass fragments, seeds, animal remains, other plant fragments and organic dust.

The detritus feeders and scavengers are the dominant group in the system by a wide margin, both in number of species represented, and total biomass end energy flow. In this respect they are found in the ecological role mostly held by primary feeders in other ecosystems. It must be kept in mind that the detritus sub-system is an incomplete cycle if the Namib Desert is to be isolated, since detritus originates largely from the inland savanna areas. With the detritus feeders at the bottom of the food chain, the dune ecosystem has a parallel in the abyssal sea.

The detritus feeders include the most highly specialized animals in the dune environment. Most characteristic of this group are the

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Tenebrionidae, while ants, termites and Thysanoptera are also represented in this group. While detail of the food preferences of the various species is often uncertain, the mere absence of any other organic food source often indicates a species as a detritus feeder. A few species with uncertain food requirements will be discussed under this group in Chapter V.

The only known non-insect animal in the area which feeds on detritus is the dune lizard Aporosaura Anchietae which feeds on seeds in the detritus deposits in the central dune area, while it is also able to live on small arthropods (Louw and Holm, in press).

A small group of dung and carrion feeders will also be discussed under this group. Two wingless scarabs occur in the area, feeding on game droppings and dry vegetable matter, and game droppings respectively. A third, alate species, appears to concentrate on lizard and small mammal droppings. Further at least two species of small sand diving, alate and nocturnal scarabs occur in the dunes. The feeding habits of these scarabs are unknown.

One species of Histeridae was recorded regularly in the experimental area. A few species of Diptera of the carrion and dung feeding families occur in the area. A few species of seed-eating birds occur in the area. These birds are hard to place in the food chain, since it appears that they migrate to areas that have had a fair shower of rain, and feed on seeds on the plants as well as on the sand. No birds are known to rely on seeds in the detritus deposits only.

As mentioned above, the larvae of Tenebrionidae in the dunes can be expected to feed on detritus deposits which have been covered with sand. All tenebrionid larvae live under the sand, and some can be found directly under detritus cushions, while any buried detritus will also contain tenebrionid larvae. A few species may feed on roots of permanent vegetation. This, however, is difficult to ascertain, since the hummocks of permanent vegetation are also packed with layer upon layer of detritus.

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V. ECOLOGICAL NICHES OF THE APTEROUS INSECTS

The apterous insects of this ecosystem can be separated into two major ecological groups, namely those that occur only (or only in significant numbers) after rain, and those that are independent of rain, such as the detritus feeders and other groups.

A. THE RAIN DEPENDENT GROUP.

This group is listed under numbers 1 to 11 on the list of species on figs. 4 and 5.

When the occurrence of these species is compared with the climate (fig. 5), the correlation between rain and polulation activity is not immediately apparent. This is due to the difference in time lapse, after the rain and before the host plants of the different species are suitable for consumption. The emergence of these phytophagous species is in every case timed to coincide with the suitable stage in the growth of the host plant.

All these species were absent in 1968, when there was no "rain" vegetation due to drought. They were present in 1967, after good rain. Since there was a fair amount of rain late in 1968, there were, however, still remnants of some populations left in February and March 1969, when the rains came (Nos. 3 and 9). The classification of these species as rain-dependent species in the ecosystem is based on these observations as well as notes on feeding behaviour as discussed below:-

No. 1. Pachynotelus albonotatus Haag

This is the largest species of the Cryptochelini, a tribe of the Tenebrionidae, in this system. The whole genus, which is distributed over the arid regions of the subcontinent, seems to be specialized on sporadic occurrence after rain. The species P. albonotatus is diurnal and frequents the more stable part of the dune slopes and the dune foot. To the knowledge of the writer, this species is endemic to the dune area, as opposed to P. renei which occurs throughout the Namib. Both species tunnel into the sand in the evening, using their curved legs, which are well equipped with bristles, to kick the sand backwards when digging. P. albonotatus was found feeding on the small rain-dependent grasses only. Of all the rain-dependent species, P. albonotatus remained active for the shortest period. They were trapped for less than one month, and observed

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for only slightly longer than one month. It is interesting to note that a small population again occurred in September after very little rain in mid-August.

No. 2. Pachynotelus renei Koch

This tenebrionid is very similar in habits to P. albonotatus, with the difference that this beetle frequents the inter-dune valleys (fig. 4) and the distribution extends to the Namib plains north of the Kuiseb, where it was found as far north as Cape Cross and Spitzkoppe by the writer. This beetle, though smaller than P. albonotatus, appeared later after the rain but was active twice as long (fig. 5). P. renei was also twice as abundant as P. albonotatus during 1969.

No. 3. Enstolopus octoseriatus Gebien

This beetle belongs to the tenebrionid tribe Adesmini, and is the only tenebrionid of this tribe in the area which is a true rain-dependent form. The feeding behaviour is similar to the Pachynotelus spp., and the distrubution coincides with that of P. renei (fig. 4). Like the Pachynotelus spp., E. octoseriatus is diurnal and tunnels into the sand in the evening. E. octoseriatus is responsible for the most spectacular population explosions in the area. During April 1967, they reached densities of as high as one per square meter in some areas on the inter-dune plains after good rains in March, and over 3,000 specimens were trapped in a pit trap (unbaited one-gallon tin) within three days. Single specimens are often found completely out of season, and this species was regarded as extremely rare until the population explosion in 1967 was recorded by the writer. Although the 1969 population was less spectacular, the correlation between rain and emergence of E. octoseriatus was again established.

No. 4. Fam. Cercopidae (Ac No. H1)

A very small cryptically coloured frog-hopper was recorded in the dunes during 1969 for the first time. This animal could not as yet be identified, and specimens are at present in the care of the British Museum of Natural History. The ecological status of this species in the system is also not yet clear, but since it belongs to a phytophagous family, it is included in this group. No clear correlation between occurrence of this species and the climate could be established (fig. 5), and the distrubution does not coincide with that of one specific host plant (fig. 4). The animal is diurnal, and hard to spot on the dune sand, since they jump very actively in

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the blowing sand and are very cryptic in colouration. The insect seems to rely on its legs exclusively for locomotion.

No. 5. Crypsicercus cubicus - Saussure

Several grasshoppers occur in the area after rain, but C. cubicus is the only completely apterous species. It is also the dominant grasshopper in the dune area. It avoids the high dunes and is mainly found on the inter-dune plains (fig. 4), where it remains on the surface at night. The only protection of this clumsy animal is its very cryptic colour and shape, which resembles a small pebble, and the red "warning" colour on the inside of the hind legs. The first peak of activity (fig. 5) was due to first instar nymphs emerging, and consequently the population activity curve was fairly regularly parabolic, regardless of climate. During the decline of the population, much predation by birds, mice and arthropod predators on C. cubicus was evident. This animal is unique in having short antennae with special grooves on the head into which they can be retracted, the purpose of which is not quite clear (Brown 1962)

No. 6. Fam. Curculionidae, sub-fam. Otiorrhynchinae

A small greenish weevil (more than one species may be involved) which was never found in the absence of rain-flora in the area. Only a few specimens were trapped during 1969, but this presumably is not an indication of their relative abundance, since they were well represented in stomach contents of Aporosaura lizards during the same time (Louw and Holm, in press). Unfortunately they were also rarely observed since they are hard to spot on their host plant, a small species of grass Stipagrostis-sp. Distribution in the area (fig. 4) is rather inconclusive on account of the small sample trapped.

No. 7. Brachycerus rotundatus Peringuey

Although B. rotundatus was identified from material from the dunes, other species of Brachycerus may also be involved, since no thorough taxonomical survey of the weevils of the area has been done as yet. This genus is decidedly rain-dependent, and the host plants are the various species of lilies that sprout in the dunes and inter dune plains after rain. Since Brachycerus spp. are very specific on lilies in this system, it would be interesting to know whether different species occur which are specific on the species of lilies in the area. All the weevils (from No. 7 to No. 11) are active throughout the daily cycle, and the main activity period depends only

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on climatic conditions. Brachycerus is distributed throughout the area (fig. 4), as are the host plants. Single specimens of Brachycerus are, like E. octoseriatus, sometimes found out of season.

No. 8. Hyomora falcipes Marshall

This weevil is most specific on Trianthema sp. as a host plant, and over 90% of the total catches of this species were made in trap No. 5, directly under a Trianthema shrub (fig. 4). Although Trianthema is a perennial plant, H. falcipes was found only after rain, when the Trianthema was in best condition (fig. 5).

No. 9. Leptostethus sp. (A yellow weevil)

This is one of the most widely adapted weevils in the area. It is very resistant, and seems to be present for a longer period of time than any of the other weevils in the system (fig. 5), while it is also least specific with regard to its host plants. A strong walker, it traverses the dunes and interdune plains from one plant to the other. It feeds mainly on grasses, including Stipagrostis sabulicola, but is also found on Trianthema sp. The high occurrence in trap No. 4 (fig. 4) is, as in the case of species No. 11, due to the channeling effect of a slipface base on the movement of these animals, which tend to avoid the soft sand of the leeward slope. All Leptostethus species in the area feign death, when in danger, by stiffening their legs and falling on their backs. They neither tunnel nor dive into the sand, but remain on the host plants during periods of inactivity. Egg laying in this species as well as Nos. 10 and 11 is done by kicking out a small crater in the sand, mostly around the stem of the host plant, and laying the eggs in the sand at the bottom of the crater.

No. 10. Black weevil near Leptostethus

A somewhat larger beetle than No. 9, and similar in appearance. While No. 9 is covered with a yellow waxy powder over the whole integument, No. 10 is black, with only two yellow stripes laterally. As indicated by fig. 4, this weevil is very specific on Trianthema as a host plant, and its period of occurrence is clearly confined (fig. 5). Behaviour is much the same as No. 9, except that this weevil is not as active and tends to aggregate on the host plant.

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No. 11. Blue weevil near Leptostethus

This large and strikingly beautiful bright blue weevil is extremely rare during spells of drought. During 1968 none were observed at all, and from 1964 to 1966 only single specimens were collected in this area. In 1967 and 1969 after good rains, however, they emerged in thousands, but only for a very short period (fig. 5). The host plant is Stipagrostis sabulicola and as in the case of H. falcipes the imagos appear to feed on this perennial plant only after good rains, when these plants are in prime condition. The behaviour is very similar to that of No. 9, and the curve of population activity is parabolic, with activity apparently positively correlated with temperature, (fig. 5). Owing to the similarity in feeding and locomotory behaviour between this weevil and No. 9, the distribution curves also coincide (fig. 5). Less were trapped near Trianthema in this case, however, while more were trapped in the dune crest system where S. sabulicola grows nearby (fig. 4).

B. THE DETRITUS FEEDERS AND OTHER GROUPS.

This group is listed as species Nos. 12 to 48 on figs. 4 and 5. The Tenebrionidae dominate this group (numbers 12 to 36), and together with the Thysanura (numbers 45 - 48), represent the true detritus feeders. The feeding habits of the Orthoptera (Nos. 37 and 38) are relatively unknown while the Scarabaeidae (Nos. 40 and 41) feed mainly on dung. The Mutillidae (Nos. 43 and 44) are the only true parasites among the insects discussed here. The single Carabid (No. 39) belongs to a myrmecophilous group, but the host in this case was not established.

The main ecological characters of the animals in the above groups will be discussed below:-

No. 12. Archinamibia peezi Koch

This appears to be a summer form, and from 1966 to 1969 it was collected only on rare occasions, and always in the period from November to February. Strictly nocturnal in habits, this sand-diving tenebrionid frequents the dune crest system area near S. sabulicola hummocks. The only specimen trapped during 1969 was in trap No. 3, under a S. sabulicola plant. It is possible that A. peezi occupies the same niche as Namibomodes serrimargo, since it is of about the same size, both are nocturnal, and both aggregate around S. sabulicola. The occurrence of these two species in the yearly

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cycle is strictly alternating.

No. 13. Namibomodes serrimargo Gebien

This species belongs to a very large genus endemic to the Namib, with many allopatric species and subspecies. The occurrence of this species coincides with the period of easterly winds. Although N. serrimargo is nocturnal and does not experience the easterly winds (which blow during the morning) on the surface, it is decidedly more active during spells of easterly winds. This may be due to the higher temperatures or to the influx of detritus caused by the easterly winds (fig. 5). The distribution of N. serrimargo coincides with the areas near S. sabulicola and owing to the attendant channeling effect of the slipface base on the movements of this species trap No. 4. was favoured, as in the case of No. 9 and 11. N. serrimargo is extremely cold-resistant, and was found walking about on the surface at night with surface temperatures as low as 3°C. During the day they lie buried in the loose sand of the S. sabulicola hummocks.

No. 14.(a) Onymacris albotesselata Koch

This beetle occurs only marginally in the experimental area, and the centre of its distribution seems to lie towards the East of the experimental area. In appearance it is subidentical to No. 15. (O. rugatipennis) the main difference being the presence of spots of white wax on the elytra and thorax. This beetle was found on the dune base mainly (fig. 4) after the rain, in March 1969 when the grass in this area was still green (fig. 5). Most probably the appearance of this species in the area is due to immigration to favourable food conditions, as in the case of O. rugatipennis, since O. albotesselata had not been recorded in this area before. All Onymacris spp. in the area are diurnal, and dive to just below the sand surface at night.

No. 14. Stenocara phalangium Gebien

S. phalangium is one of the Adesmini, a tribe of Tenebrionidae represented mainly by the genus Onymacris in the dune ecosystem. It is characterised by extremely long and slender legs, enabling this diurnal animal to remain active at high surface temperatures, since it can run with the body held at more than ten mm from the surface, where the ambient temperature is several degrees below that of the surface. This beetle belongs in the well defined niche of small, fast moving diurnal detritus feeders, together with C. hereroensis

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(No. 24) and Gyrosis moralesi (No. 22). While G. moralesi is a summer animal, C. hereroensis and S. phalangium are winter animals (fig. 5). The distribution in place of the last two species is very clearly separated, with S. phalangium on the inter-dune plains, and C. hereroensis on the dune slopes, while G. moralesi, the summer form, occurs on the plains (fig. 4). These three species illustrate how well the available niches in the system are filled, since detritus, which is brought in by the easterly wind, is much more abundant during the winter and permits two species to share the niche in winter, which is held by one species during the summer, when the bare dune slopes are devoid of detritus, and only the remaining grass clumps in the inter-dune valleys are available as food.

Owing to its exposed environment and slender build, S. phalangium is prevented from being active during easterly storms and consequently its activity peaks follow just after spells of easterly winds. Apparently these peaks are then correlated with the deposition of detritus, and not with temperature (fig. 5).

Note: The histogram of No. 14 is at 1/10th scale, i.e. one mm vertically indicates 10 individuals trapped.

No. 15. Onymacris rugatipennis Haag

This tenebrionid is a broadly adapted species which occurs mainly in the dry riverbeds of the Namib, but will enter the dune system and the plains opportunistically for food. It seems to be a rather omnivorous species, feeding on green grass, detritus or dead animal matter. The histogram in fig. 5 demonstrates an influx of this species after the rain, when the dune area has a good stand of vegetation. The distribution is very similar to that of O. plana (No. 18) the species which is normally encountered in the niche of large diurnal detritus feeders and scavengers in the dune area, with the only difference that O. rugatipennis occurs more often near the dune base and in the inter-dune valleys than O. plana. With food supply dropping in August when the rain flora had been destroyed by the weather, O. rugatipennis disappeared completely from the dune system and plains although still present in the adjoining riverbed.

No. 16. Onymacris unguicularis Haag

O. unguicularis and O. laeviceps (No. 17) both fill the niche of large detritus feeders and scavengers with a bimodal morning and afternoon activity cycle. While O. unguicularis alone is found on the coastal dunes, O. laeviceps alone occurs on the inland dunes. The area in

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which the two species overlap is apparently not stable, since O. laeviceps alone was present at Gobabeb until 1968, when the first individuals of O. unguicularis were noted in the area. During 1969, O. unguicularis became quite well established in the experimental area. The only difference in distribution of the two species is a preference by O. laeviceps for the slip-faces, while O. unguicularis favoured the slip-face base. (Fig. 4). While O. unguicularis was slightly more active in the winter months, probably owing to adaptation to the colder coastal climate, O. laeviceps is predominantly a summer animal (fig. 5). Neither of the populations benefited from the rain flora, since both are peculiar to the dune areas where rain-flora cannot grow.

No. 17. Onymacris laeviceps Gebien

Two interesting behaviour patterns make O. laeviceps unique in this genus. Firstly they climb onto the grass, S. sabulicula, to feed on the seeds, a feat for which their sand-diving morphology is very badly suited, and secondly they are sometimes active during warm and humid nights. Although their habitat and food requirements are similar to that of the sympatric O. plana (No. 18), their main period of activity is before and after the main activity period of O. plana, resulting in this case in a division of the niche into different segments of the day.

No. 18. Onymacris plana Peringuey

O. Plana is an extremely fast diurnal runner, and can tolerate high temperatures by sprinting from the shade of one plant to that of another. Because these beetles are so active, trap No. 4 again caught a higher proportion, for the same reason as mentioned for Nos. 9, 11 and 13. O. Plana is omnivorous, and will feed on dead or disabled animals, as well as on green plants after the rain, or on detritus. Of the plants, O. plana frequents the Narra (trap No. 6), since the beetle also feeds on the Narra which drop to the sand (fig. 4). The effect of the rain flora on the population of O. plana is apparent from fig. 5. During the winter, O. plana is most active during hot spells. It is predominantly a summer animal (fig. 5), and strictly diurnal.

Note: As in No. 14, the histogram on fig. 5 is on 1/10th scale.

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The Zophosini:

Numbers 19 to 24 represent species of the pan-African tenebrionid tribe of the Zophosini. All species of this tribe are rather similar in appearance and behaviour, except in case of the Namib forms, where the tribe is differentiated into many genera. All the species of this tribe in the dune ecosystem have retained the main characteristics of the group in being small, fast moving diurnal runners, except the blind nocturnal Dactilocalcar caecus (No. 21.)

No. 19. Cardiosis fairmairei Peringuey

C. fairmairei is a strikingly black and yellow coloured species, and next to the Lepidochora spp., perhaps the most extremely adapted animal of the dunes. They are very efficient sand divers, and are never found far from the dune crest system (fig. 4). They are most active in wind (fig. 5), and have the habit of letting themselves be swept along with the wind on the slip-face of the dune, thus eventually landing up together with the wind born detritus on which they feed. Whirling around on the slip-face with the detritus, these beetles are hard to spot from a distance.

No. 20. Cardiosis hamiltonulus Koch

This very interesting species was only discovered in 1968, and has a very narrow niche. It is the smallest diurnal beetle in the system and inhabits only the rippled sands of the dune base, with very little overlap with C. fairmairei on the dune slopes, where both species occur marginally (fig. 4). C. hamiltonulus is also the only diurnal tenebrionid in the experimental area which is truly cryptic in colouration. Both Cardiosis species occur throughout the year (fig. 5).

No. 21. Dactilocalcar caecus Gebien

This is the smallest of the Zophosini in the area, and the only nocturnal one. Being blind and unpigmented, this beetle is rarely found on the surface and probably spends most of the time under the sand. The shape of the legs reminds one of the Dytiscidae, and in the case of D. caecus, are used for "swimming" through the sand. The species seems to occur throughout the year, and is distributed mainly on the dunes rather than on the plains, although the sample collected was not adequate for conclusive deductions (Figs. 4 and 5).

No. 22. Gyrosis moralesi Koch

The ecological role of this species has already been outlined above

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(vide No. 14). This species is strictly diurnal, and a runner of the inter-dune valleys (fig. 4). Although it occurs throughout the year, it is mainly a summer form (fig. 5). They were repeatedly observed feeding on the remains of grass clumps, and are often found under these grass tufts, digging to the roots, either for feeding or egg-laying.

No. 23. Gyrosis orbicularis Deyrolle

In appearance this species is very similar to No. 22, being only slightly larger in size, and occurs mainly in the riverbed. Single specimens enter the experimental area and are then found together with G. moralesi as well as on the dunes (fig. 4). A permanent population of this species never got established in the dune area, and it is never found far south of the river.

No. 24. Cerosis hereroensis Gebien

This is the dominant species of the whole dune ecosystem, and occurs all over the area, decreasing in numbers only towards the slip-faces, and in the plains where it has to compete with S. phalangium (No. 14), and G. moralesi (No. 22). The ecological niche was discussed under No. 14 above. This animal has an advantage over S. phalangium in being able to be active during spells of easterly winds (fig. 5), thus having the benefit of first choice on the detritus imported into the system.

Note: Histogram on fig. 5 is at $^{1}/10$th scale

The Caenocrypticini:

The species from Nos. 25 to 29 belong to the tenebrionid tribe Caenocrypticini. They are all very small nocturnal tenebrionids that spend the day submerged in the sand. No members of this tribe are found in the inter-dune valleys.

No. 25. Caenocrypticus phaleroides Koch

C. phaleroides was found predominantly under Trianthema sp. (trap No. 5), indicating a relationship between the beetle and plant which could not as yet be defined (fig. 4). No clear correlation between the activity of this species, which occurs throughout the year, and the climate could be established (fig. 5).

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No. 26. Vernayella noctivaga Koch

This is the largest species of the Ceaenocrypticini in the area, and may be found roaming all over the dune crest area, whereas the other species of Vernayella tend to remain near the slip-faces of the dune (fig. 4). The animal was found throughout the year, although trapping data are somewhat scanty (fig. 5).

No. 27. Vernayella delabati Koch

A very delicate and unpigmented beetle, found only on, or very close to, the slip-faces (fig. 4). Like the other Ceaenocrypticini, it appears to feed on fine organic particles in the detritus, since this is often the only manageable organic foodstuff present in the environment of these animals. V. delabati was found throughout 1969 (fig. 5).

No. 28. Vernayella pauliani Koch

V. pauliani is the dominant species in this group, and also an inhabitant of the slip-face system. Being a bit more robust than V. delabati, it roams around near the slip-face, and is most frequently found at the slip-face base, where it feeds on detritus particles (fig. 4). This species showed a significant increase in population activity directly after the rains in February/March, and also during the winter easterly wind period (fig. 5).

No. 29. Vernayella ephialtes Koch

This species is restricted to the slip-face, and is found in greatest numbers near the highest crest of a dune range (fig. 4). It was not recorded during the last half of 1969, and the appearance of this animal seems to be fairly closely correlated with high velocity winds (fig. 5).

No. 30. Derosphaerius humilis Koch

This tenebrionid prefers the denser vegetation of the marginal dune areas, near the riverbeds and towards the inland. Only one specimen was trapped in the dune area after the rains, under a clump of Stipagrostis sabulicola (trap no. 3).

No. 31. Carchares macer Pascoe

This tenebrionid also prefers the marginal dune area next to the river beds, where it is found under shrubs of A. horrida and Salvadora perisca. One specimen was trapped during April under A. horrida (trap no. 6). Both No. 30 and No. 31 are nocturnal.

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No. 32. Psamogaster malani Koch

This member of the tribe Opatrini of the Tenebrionidae emerges towards sunset and was never found to be active late at night. It prefers sheltered depressions in the dunes, where detritus collects, but may be found as single individuals, all over the area. It is a sluggish beetle and seems to spend most of the time under the sand. It occurs throughout the year (fig. 5).

The Eurychorini:

Species Nos. 33-36 belong to the tribe Enrychorini. All the Eurychorini have the body dorso-ventrally depressed. The genera in the interior of the continent are mostly petrophilous, and have evolved flat bodies to fit into stone crevices. The genera in the Namib use their depressed bodies very effectively for sand diving, since the disc-shape thereof offers little resistance to the sand.

No. 33. Stips stali Haag

S. stali is, like Nos. 30 and 31, a plant satellite of the marginal dune areas, but is comparatively successful in the dune base area, where there is some vegetation (fig. 4). It is strictly nocturnal and in its central distribution area, at least. occurs throughout the year.

No. 34. Lepidochora kahani Koch

The genus Lepidochora is further adapted to a sand-diving mode of life than Stips, since in this genus the elaborate sculpture on thorax and elytra which is characteristic of the tribe as a whole, has been replaced by a smooth and scaly integument. L. kahani is the largest of the three sympatric species in the area, and is strictly nocturnal. It is also the rarest of the three species, and inhabits by preference the highest slip-faces of the dune ranges (fig. 4), where it feeds on wind-blown detritus.

No. 35. Lepidochora argentogrisea Koch

This is the most common species of Lepidochora in this area, and the only one that is facultatively diurnal. Diurnal activity in this species occurs only during strong winds, and has the ecological advantage of giving this species first choice of the imported detritus. Usually, however, this species is active at night. It is the smallest and most heavily pigmented of the three Lepidochora species in this system. It leaves the slip-face only when moving towards another slip-

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face, and is never found beyond the dune foot (fig. 4). Like the other Lepidochora species, it occurs throughout the year, although the increase in population activity coincides very markedly with the easterly wind period. Every peak in the velocity of the easterly wind is accompanied by a corresponding peak in population activity (fig. 5). Rain also appears to cause an increase in population activity. Because of its abundance and interesting morphology and ecology, this species has been studied most intensively of all the tenebrionids in the area (LOUW, in prep., KÜHNELT, 1969).

No. 36. Lepidochora porti - Koch

This species is rarely found on the slip-face, and is more common on the dune foot and dune base areas than Nos. 34 and 35 (fig. 4). It resembles L. kahani in appearance, but is a little smaller and more convex. Like L. kahani it is strictly nocturnal. It appears to be more common during the summer months, but is, like No. 13, able to withstand temperatures as low as 3°C on the surface.

The Orthoptera: Species Nos. 37 and 38 are ground crickets of the family Tettigoniidae.

No. 37. Acanthoplus sp.

Acanthoplus is a verly large species, which lives only under A. horrida shrubs (fig. 4), where it feeds on the fruit of this plant and possibly also on insects which use these plants as shelter. Insect remains are often found in the burrows inhabited by this cricket, which lives semi-socially in collective burrows. This cricket covers great distances at night between shrubs of A. horrida, and is active throughout the year.

No. 38. Comicus sp.

This cricket is smaller than the Acanthoplus sp. and is marked by lack of pigments in the integument, extraordinary long antennae and intricate tarsi with comb-like projections on the tarsal segments. These projections enlarge the area of the tarsi to facilitate sand digging and jumping on the sand. This species occurs fairly evenly over the whole area (fig. 4) and throughout the year, with a slight increase in numbers after the rain (fig. 5). They tunnel into semi-stable dune sand for the day, and are often found at night in shallow depressions in the stable dune slopes, with the long antennae stretched out forward on the surface of the sand. The purpose of this behaviour is not quite clear. The animal is little known, but appears to be widely distributed in the arid regions of the subcontinent, possibly as several species or subspecies. (Brown pers. comm.)

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No. 39. Family Carabidae

A small brown carabid, which belongs to a myrmecophilous group of Carabidae, possibly associated with the dune ant, Camponotus sp. which occurs in the dune area. (KOCH, pers. comm.) This beetle occurs mainly near vegetation hummocks on the dunes (fig. 4), and is active throughout the year. A very significant increase in population activity was recorded after the rains in February/March 1969 (fig. 5).

The Scarabaeidae:

Species Nos. 40 and 41 are scarabs of the apterous genus Neopachysoma. These scarabs have changed their way of life considerably in order to adapt do desert conditions, because the loss of flight necessitates strong and fast walking.

No. 40. Neopachysoma denticol Peringuey

N. denticol is the smaller of the two Neopachysoma species, which are very similar in behaviour. It has brown elytra, whereas N. rodriguesi is completely black, and it is not as specific with regard to its food requirements. It will take grass fragments, leaves and even dead insects as well as droppings of hare and Oryx. Since these objects cannot be formed into a ball the beetle holds the food with the hind legs, while running forward with the remaining four legs. The food is either dragged forward or, in the case of grass and leaves, pressed against the abdomen and carried. N. denticol was often seen carrying leaves of Monsonia ignorata. Both species make burrows into semi-stable dune sand by digging and pushing the sand away with the front legs, head and thorax. When selecting a site for a burrow, the beetles 'test' the stability of the sand with their front legs, by digging a little and then patting the overhanging edge of the burrow. If the sand caves in, they will select another site. N. denticol was found regularly in the area after the rains, and mostly in trap No. 4 (fig. 4), since they run mainly along depressions in the dune area in search of food.

No. 41. Neopachysoma rodriguesi Ferriera

This species is found in greatest numbers near grazing areas of Oryx, the droppings of which they prefer. They transport their food in the same way as N. denticol, but were never found to take vegetable matter. Hare droppings are also taken by this species, in which case they cradle several pellets in the circle formed by the two hind legs, and drag them forward. Only three specimens were trapped during 1969, since the Oryx rarely come as far North as the experimental area, and all the specimens

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were trapped in trap No. 4. Both species of Neopachysoma occur throughout the year, according to observations made in their centre of distribution, south of the experimental area.

No. 43. Family Mutillidae (large species)

Two species of apterous mutilids were recorded during 1969. These species could unfortunately not be classified further than the family level, and can therefore only be distinguished by referring to the "large" and "small" species. The larger species was captured only under Trianthema and A. horrida plants, and appears to occur throughout the year (figs. 4 and 5). Since the family as such is parasitic these wasps may be presumed to be parasites as well. No host records are available. Males of this species are alate.

No. 44. Family Mutillidae (small species.)

This species was encountered both on the stable dune slopes and the inter-dune valleys (fig. 4). Most specimens were trapped within the first few months after the rains, but they were also recorded in October and November (fig. 5). Males of this species are alate.

The Thysanura:

Several species of Thysanura are found in the experimental area (Nos. 45 to 48). They are all detritus feeders, and free-living. It is very likely that other species occur as myrmecophiles and termitophiles in the nests of ants and termites, but these were not recorded in this survey. (COATON, pers. comm.)

No. 45. Ctenolepisma pauliani Wygodzinsky

C. pauliani is fairly evenly distributed over the whole area, with a slightly denser concentration on the dune base and dune foot. It is the largest of the local Thysanura, and banded in black and ochre scales. Cerci and antennae are exceptionally long, and these insects have the same habit as Comicus (No. 38), lying in shallow hollows on the dune slopes, with antennae and cerci stretched out upon the sand. They can dive into the sand, but are also found to dig tunnels. C. pauliani is nocturnal.

No. 46. Ctenolepisma terebrans Silvestri

This is the most common species of Thysanura in the system, and is

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found all over the area. It prefers the accumulations of detritus under A. horrida (trap 6) and S. sabulicola (trap 3 & 4), (fig. 4.) Like most detritus feeders, this species is more active during spells of easterly winds. Rain also had a positive effect on population activity (fig. 5). This species is smaller than No. 45, and covered with grey to black scales. C. tenebrans is also nocturnal.

No. 47. Morisma sp.

A very broad and flat species of Thysanura which occurs only on the dunes in loose sand (fig. 4). Specimens are at present in the care of Dr. Wygodzinsky (American Museum of Natural History, New York), who informed the writer that it is a new species. This species is sand diving and was never found to tunnel. Its activity is strongly correlated with high velocity winds (fig. 5). Like L. argentogrisea (No. 35), this species is nocturnal, but, with strong winds, will emerge in daytime.

No. 48. Hyperlepisma australis Wygodzinsky

This very smooth and silvery scaled species occurs mainly on the interdune valleys (fig. 4). It is nocturnal, and was trapped throughout the year (fig. 5). This was found to be the rarest species of the Thysanura in the area.

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VI. DISTRIBUTION OF THE APTEROUS INSECTS IN PLACE

The degree of habitat specialization of the species in the system is very high. Although some of the curves in fig. 4 are unreliable because of too small samples, it will be noticed that distribution patterns are often repeated (vide Nos. 2, 3 and 5, Nos. 19, 27, 28 and 35, Nos. 7, 38 and 45, Nos. 9 and 11, etc.). This indicates that the apterous insects can be divided into habitat groups, which can be circumscribed as follows:-

The dune crest fauna:

These insects depend on the loose sand of the slip-faces for shelter against weather and enemies. They are mostly highly adapted sand-divers and detritus feeders. This group is not readily distinguished, by referring to the distribution curves, firstly because many plant-satellites specific on S. sabulicola are found in the dune crest area, where this plant occurs nearby (vide No. 11), and secondly because trap No. 7 was on a slip-face only during westerly winds, (the slope changing to a hard bare slope during easterly winds), and therefore its catches give an under-estimate in the case of slip-face animals, and an over-estimate in the case of other animals. From the many observations made over three years, the true slip-face fauna could, however, be identified with certainty.

Species in this group are represented by the following numbers:- 16, 17, 19, 26, 27, 28, 29, 34, 35, 47. Although some of these species may roam far from the slip-face of the dune (vide Nos. 16 and 17), they all depend on the slip-face for shelter, and return to this habitat for periods of inactivity.

The satellites of perennial vegetation:

Species associated with S. sabulicola are Nos. 9, 11, 12 and 13, while the species associated with A. horrida are Nos. 31 and 37.

The satellites of Trianthema sp. are Nos. 8, 10 and 25. Species which occur with permanent vegetation, but which are non-specific as to the plant species, are Nos. 18, 24, 39, 43 and 46.

While the specific groups can be expected to be in some or other ecological inter-action with the specific plant, the last mentioned group is dependent on the permanent vegetation for shade and/or for the accumulation of detritus found below these plant hummocks.

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Species of the dune foot and base:

This area, which is characterised by coarse sand with a rippled surface, sustains a group of species which seem to live on detritus deposits in these ripples. Species concerned are Nos. 14(a), 20 and 33.

The fauna of the dune slopes and foot:

These are animals that occur all over the dunes, but avoid the inter-dune valleys, being less specific in their habitat requirements than the groups mentioned above. Species in this group are Nos. 1, 4, 24, 32, 36, 40 and 41.

The inter-dune valley fauna:

This is a clearly separated group of animals that prefers the more stable and exposed habitat of the inter-dune valleys. Species that never enter the dune habitat are Nos. 14, 22 and 48, while Nos 2, 3, 5 and 44 are sometimes found on the dunes, while their centre of distribution is decidedly the inter-dune valley habitat.

The broadly distributed species:

A few species occur all over the area and are largely non-specific to the type of substratum. Most of these species have a wide distribution beyond the experimental area, and even beyond the Namib Desert. Species concerned are Nos. 7, 15, 23, 38 and 45. Numbers 15 and 23 are marginal populations from adjoining systems, which do not fill a well-defined niche in the area and roam about at random.

The habitat preferences of some of the rare species in the area are not quite clear. This refers to Nos. 6, 21 and 30, not listed above, and Nos. 14(a) and 31, listed above under "Species of the dune foot" and "plant satellite" groups respectively.

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VII. DISTRIBUTION OF THE APTEROUS INSECTS IN TIME

The main activity during the yearly cycle in this system centres around two periods, namely the after-rain period of about four months, if rain does occur in sufficient amounts to give rise to the rain flora during that year, and secondly the easterly wind period during winter. Since both these climatic factors are directly linked with food supply, it may be presumed that food supply is the principal limiting factor of the fauna of the system, and that climate regulates populations rather indirectly through the food supply. Access to the food for the various species, which can be active only under special climatic conditions, also plays an important role in this connection. As in the case of habitat-distribution, the species in the system fall into characteristic seasonal groups:-

The rain fauna:

As discussed in Chapter IV, two groups may be distinguished, viz. those that occur only after rain and feed on the green "rain-flora", comprising species Nos. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11 and 44 and secondly those that are normally all-the-year-round species, but which benefit significantly from rain, comprising species Nos. 14(a), 15, 18, 28, 33, 35, 38, 39 and 46. Of the latter group species Nos. 28 and 35 also benefit from easterly winds, and will be listed under the easterly wind group.

The winter fauna or easterly wind group:

This group is dominant in the system in terms of biomass and activity. Species which occur only during the easterly wind period are Nos. 13, 14 and 24, while Nos. 19, 28, 34, 35 and 37 show marked increases in population activity during the easterly winds.

Summer species:

Three species in the system, Nos. 12, 17 and 22 are most active during the summer months. These are forms which utilize the available food during the summer and which seem to thrive in the absence of the winter fauna.

Species occuring throughout the year:

A number of species maintain a fair measure of activity throughout the year, vide Nos. 16, 20, 25, 26, 27, 32, 36, 47 and 48. The samples trapped of many of these species, are, however, not large enough to be conclusive.

Species not listed above, have not been trapped or observed regularly

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enough to come to any conclusions as to their yearly activity cycles (Nos. 20, 26, 27, 32 and 48). Others prefer specific types of weather for activity, as discussed in Chapter V above (No. 47).

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VIII. SUMMARY AND CONCLUSION

When it is considered that the cross-section of the area covered by this trapping experiment is only 700 meter, and how homogeneous the area is in comparison with other ecosystems, the most striking feature of this ecosystem is the variety of species it contains. Moreover, a large portion of the species are closely related forms. (Vid. the Lepidochora spp., the Onymacris spp., the Zophosini, the Thysanura, etc.)

An ecosystem can only support as many species as there are niches available, but the number of niches available are in most natural systems nearly unlimited. If a system consists of a great number of very specialized forms, it is not necessarily an indication of a complex environment, but rather of the relative evolutionary 'age' of the system. This 'age' may be measured in terms of time, if the rate of evolution is taken to be the same in the populations of different systems. In this case, it would have to be presumed that this Namib Desert ecosystem is older in time than, for instance the Kalahari or Sahara ecosystems (KOCH, pers. comm.)

The alternative is that evolution in the Namib Desert did not proceed at the same rate as in comparable situations elsewhere. This possibility cannot be excluded, since selective forces in the hostile environment of a desert on an unspecialized species are severe, and provided that a series of events occurred which separated parts of populations from each other temporarily, could well lead to the complex configuration of closely related species as they are encountered today.

The geology of the area could provide the answer to the geological age of the desert, as compared to other deserts of the world. Complete records of distribution of species in the desert could provide clues to the eventual historical border lines which made speciation possible. Until these data have been collected and studied, both the above-mentioned suggested solutions to the problem of the exceptionally diversified fauna of the area must remain hypothetical.

This paper, therefore, attempts only to map the ecological situation in one selected spot in the Namib Desert as accurately as was technically possible under the circumstances. The fact that the area is extraordinarily rich in species was already demonstrated by Koch (1961). It has now been shown that all these species, many of which are sub-identical, occupy different niches within the area by dividing the biome in time and/or space.

The correlations between activity of populations and the weather reveal

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two important aspects of the ecology of the Namib Desert. Firstly,it is apparent that the wind is the critical weather factor in the ecology of the area because it controls both the influx of the most important food supply, the wind-blown detritus, and the humidity of the environment, while it is also responsible for most of the significant changes in temperature. Secondly, the weather has a markedly different effect on every individual species, to such an extent that no weather phenomenon can be described as beneficial or hostile to life in the area as such.

Much more knowledge of the behaviour and physiology of the various species is needed to understand fully the mechanisms by which these animals turn such an apparent hostile environment with its droughts, vegetationless sand substrata, heat and desert storms to their advantage. The behaviour patterns pointed out above are only casual observations, but may serve as an introduction to future behavourial studies on dune arthropods.

As by-products of this study, a technique for trapping terrestrial arthropods by unbaited and timed pit traps was evolved. This technique may be useful in similar studies elsewhere, and is already being used by workers in the U.S.A. Furthermore a number of new taxa were described as a result of this survey.

With the information contained in this paper for comparison, it may be possible to establish the critical difference between this ecosystem and other desert ecosystems, which may lead to a better understanding of the unique biological situation encountered in the Namib Desert.

It was, furthermore, attempted to list the species, the micro-habitats and the times of occurrence of species as related to the climate, as accurately as possible for the benefit of workers who want to investigate the many unexplored behavourial, physiological and ecological mechanisms and principles that make life possible for the inhabitants of the Namib Desert dunes.

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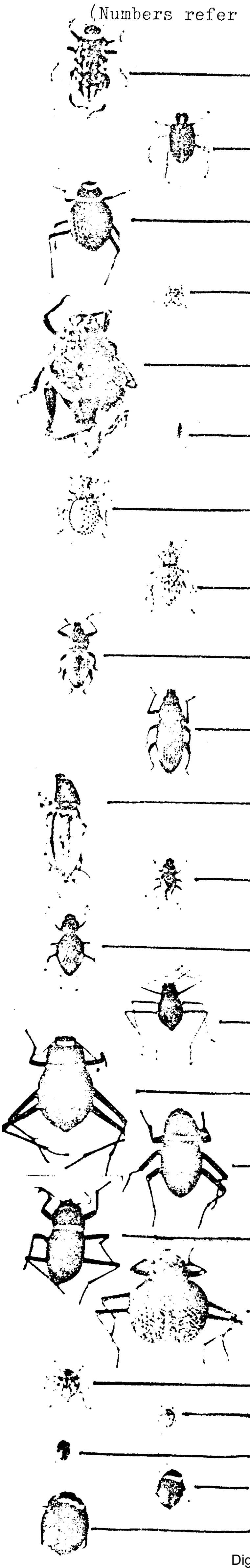
NUMBERED LIST OF SPECIES

(Numbers refer to numbers on figs. 4 and 5, - insects are depicted life size)



1 *Pachynotelus albonotatus* Haag.

2 *Pachynotelus renei* Koch.

3 *Eustolopus octoseriatus* Gebien.

4 fam. Cercopidae

5 *Crypsicercus cubicus* Saussure.

6 fam. Curculionidae
subfam. Otiorrhynchinae.

7 *Brachycerus rotundatus* Peringuey.

8 *Hyomora falcipes* Marschall.

9 Yellow weevil *Leptostethus* sp.

10 Black weevil near *Leptostethus*

11 Blue weevil near *Leptostethus*

12 *Archinamibia peezi* Koch.

13 *Namibomodes serrimargo* Gebien.

14a. *Onymacris albotesselata* Koch.

14 *Stenocara phalangium* Gebien

15 *Onymacris rugatipennis* Haag.

16 *Onymacris unguicularis* Haag.

17 *Onymacris laeviceps* Gebien.

18 *Onymacris plana* Peringuey

19 *Cardiosis fairmairei* Peringuey.

20 *Cardiosis hamiltonulus* Koch.

21 *Dactilocalcar caecus* Gebien.

22 *Gyrosis moralesi* Koch.

23 *Gyrosis orbicularis* Deyrolle

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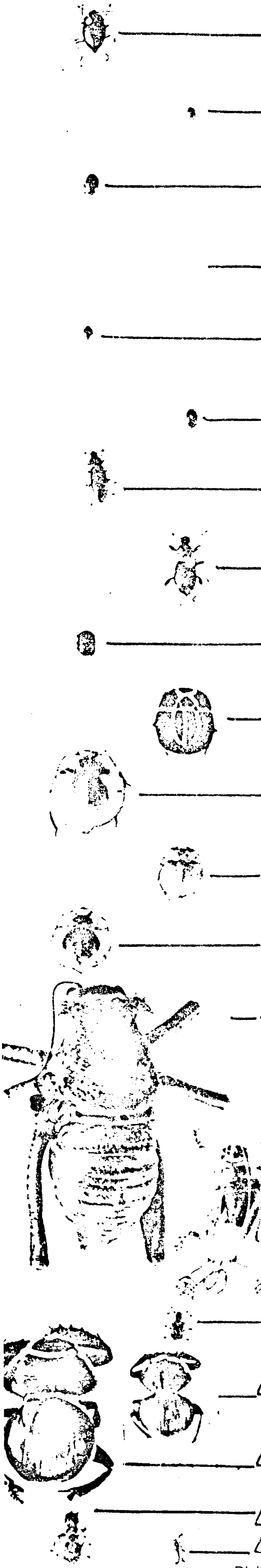

24 Cerosis hereroensis Gebien.

25 Caenocripticus phaleroides Koch.

26 Vernayella noctivaga Koch.

27 Vernayella delabati Koch.

28 Vernayella pauliani Koch.

29 Vernayella ephialtes Koch.

30 Derosphaerius humilis Koch.

31 Carchares macer Pascoe.

32 Psamogaster malani Koch.

33 Stips stali Haag.

34 Lepidochora kahani Koch.

35 Lepidochora argentogrisea Koch.

36 Lepidochora porti Koch.

37 Acanthoplus sp.

38 Comicus sp.

39 fam. Carabidae

40 Neopachysoma denticol Peringuey

41 Neopachysoma rodriguesi Ferriera

43 Large species of Mutilidae

44 Small species of Mutilidae

45 Ctenolepisma pauliani Wygodzinsky.

46 Ctenolepisma terebrans Silvestri.

47 Morisma sp.

48 Hyperlepisma australis Wygodzinsky.

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F I G U R E   4

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TEXT TO FIG. 4 : DISTRIBUTION OF APTEROUS INSECTS IN PLACE.

(Please fold out plate at end of diagrams)

Curves 1 to 48 represent the percentages of species Nos. 1 to 48 trapped at the nine trapping stations. The vertical lines represent trapping sites, and correspond with the fold-out plate. One cm. vertically represents 40% of the total catch of the species, and the vertical height of the curve on the nine lines adds up to 100% for every species.

Some species which were trapped in one trap only, are indicated by "100%" written over the line of that trap.

FOLD-OUT:

1. Photos:

   The immediate vicinity of every trap was photographed, and the numbers 1 to 9 were used to distinguish between traps.

2. Diagramatic cross section:

   The silhouette represents a diagramatic cross section of the dune range and interdune valley, with the lines from the traps crossing this diagram at the relative position of the traps on the dune slope. The cross section is not on scale, vertical elevation being exaggerated.

   Symbols on silhouette of dune represent the vegetation, large letter "V" stands for *A. Sabulicola*, small letter "v" for "rain"-grasses, large letter "O" for *A. horrida*, small letter "o" for *M. ignorata* and small letter "t" for *I. hereroensis*.

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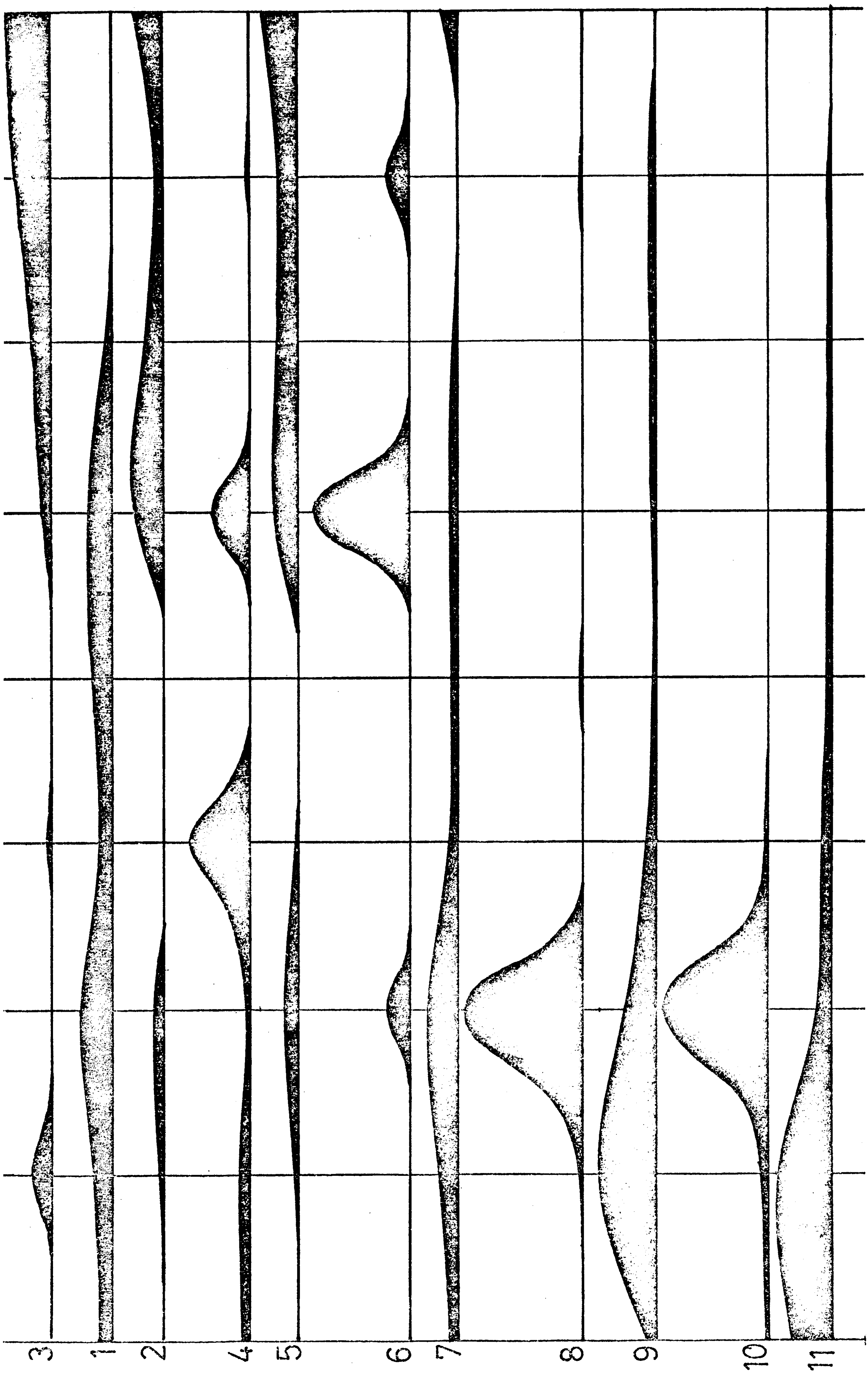

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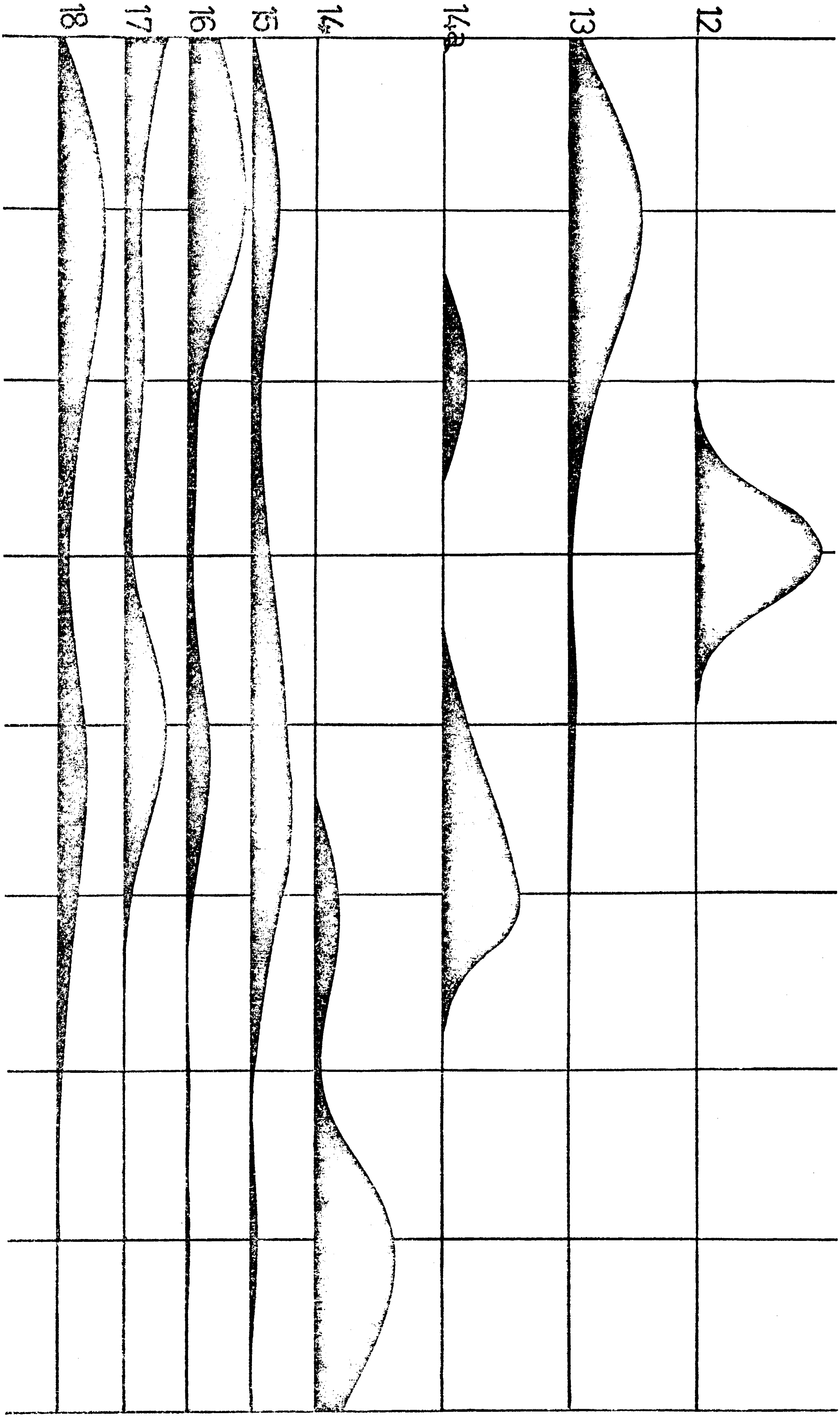

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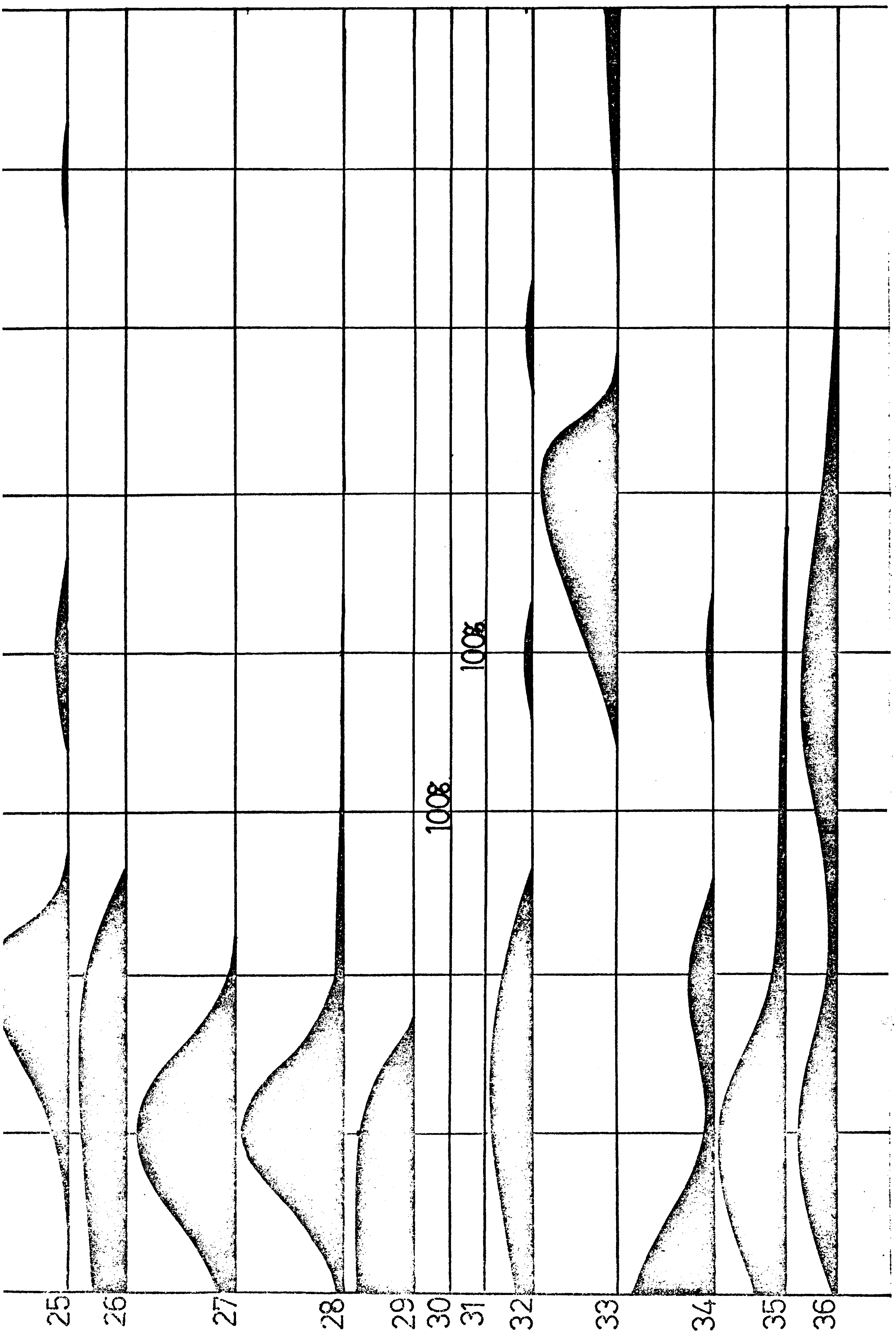

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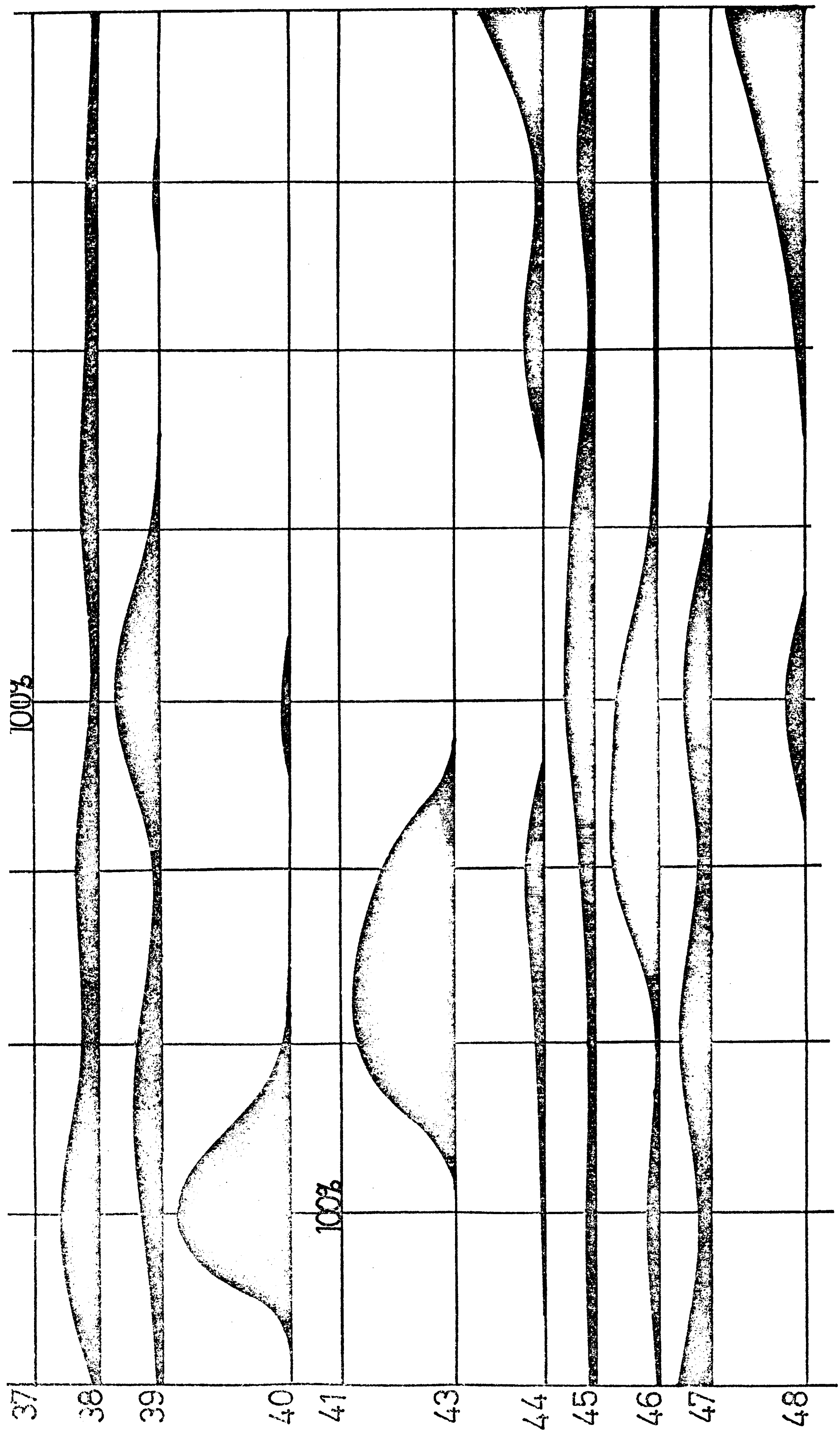

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F I G U R E 5

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TEXT TO FIG. 5 : DISTRIBUTION OF APTEROUS INSECTS IN TIME.

(Please fold out plate at end of diagrams).

Histograms Nos. 1 to 48 represent the total numbers of individuals of species Nos. 1 to 48 trapped every day of the year 1969. Days correspond to days on fold-out plate.

One mm vertically represents 1 individual trapped, except in the case of Nos. 14, 18 and 24, which are at $^{1}/10$th scale (i.e. one mm represents 10 individuals trapped.)

Crosses on individual days represent sightings of that species on the particular day, but no trapping of that species.

When traps were not emptied every day, the average catch over the period of two or more days is recorded on the histograms (26 Feb. - 1 Mar., 4 Mar. - 8 Mar., 23 Mar. - 2 Apr., 24 Jul. - 26 Jul, 12 Sept. - 14 Sept., 12 Oct. - 14 Oct., 30 Oct. - 31 Oct.)

FOLD-OUT:

1. Temperatures:

   The daily histograms indicate minimum temperatures on the top of the lower black column, while maximum temperatures are to be read at the bottom of the upper black columns. The unshaded portion of every day therefore indicates the temperature range of that particular day. Temperatures were measured in a Stevenson screen.

2. Wind:

   The winds above the 0-line are the easterly group, while westerly winds are indicated below the 0-line. The shades (from light to dark) represent SE, E, NE and N above the line, and in the same order S, SW, W and NW below the line. Darker shades therefore indicate a northerly tendency in the wind regime, while the lighter shades represent a southerly tendency. Histograms indicate kilometres windway per day.

   For the periods marked with a question mark, no data are available.

3. Precipitation:

   Heavy black indicates rain, dark grey fog precipitation and circles, dew. The latter is indicated in increasing quantities, viz. one to three circles, which do, however, not indicate exact amounts, since dew could not be measured.

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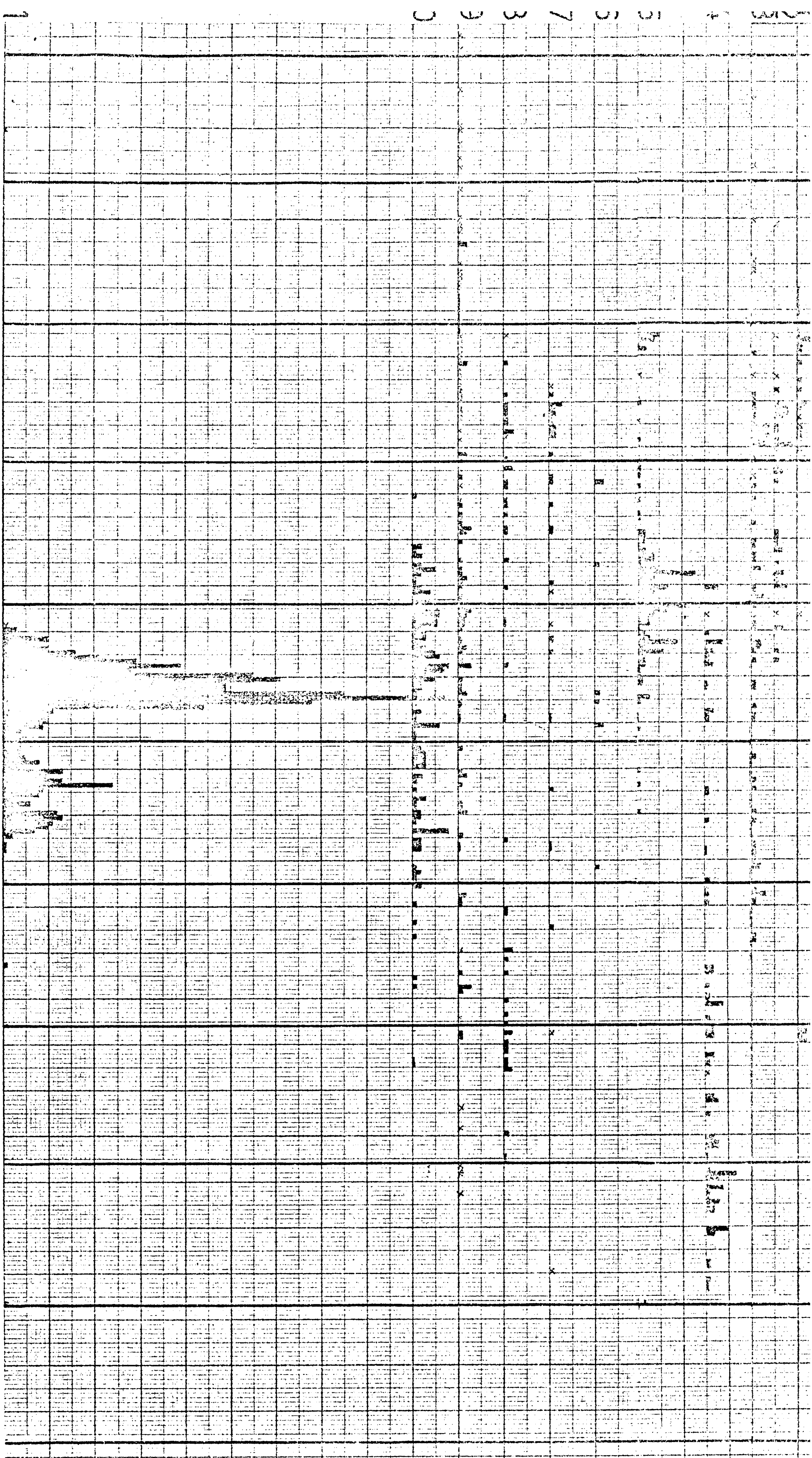

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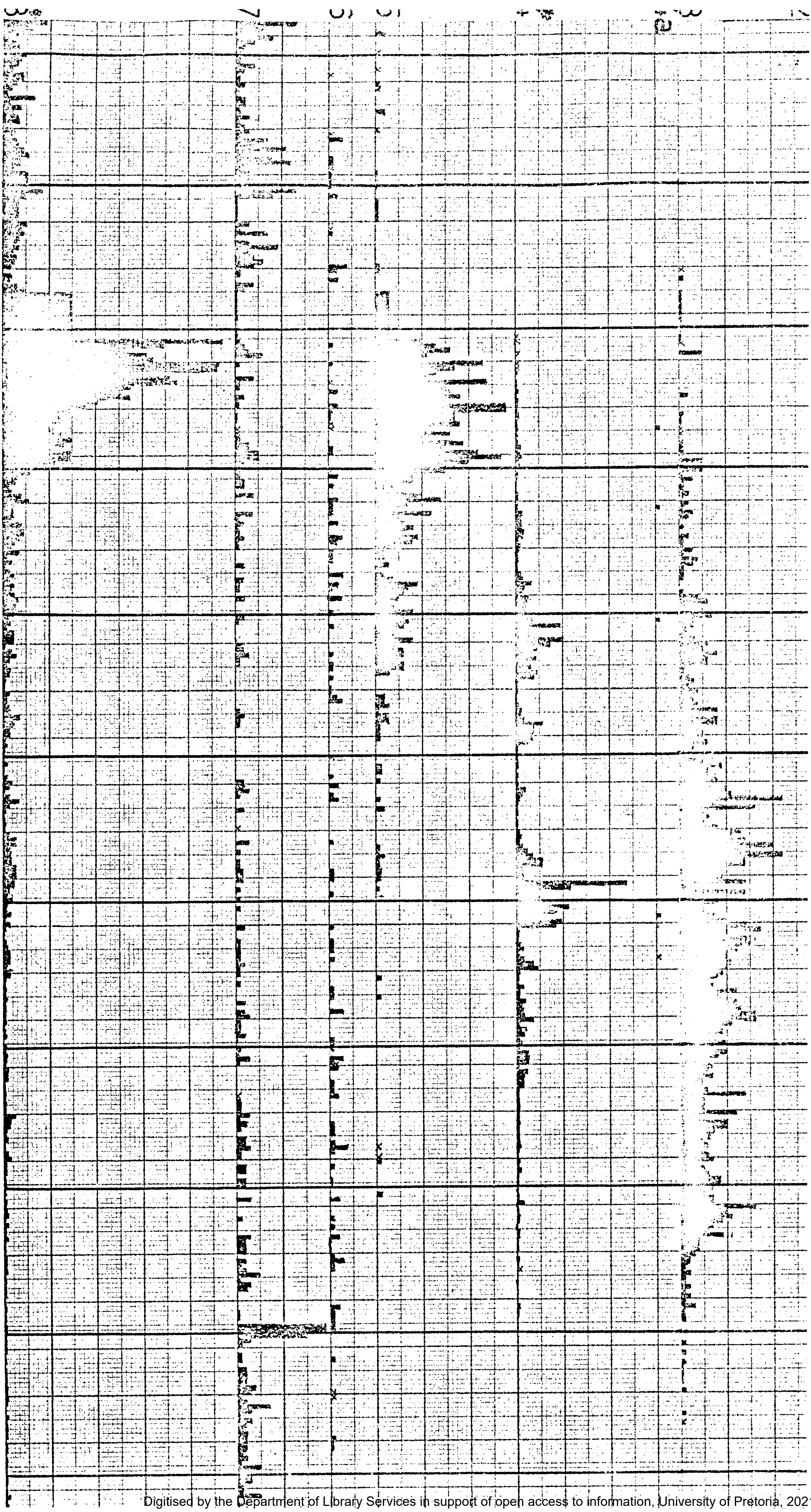

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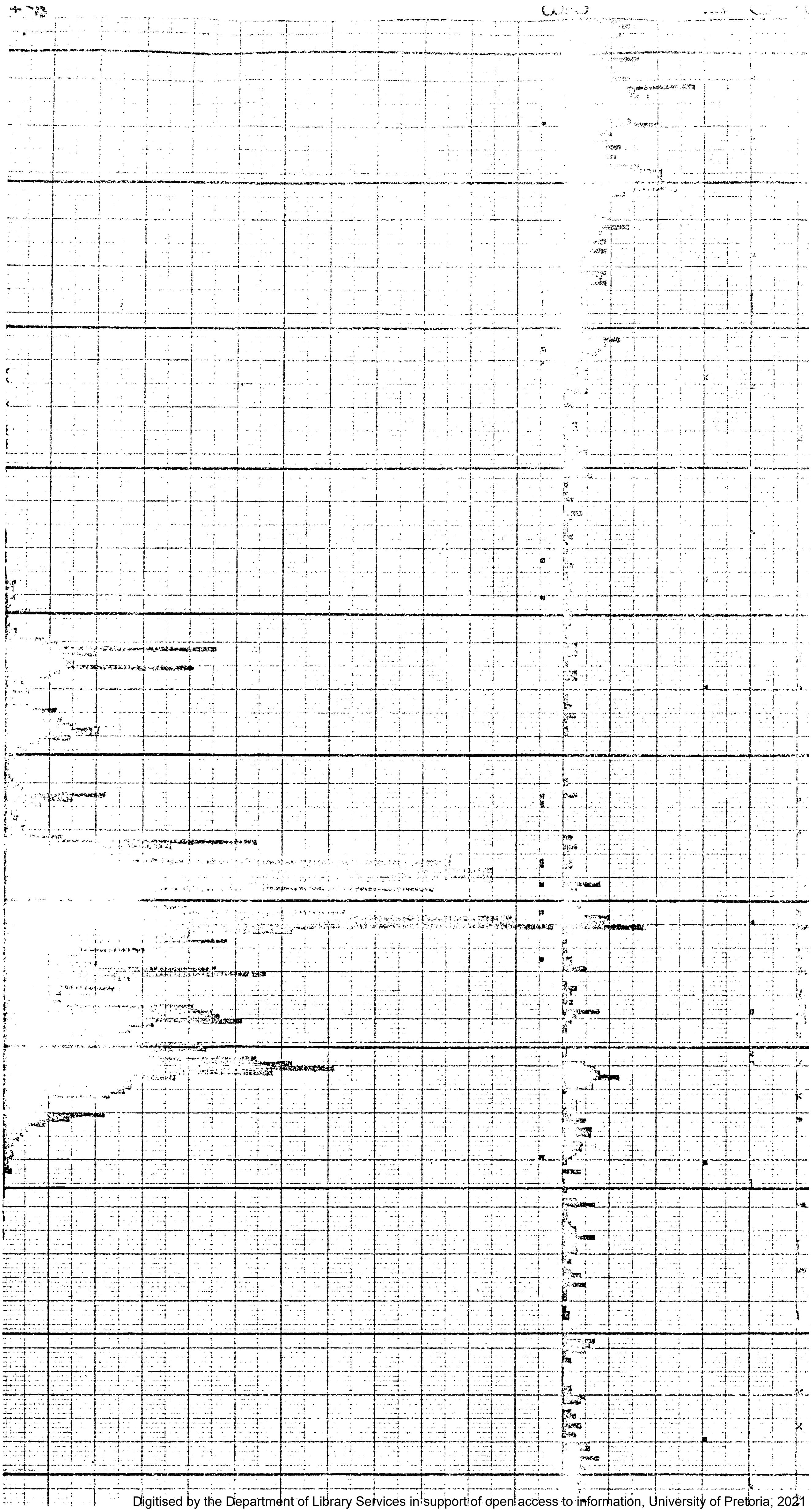

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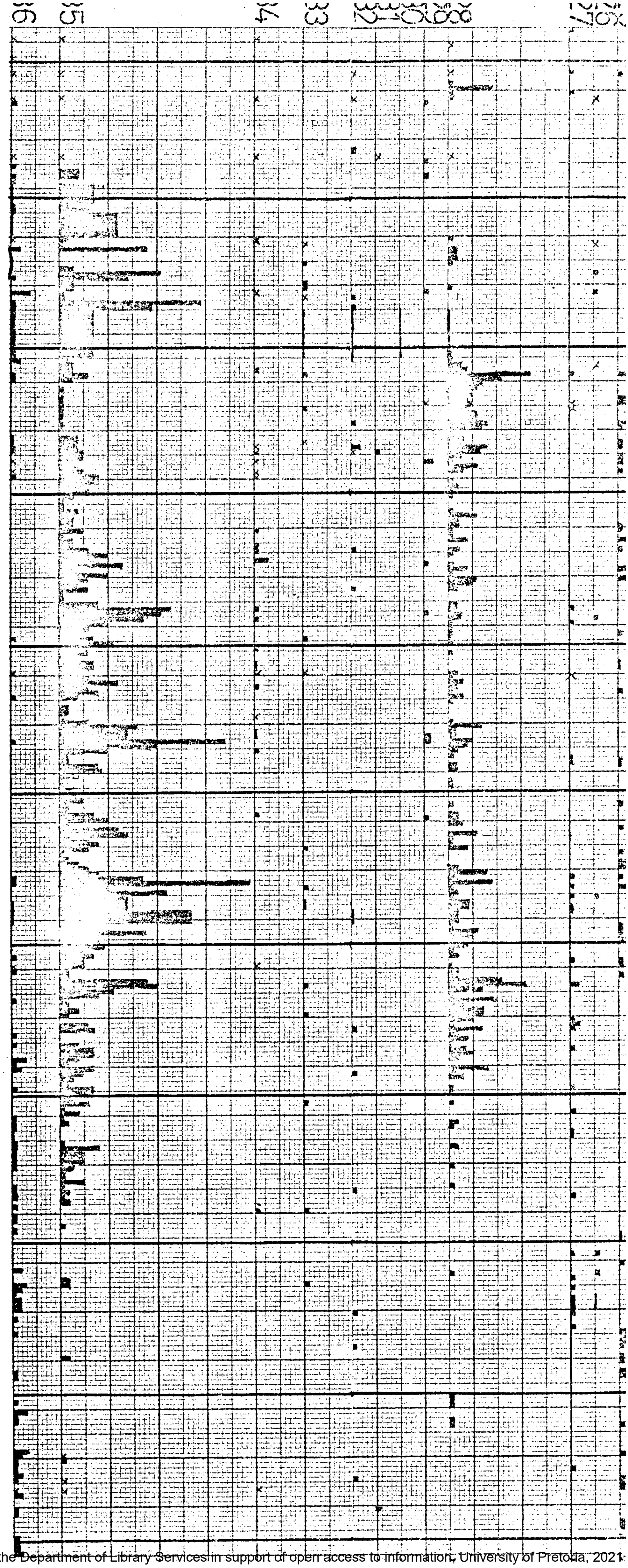

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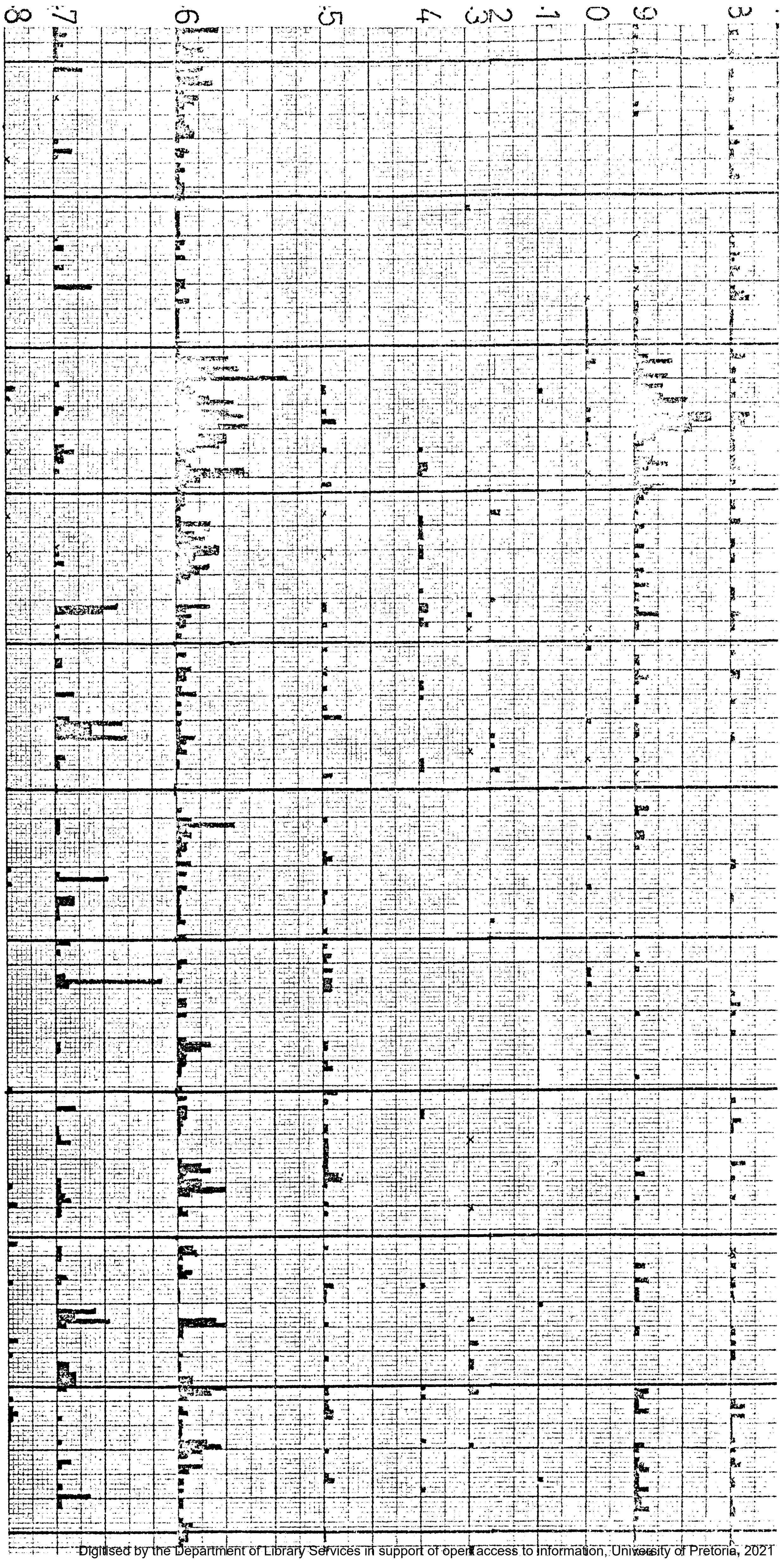

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A C K N O W L E D G E M E N T S

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I also wish to thank the other people, too numerous to mention, who helped me with the identification of material, and who contributed to this paper through stimulating discussions. I want to thank Miss Alice Mertens for the superb photographs, which I unfortunately had to mutilate for the purposes of this paper!

Lastly I want to thank my wife for the unselfish way in which she assisted me during our three years of study in the desert. A large share of the routine work on this project was done by her, for which she never expected any recognition or remuneration.

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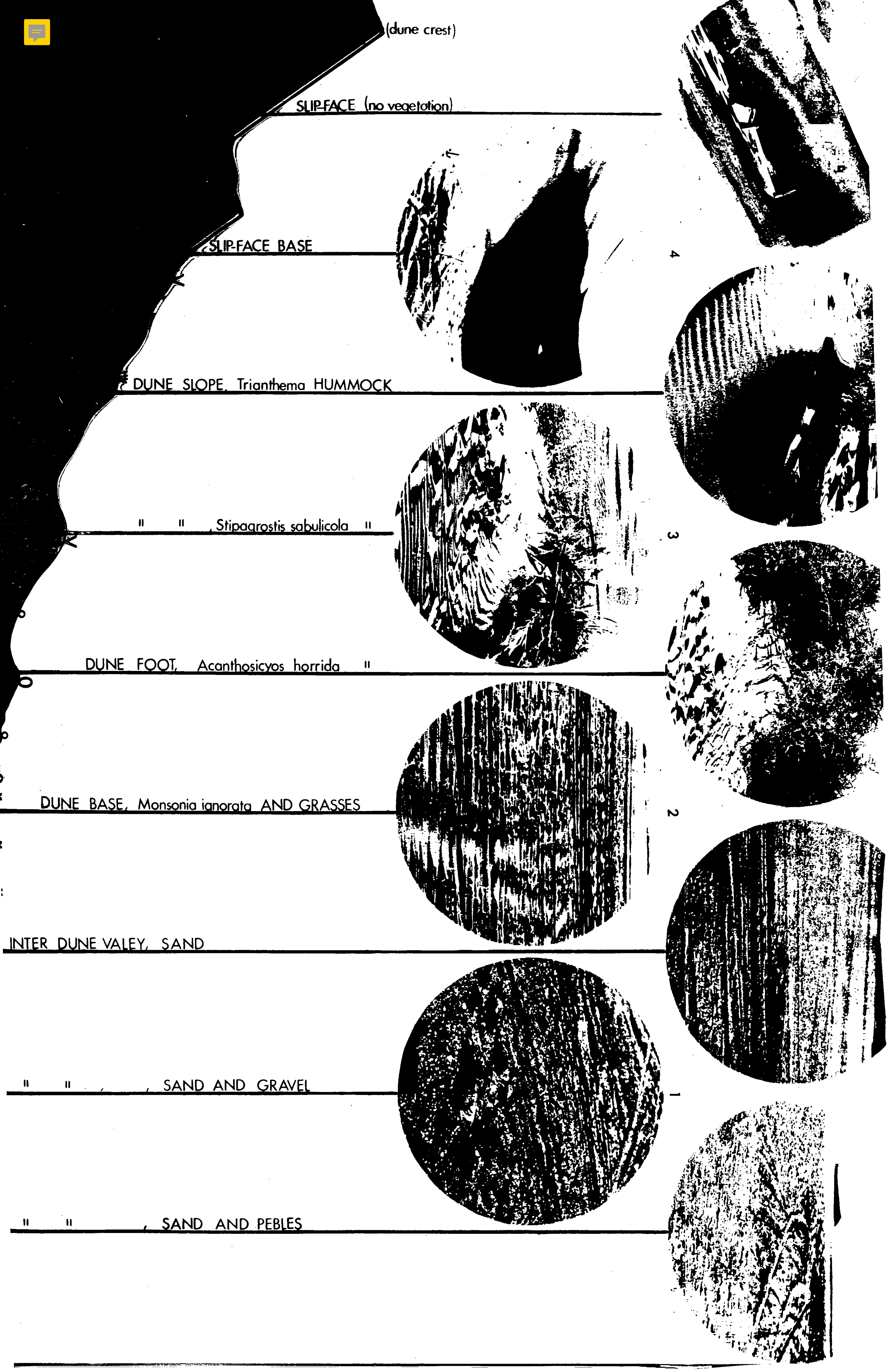

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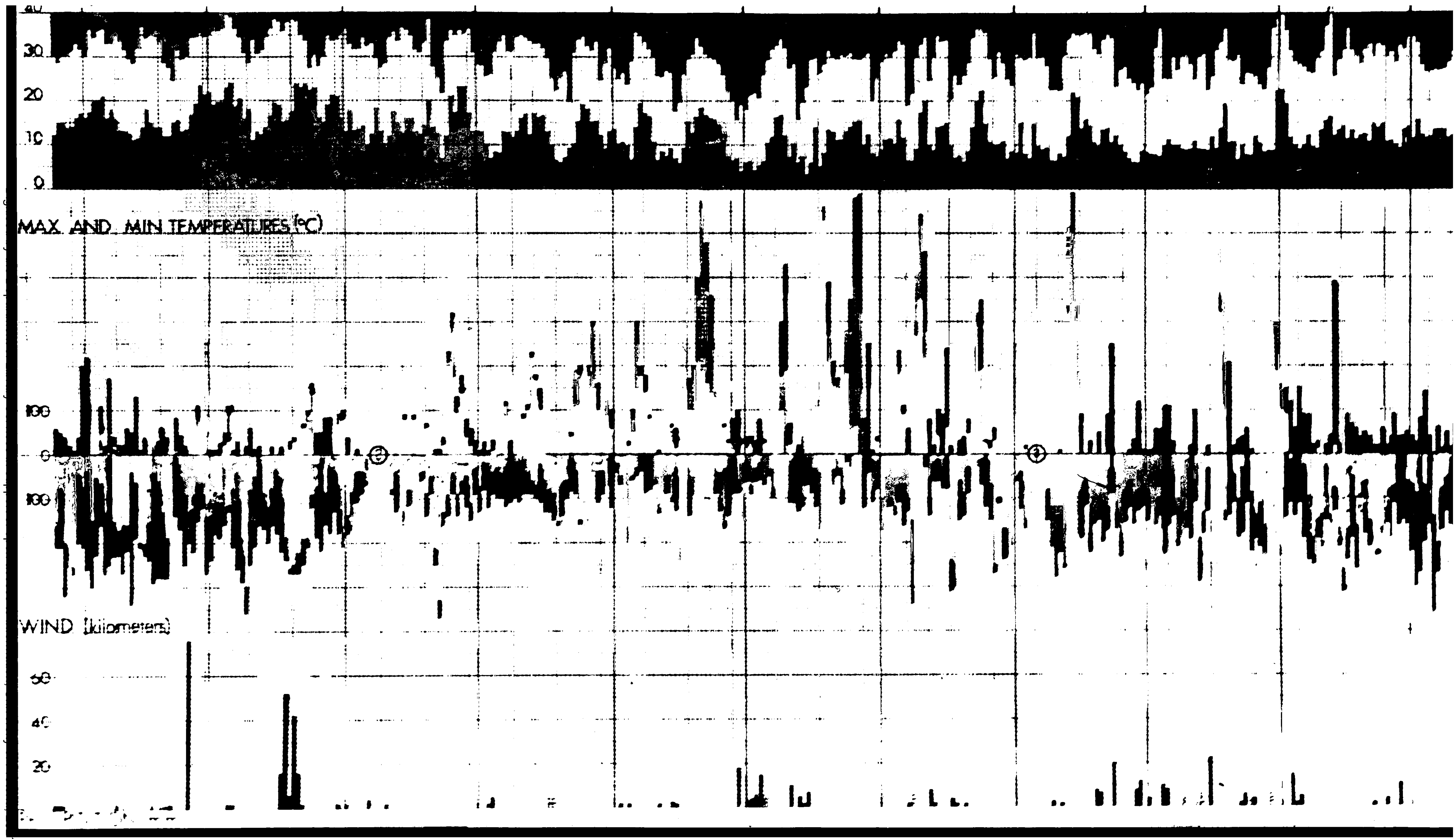
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30
20
10
0
MAX. AND MIN TEMPERATURES (°C)
100
0
100
WIND (kilometers)
60
40
20