EVOLUTION AND ECOLOGY

OF

GUINEAFOWL

T.M. CROWE

Submitted for the degree of Ph.D.
in the Faculty of Science (Dept. of Zoology)
University of Cape Town

May 1978

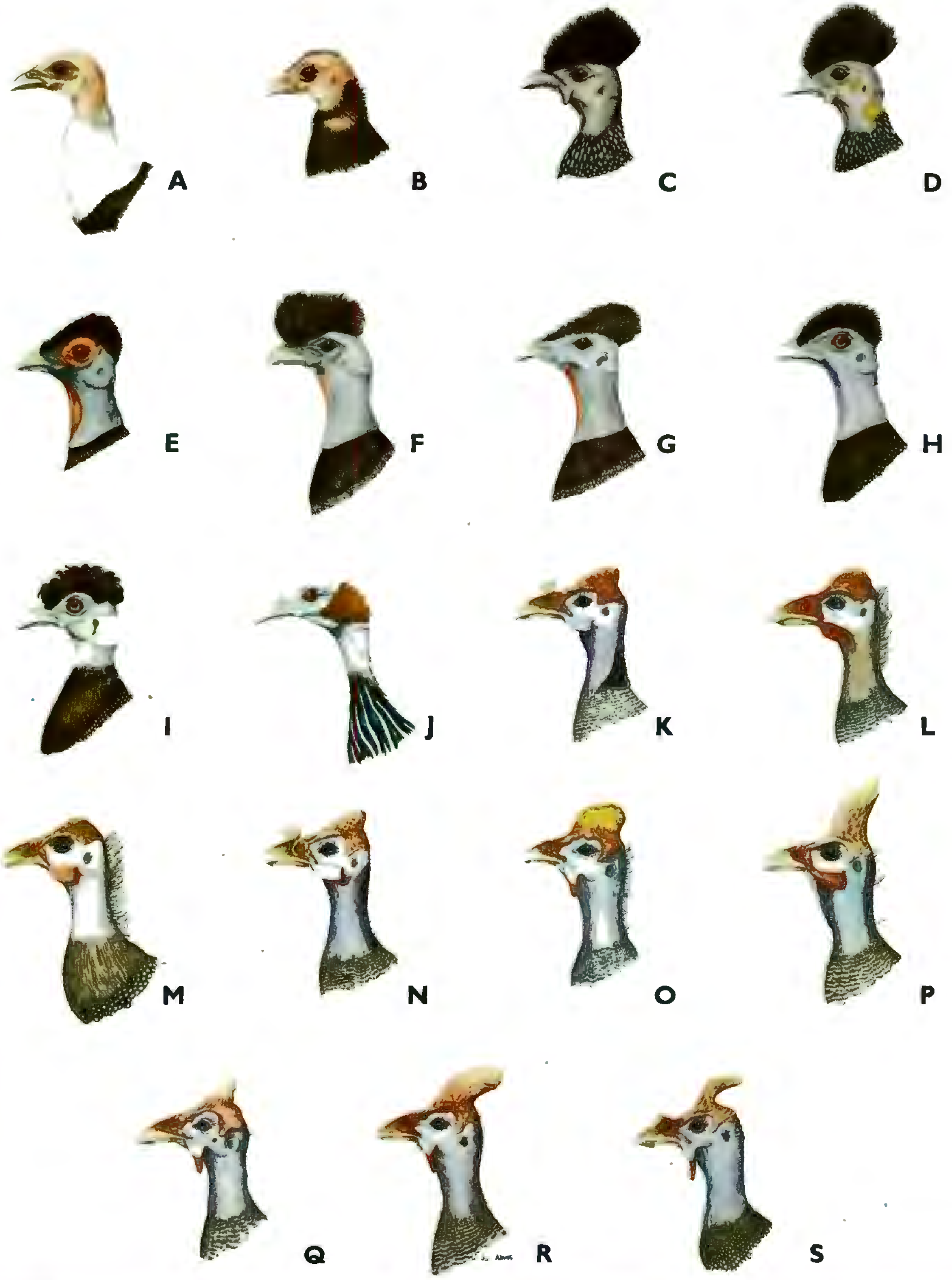

Plate 1. Guineafowl taxa recognised in Paper 1.
A = Agelastes meleagrides, B = A. niger, C = Guttera plumifera plumifera, D = G. p. schubotzi, E = G. pucherani pucherani, F = G. p. verreauxi, G = G. p. sclateri, H = G. p. barbata, I = G. p. edouardi, J = Acryllium vulturinum, K = Numida meleagris meleagris, L = N. m. sabyi, M = N. m. galeata, N = N. m. somaliensis, O = N. m. marungensis, P = N. m. reichenowi, Q = N. m. mitrata, R = N. m. coronata, S = N. m. damarensis.

CONTENTS

INTRODUCTION

By almost any definition, guineafowl (Numidinae) are characteristically African birds. This small subfamily (4–5 genera, 5–8 species) is endemic to, and possibly evolved, in Africa (Ghigi 1936). Nearly every major African biome and biotope has an associated guineafowl taxon (Crowe & Snow 1978). Guineafowl are sedentary birds (Chapin 1932; Elgood et al. 1973), and therefore should be more susceptible to local selection pressures than would be more mobile taxa (Ehrlich & Raven 1969). At least some inter- and intra-specific phenetic variation appears to be correlated with variation in the environment (Crowe & Snow 1978). In this dissertation, I investigate aspects of the evolution and ecology of guineafowl, and use the results of my analyses to formulate or test hypotheses concerning broad patterns of evolution and ecology of birds in Africa. Specifically, my seven aims are to:

1. re-evaluate the rather confused taxonomy of the subfamily,
2. produce a parsimonious phylogeny based on the analysis of shared derived character-states,
3. develop models of speciation which are consistent with the above phylogeny and the likely geological and climatological history of Africa,
4. suggest a scheme of avifaunal zones based on the analysis of the distributions of, and phylogenetic relationships between recognized guineafowl taxa,

5. discover the possible adaptive significance of phenetic variation in polytypic guineafowl species,
6. demonstrate possible anatomical adaptations in the vascular system of the head and neck of *Numida meleagris*,
7. determine the likely mechanism of population limitation in *N. meleagris*.

This dissertation consists of seven published or submitted papers which relate to one or more of the aims listed above. I have followed this format rather than the more traditional one, so that my results may be communicated as quickly as possible. I apologize for the necessary inconsistent layout of the various papers, and the repetition of information. The following summary and synthesis will, I hope, facilitate the digestion of a rather diverse array of information, and provide a thread which links it into a more cohesive unit.

References

Chapin, J.P. 1932. The birds of the Belgian Congo. Part I. *Bull. Amer. Mus. Nat. Hist.* 65: 1-756.

Crowe, T.M. & Snow, D.W. 1978. Numidinae. *In*: Snow, D., ed. *An atlas of speciation in African non-passerine birds*. London: British Museum (Natural History).

Ehrlich, P. & Raven, P. 1969. Differentiation of populations. *Science* 165: 1228-1232.

Elgood, J.H., Fry, C.H. & Dowsett, R.J. 1973. African migrants in Nigeria. *Ibis* 115: 1-45.

Ghigi, A. 1936. *Galline di Faraone e Tacchini*. Milano: V. Hoepli.

SUMMARY AND SYNTHESIS

The Numidinae have been 'over-split', particularly at the subspecies level. Nearly 50 taxa have been ascribed to the subfamily. In paper 1 I admit only 19 taxa. In this paper, I analyze patterns of qualitative and quantitive character variation to produce a hypothetical taxonomy and phylogeny for the subfamily; and speculate as to the origin, ecology and phenotype of the ancestral guineafowl, and the value of evolutionary patterns found in guineafowl in predicting broad biogeographic patterns for African birds as a whole (i.e. aims 1-4). Quantitative and ecologically defined genus, species and subspecies concepts are applied in erecting the taxonomy. A cladistic approach, based on postulated primitive-derived character sequences, is used in developing the phylogeny.

Although the likely ancestral guineafowl was an Asiatic francolin-like phasianid, the evolution that has produced the recognized taxa occurred solely in Africa. Moreover, preliminary results suggest that avifaunal zones derived from patterns of evolution in guineafowl closely parallel, and therefore may be taken to be representative of broad biogeographic trends found in African birds as a whole. The ancestral guineafowl was probably a savanna-living bird, which traversed the arid-savanna corridor that linked Asia and Africa during the mid-Miocene. Upon its arrival in Africa, this open-country bird encountered a continent dominated by forest, possibly unoccupied by potential competitors. Such conditions would have favoured radiation into forest biome, and it is likely that Agelastes, the most primitive (i.e. most francolin-like) guineafowl genus is the result of such a radiation.

Relatively soon (on a geological time scale) after this successful invasion of forest, the climate of Africa became more arid. Throughout the latter Miocene and the Pliocene, savanna and desert biome expanded at the expense of forest. Such a situation favoured radiation in non-forest biomes, and into the expanding forest edge biotope. It is possible that proto-*Numida*, *Acryllium* and *Guttera* were the result of such radiations. The relatively uniformly arid conditions of the Pliocene subjected the four guineafowl lineages to strongly divergent selection pressures, and it is probable that the genera recognized herein were already well-defined at the beginning of the Pleistocene.

The arid climate of the Pliocene was replaced by a fluctuating wet-dry climate in the Pleistocene. These climatic fluctuations had profound effects on the distribution of Africa biomes. During moist phases, forest biomes expanded considerably beyond their present extent, partitioning non-forested biomes into more or less isolated tracts. Desert was confined to relatively small areas, and savanna biome bridged the western Sahara, allowing dispersal of *Numida meleagris* into North Africa. Sub-Saharan subspecies of *N. meleagris* are a result of divergence in these wet-phase isolated tracts. Also, expanded forest during mesic phases could have allowed a second radiation into lowland forest, culminating in *Guttera plumifera*. During arid phases, the forest contracted into island-like refugia, and *N. m. sabyi* was isolated, and presumably diverged from sub-Saharan populations. The species *Agelastes meleagrides* and *A. niger*, and subspecies in the genus *Guttera* are also a result of divergence in forest refugia. The fact that *Guttera* subspecies are much more well-marked than are those of *N. meleagris* suggests that isolation in forest refugia has been more effective than in tracts of savanna biome partitioned during mesic phases.

In paper 2, I investigate the possible adaptive significance of intra-specific phenetic variation in *Guttera pucherani*, a forest-living guineafowl, and *Numida meleagris*, a characteristic bird of savanna biome. In this paper, I use regression and correlation analyses to determine possible adaptive relations between phenetic characters, which descriminate subspecies in paper 1, and measures of the environment (i.e. aim 5). Variation in most of the 28 characters studied is statistically related to variation in the environment. In *N. meleagris*, six phenetic trends emerge.

1. Variation in wing length, an index of body size, follows predictions of Bergmann's Rule, i.e. is inversely related to measures of temperature and positively related to elevation.
2. Exposed structures of the head tend to be smaller at hotter and drier sampling localities. The reduction of exposed surface area may help uptake of radiative heat, and/or limit loss of body water through cutaneous evaporation.
3. The amount of white in the body plumage tends to be greater at hotter sampling localities. This may help the birds to reflect some of the heat of radiation.

4. Collar plumage appears to follow predictions of Gloger's Rule, i.e. tends to be darker at relatively moist and warm localities.
5. The amount of nape covered by filoplumes tends to be greater at hotter localities. Since filoplumes may be sensory structures which allow the monitoring of environmental disturbers, such as wind, and since dense dark feathers may be used as a thermal shield, filoplumes may serve a dual function in aiding guineafowl to orient their head and neck optimally, relative to the wind and sun, so that heat of radiation may be absorbed and dissipated before it reaches the skin.
6. Wattles tend to be wider at localities at which there is greater visibility. Since the subspecies with the widest wattles, N. m. galeata, also has the greatest amount of red pigment in its wattles, it is possible that this increased wattle width may facilitate individual and/or incipient species recognition.

As with N. meleagris, temperature, moisture and visibility seem to have played an important, although somewhat different role in shaping G. pucherani phenotype. Four basic trends emerge.

1. Variation in wing and tarsus length is significantly related to measures of the amount of moisture in the air, the former inversely, the latter directly. Since an increase in tarsus length and a decrease in overall size results in an increase in the surface to volume ratio, it is possible that this may be an adaptation which allows more effective non-evaporative cooling

in relatively moist areas.

2. The amount of white in the collar is greater at hotter localities, and may allow greater reflectance of radiation.
3. The degree of curliness of crest feathers is greatest at hotter areas, and may enhance the value of the crest as a thermal shield.
4. Overall crest size is greater at localities with low visibility. This result suggests that the crest may be a "close-in" signalling device in dense vegetation.

Lastly, I stress that a statistical correlation is poor evidence for an adaptive relation, and that phenetic variation in these species may also have been affected by non-physiological pressures. More detailed anatomical, physiological and behavioural research is needed to test the hypotheses developed in this paper.

In papers 3 and 4, I collaborate (as senior author) with colleagues to investigate the advantages and disadvantages of having a largely unfeathered head and neck (i.e. aim 6). Paper 3 (done jointly with A.A. Crowe) is an anatomical study of the cervico-cephalic vascular system of _N_. _meleagris_. My _a priori_ hypothesis, developed from observations of guineafowl in the field and from the results of paper 2, is that the head and neck of _N_. _meleagris_ acts as a thermal window. In other words, _N_. _meleagris_ can facilitate the uptake and/or dissipation of heat through optimal orientation of the head and neck, coupled with controlled patterns of blood flow. In paper 3 we show that _N_. _meleagris_ possesses several vascular arrangements, most notably a nape-cheek rete, which we feel may help this species to regulate brain temperature. Although there are only tenous direct connections between these vascular arrangements and the brain, we suggest several alternate pathways of blood flow which would allow the regulation of the temperature of arterial blood before it reaches the brain.

In paper 4 (done with P.C. Withers), we test the hypothesis that the head-neck thermal window helps to cool brain temperature by means of convective cooling, and comment on the basic mechanisms used by _N_. _meleagris_ in regulating its brain and body temperatures. We examined the brain temperature, deep body temperature, the metabolic rate, and/or respiratory quotient for nine captive guineafowl exposed to ambient temperatures ranging from 12 to 43°C, and both with and without simulated solar radiation and convection. Our results are consistent with the convective cooling hypothesis, and we reach six major conclusions concerning temperature regulation in _N_. _meleagris_.

1. At low ambient temperatures, body temperature is maintained by increased production of metabolic heat.
2. At high ambient temperatures, _N_. _meleagris_ regulates body temperature by lowering metabolic heat production, and by promoting evaporative heat loss by panting and gular fluttering.
3. Since there was little variation in the respiratory quotient (i.e. no evidence of alkalosis), evaporative water loss does not occur at important sites of respiratory gas exchange.
4. In the absence of flutter-panting with an open gape, _N_. _meleagris_ can regulate brain temperature through

evaporative water loss in the nasal mucosa.

5. This mechanism for brain temperature regulation becomes ineffective when heat-stressed guineafowl pant and gular flutter through the mouth.
6. Convective heat loss through the thermal windows of the head and neck becomes critical to brain temperature regulation under these conditions.

In papers 5-7, I formulate and test hypotheses concerning population regulation in _N. meleagris_ (i.e. aim 7). Paper 5, a joint effort with W.R. Siegfried, consists of a statistical analysis of rainfall and guineafowl hunting data for Rooipoort, an estate near Kimberley, South Africa. We show that frequency of rainfall during the 12 months prior to the hunting season is the best predictor of a shooting index (no. of guineafowl shot/ no. of hunting days). We offer two possible hypotheses to explain this result.

1. Guineafowl population at Rooipoort is limited in a density independent manner by some direct consequence of frequent rainfall.
2. Guineafowl population at Rooipoort is limited in a density dependent manner by some indirect consequence of frequent rainfall (e.g. increased abundance of food or other critical resources).

In paper 6, I test these hypotheses by reanalyzing the data from paper 5 in the light of ecological and behavioural data collected during a 28 month intensive study of the Rooipoort guineafowl population. I reject the density independent hypothesis, since changes in population are statistically dependent on, and inversely related to the estimate of population (shooting index), and since frequency of rainfall is also a significant predictor of food availability. The density dependent hypothesis is modified to include possible effects of rainfall in guineafowl physiology and behaviour.

In paper 7, I test the hypothesis that high levels of intestinal helminth infestation can limit the Rooipoort guineafowl population in a density dependent manner. Although there were higher levels of infestation at higher population densities, particularly among birds living in relatively mesic habitat, there was no indication of any pathological condition that could be a result of damage by helminths. Therefore the hypothesis is rejected.

Throughout this thesis two factors, temperature and rainfall, emerge again and again as playing, or having played, important roles in the ecology and evolution of guineafowl. In the short term, year-to-year variation in the temperature/ rainfall regime influences population (papers 5 & 6) and intestinal helminth burdens (paper 7) in N. meleagris, probably through its effects on the availability of food and drinking water, and on the survival of growth stages of the parasites. Long term variation (i.e. on a geological time scale) in temperature and rainfall patterns has affected guineafowl evolution both relatively directly and indirectly. The significant statistical relationship between variation in N. meleagris and G. pucherani and variation in temperature and rainfall (paper 2) suggests that the phenotype of guineafowl may be largely a response to selection pressures dictated by temperature and rainfall. This hypothesis is supported, in part, by anatomical and experimental studies (papers 3 & 4) which show that the largely naked head and neck of N. meleagris helps this species to regulate brain temperature.

Indirectly, temperature and rainfall have influenced guineafowl evolution through their effect on the distribution of vegetation. Since guineafowl are "tied" to their associated biomes, expansion of any of these would have provided corridors of dispersal for some species and barriers to others. Wet-dry and/or cool-warm climatic fluctuations that occurred during the Pleistocene promoted the expansion and contraction of all extant African biomes. I believe that guineafowl taxa as we know them today, are a result of adaptive divergence during isolation due to the spread of unsuitable biomes (paper 1).

THE EVOLUTION OF GUINEAFOWL (GALLIFORMES, PHASIANIDAE, NUMIDINAE). I. TAXONOMY, PHYLOGENY, SPECIATION AND BIOGEOGRAPHY

BY

T.M. CROWE

FitzPatrick Institute, University of Cape Town

(With 1 plate, 52 figures, 11 tables and 2 appendices)

ABSTRACT

Patterns of qualitative and quantitative character variation in 1833 museum specimens encompassing all taxa attributed to the Numidinae are analyzed to produce a hypothetical taxonomy and phylogeny for the subfamily. Quantitatively and ecologically defined genus, species and subspecies concepts are applied in erecting the taxonomy. A cladistic approach, based on postulated primitive-derived character sequences, is used in developing the phylogeny. Four genera, six species and 15 subspecies are recognized. Cladistic events are linked to likely causal geological and paleoecological events to determine a possible evolutionary chronology. Genera are thought to have arisen as a consequence of Miocene and Pliocene radiations; species and subspecies as a result of Pleistocene divergence. A hypothetical map of African avifaunal zones, based on evolutionary patterns found in guineafowl, is offered. Comparisons of this map with other African avifaunal maps and with distribution maps of selected francolin taxa suggest that biogeographic patterns found in guineafowl reflect broad patterns found in many

African birds. A hypothesis as to the causes of relatively high species richness in francolin is offered.

CONTENTS

INTRODUCTION

There are many reasons why an understanding of the evolution of guineafowl (Numidinae; Sibley & Ahlquist 1972) should provide an insight into patterns of avian evolution and biogeography in Africa.

1. The Numidinae are endemic to Africa, and presumably evolved and/or radiated there from a francolin-like ancestor (Ghigi 1936; Cracraft 1973; Olson 1974).
2. At least one guineafowl species has become adapted to life in each major terrestrial African biome outside of desert, Mediterranean vegetation and montane forest (Crowe & Snow 1978).
3. Guineafowl are sedentary birds (Chapin 1932; Priest 1933; Archer & Godman 1937; Elgood _et_ _al_. 1973), and thus should be more susceptable to local selection pressures than would be more mobile species (Ehrlich & Raven 1969).
4. The distributions of some guineafowl taxa do not correlate well with present-day vegetation and topography (Chapin 1932). Such anamalous distributions of plants and animals can be used to infer environmental conditions and the distributions of African biomes, during the Tertiary and Quarternary (Chapin 1932; Moreau 1963, 1966; Roberts 1975; Hamilton 1974 and Axelrod & Raven in press).
5. The genetic basis of morphological variation in several guineafowl species is relatively well understood (Ghigi 1936).

6. Perhaps most importantly, guineafowl species are relatively well represented in museum collections and, accordingly, lend themselves to quantitative analysis, which is desirable in formulating precise evolutionary and biogeographic hypotheses (Mayr et al. 1953; F. Vuilleumier 1975).

Thus, guineafowl provide a simple, characteristically African system from which evolutionary and biogeographic hypotheses may be derived. The aims of the present study are to:

1. re-examine and revise, if necessary, the rather confused taxonomy within the subfamily (Table 1), using a repeatable, relatively objective quantitative methodology;
2. produce a parsimonious phylogeny based on the analysis of shared derived character-states;
3. develop models of speciation, which are consistent with the phylogeny developed herein and the likely past geological and climatic history of Africa;
4. suggest tentative avifaunal sub-regions, provinces and districts for Africa, based on analysis of the distributions of recognized guineafowl taxa.

The possible familial status of the subfamily (Wetmore 1960), the adaptiveness of inter- and intra-specific morphological variation in guineafowl, and the predictive value of evolutionary and biogeographic models based on patterns found in guineafowl, will be discussed briefly, if at all, herein. These topics will be dealt with in greater detail in future papers.

Table 1

A history of the taxonomy of guineafowl[1].

Taxa			Chapin (1932 & *in litt.*)	Peters (1934)	Ghigi (1936)	Boetticher (1954)	Macworth-Praed & Grant (1952; 1962; 1970)	White (1965)	Crowe (this study)
Phasidus	*niger*		X	X	X	X	X		
Agelastes	*niger*							X	X
	meleagrides		X	X	X	X	X	X	X
Acryllium	*vulturinum*		X	X	X	X	X	X	X
Guttera	*plumifera*	*plumifera*	X	X	X	X	X	X	X
		schubotzi	X	X	X	X	X	X	X
	pucherani[4]		X	X			X	X	
	edouardi[4]	*edouardi*	X	X	X	X	X	X	X
		suahelica		X	X	X			
		schoutedeni	X	X	X	X	X	X	
		seth-smithi	X	X	X	X	X	X	
		verreauxi[2]	X	X	X	X	X	X	X
		sclateri	X	X	X	X	X	X	X
		chapini	X	X		X	X	X	
		granti	X		X			X	
		barbata		X	X	X	X	X	X
		lividicollis			X	X			
		kathleenae[3]	X				X	X	
		symonsi					X		
		pucherani			X	X			X

Numida	meleagris	meleagris	X	X	X	X	X	X	X
		major	X	X	X	X	X	X	
		macroceras	X	X	X	X	X	X	
		somaliensis	X	X	X	X	X	X	X
		intermedia	X	X	X	X	X	X	
		toruensis	X	X	X	X	X	X	
		neumanni			X				
		omoensis			X				
		ansorgei			X				
		inermis							
		sabyi	X	X	X	X			X
		galeata	X	X	X	X	X	X	X
		marchei	X	X	X	X	X		
		strasseni	X	X	X	X	X	X	
		mitrata	X	X	X	X	X	X	X
		reichenowi	X	X	X	X	X		X
		marungensis	X	X	X	X	X	X	X
		callewaerti	X	X	X	X	X	X	
		maxima	X	X	X	X			
		uhehensis			X	X			
		rikwae			X	X			
		frommi			X				
		coronata	X	X	X	X		X	X
		limpopoensis		X		X			
		transvaalensis				X			
		papillosa	X	X	X	X	X	X	
		damarensis	X	X	X	X	X	X	X
		blancoui[3]				X			
	reichenowi							X	

[1] unless otherwise specified, nomenclature follows Peters (1934)

[2] *G.e. verreauxi* = *G.e. pallasi*, see White (1965)

[3] see White (1965)

[4] since these two taxa are considered to be conspecific in the present study, following the principle of priority the specific name recognized is *G. pucherani*.

METHODS

Material and characters

The author examined 1 833 museum specimens including all taxa attributed to the subfamily in Table 1. All characters investigated (Appendices 1 and 2, Figs. 1-3) appear to have a genetic basis (Ghigi 1936), and have been discussed in previous studies (e.g. Beddard 1898; Bannerman 1930; Chapin 1932; Ghigi 1936; Archer & Godman 1937; Jackson 1938; Boetticher 1954; Mackworth-Praed & Grant 1952, 1962, 1970). Therefore, they need not be described again in detail. Characters were chosen to reflect as much of the phenotype as possible, while eliminating the necessity of close comparisons of specimens from different collections. Due to logistical constraints (e.g. small sample sizes of each sex, time allotted for examination of specimens, and variation in the detail of collectors' notes and care in specimen preparation) some of the quantitative characters listed in Appendix 1 were assessed relatively subjectively, and data for both sexes were lumped. This introduces a certain amount of imprecision into the analysis. But, subjective assessments were made against a set of reference specimens, photographs or drawings encompassing the range of observed variation. Also, the previous studies mentioned above have stated that sexual dimorphism is absent, or relatively minor in comparison with geographical variation in guineafowl. Moreover, it was felt that the advantages accruing from considering a large number of characters for many specimens outweighed any sampling bias due to imprecise measurement

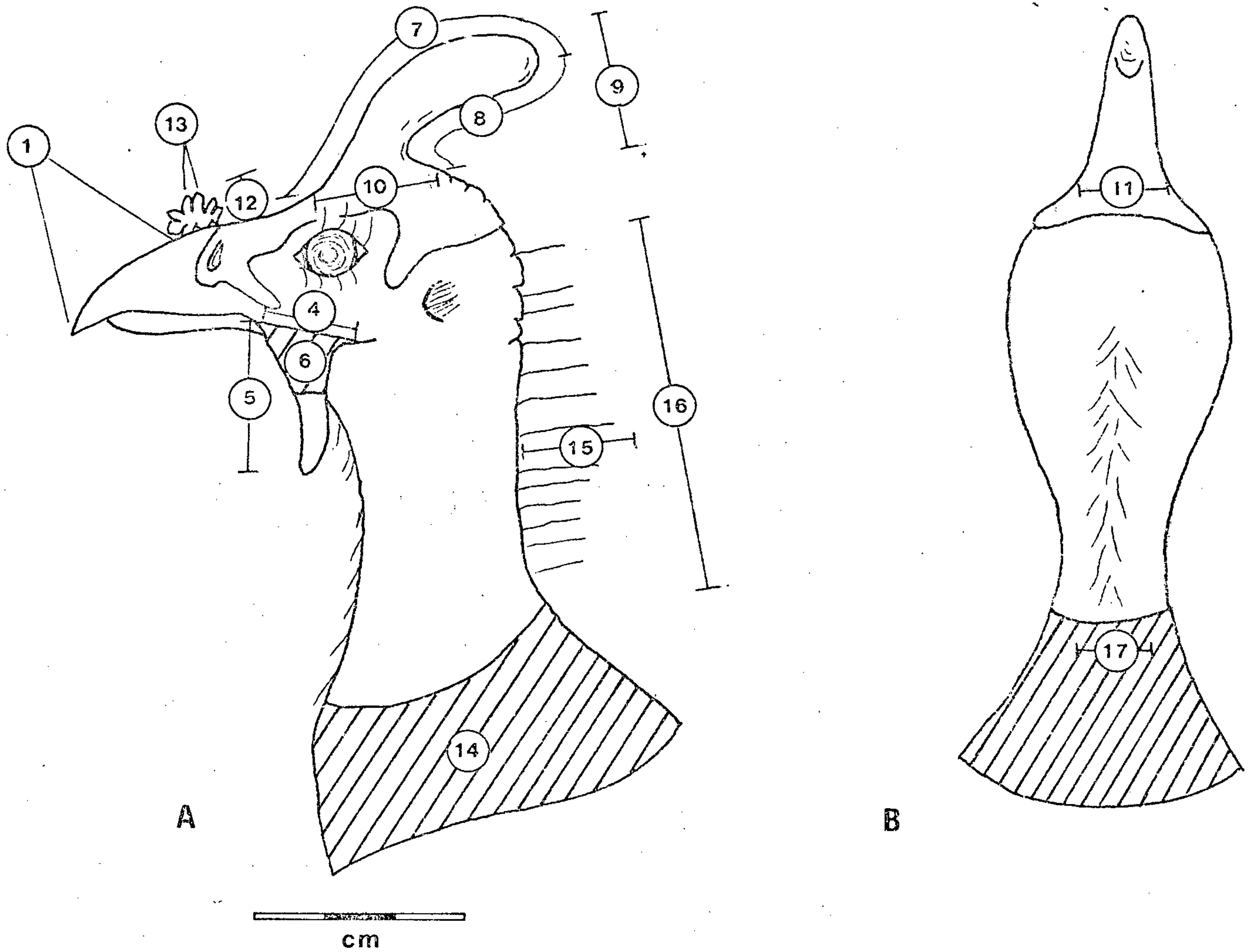

Fig. 1. Quantitative characters 1, 2-17. A. Lateral view of head, neck and collar of *Numida meleagris*. B. Dorsal view of same.

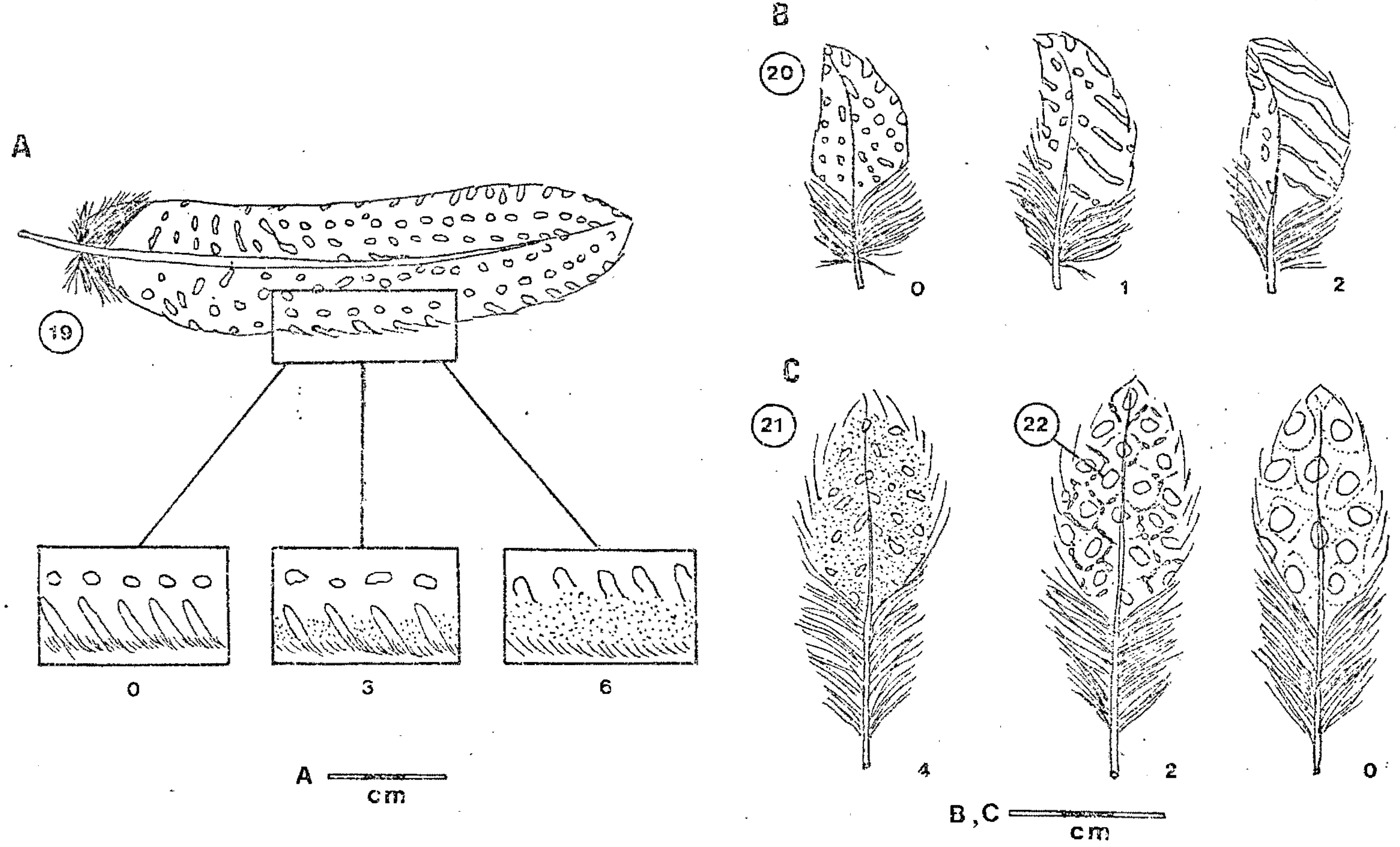

Fig. 2. Quantitative characters 19–22. A. Secondary remex from *Numida meleagris*. B. Wing covert from *N. meleagris*. C. Mid-dorsal feather of same.

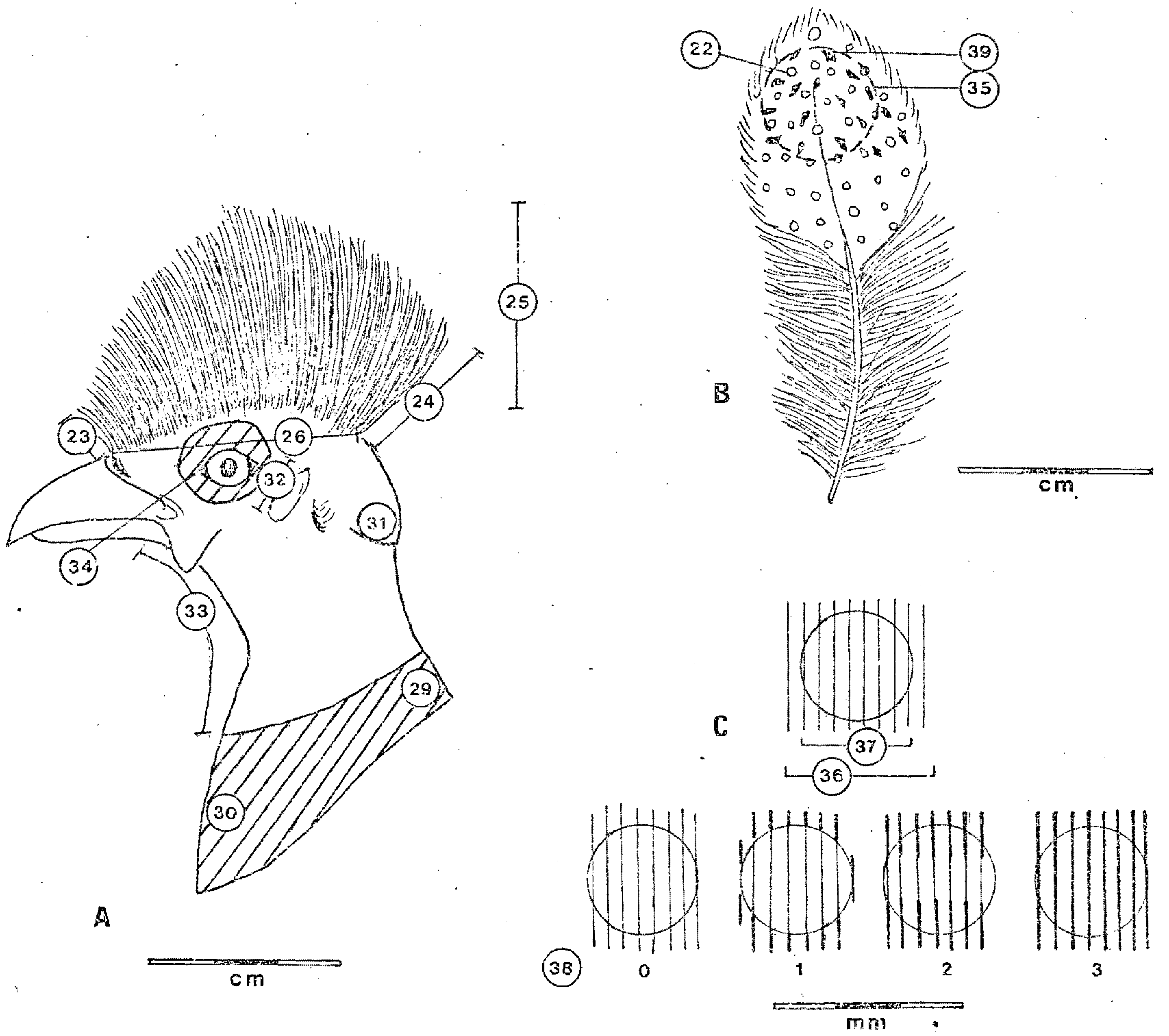

Fig. 3. Quantitative characters 22-26, 29-39. A. Lateral view of head, neck and collar of *Guttera plumifera*. B. Mid-dorsal feather of *G. pucherani edouardi*. C. Spots on mid-dorsal feathers of *Guttera* spp.

and sexual dimorphism.

Taxonomic philosophy

The taxonomic philosophy adhered to in the present study follows that outlined by Mayr et al. (1953). A species is a group of actually or potentially interbreeding individuals which has diverged sufficiently in allopatry to have become reproductively isolated from other such groups. A genus is a monophyletic taxon which is decidedly qualitatively distinct, and is adapted to a particular mode of life, i.e. a generic "niche".

The subspecies is much more difficult to define. Table 1 shows that much of the "taxonomic variation" in guineafowl systematics is at the subspecies level. Some systematists (e.g. Wilson & Brown 1953; Moreau 1957; Selander 1971; Gould & Johnston 1972) state that the category is useless, and even detrimental to the understanding of geographic variation and intra-specific evolution. These critics maintain that:

1. characters used to delineate subspecies usually have patterns of geographic variation which are discordant with each other and with the distribution attributed to the taxon;
2. indistinguishable phenotypes occur in geographically isolated areas, presumably due to parallel evolution under similar selective regimes;
3. no objective degree of difference can be offered to distinguish subspecies from slightly differentiated local populations.

In an attempt to satisfy these legitimate criticisms, Ford (1974) offers the taxo-evolutionary subspecies concept, the concept adhered to in the present study. This concept limits the awarding of subspecies status to geographic aggregates of populations which appear to have undergone genetic and phenotypic divergence in allopatry. Past allopatric divergence may be inferred for presently parapatric taxa if their distributions can be derived from concordant character variation, and if they are separated by a zone of secondary intergradation (Ford 1974).

Taxonomic methodology

Since both the recognition of taxa and their assignment to taxonomic categories (with the possible exception of the species) are ultimately subjective processes (Mayr *et al*. 1953; Selander 1971; Ford 1974), it is of utmost importance to outline the methodology underlying taxonomic decisions.

With the foregoing taxonomic philosophy in mind, the procedure used to determine genera involved four steps:

1. a sorting of specimens into groups which consisted of members of both sexes, and which possessed unique combinations of qualitative characters;
2. a cluster analysis of these groups according to the number of shared qualitative character states;
3. presentation of the clustering similarity matrix in the form of a phenogram;
4. interpretation of the matrix and the phenogram, according to the taxonomic philosophy outlined above, to determine genera.

Once genera were identified, each was analyzed separately to determine species and subspecies. Two multivariate statistical computer programmes were used in tandem in these analyses. The first programme, BMDP2M (Dixon 1975), was used to cluster specimens into operational taxonomic units (OTUs, Sneath & Sokal 1973). In BMDP2M, the clustering algorithm first amalgamates the two specimens which are most similar. The amalgamated specimens are then treated as one case in future comparisons. This clustering algorithm continues until all specimens are grouped into one large cluster. The similarity measure used is the Euclidean distance, and the clustering method is the weighted average pair group method (Sneath & Sokal 1973). The printed output of BMDP2M includes a phenogram which illustrates the results of the cluster analysis in a hierarchical manner. OTUs were identified from examination of these phenograms. In a phenogram, OTU status was awarded to any specimen cluster which contained members of both sexes from several geographically contiguous localities, and which was morphologically more distinct (i.e. linked up with other such groups at a lower similarity) than was a group of specimens from a single, relatively well-sampled locality within the range of an undisputed taxon listed in Table 1.

OTUs were compared using stepwise multiple discriminant analysis programme BMDP7M (Dixon 1975). This programme calculates a series of linear classification functions in a stepwise manner, such that within-OTU variance is minimized and between-OTU variance maximized. At each step in the analysis, the character not yet entered into the functions that best separates OTUs is included. This procedure continues until all significant ($P < 0,05$) characters are included in the functions. The printed output of BMDP7M includes a probabilistic statement as to the OTU membership of each specimen. In the final step, BMDP7M computes canonical discriminant functions between OTUs, and plots the first two so as to give an optimal two-dimensional picture of the separation of the OTUs. This plot consists of a multivariate centroid for each OTU, surrounded by a cloud of individual points corresponding to specimens in that OTU. In this study, an OTU, or group of OTUs, was awarded species rank if none of the component specimens were intermediate between two OTUs (i.e. were assigned a probability greater than 0,05 of belonging to another OTU).

Once species were identified, character variation within each species consisting of several OTUs was analyzed to determine if any component OTUs merited subspecies status. The taxonomic procedure used in these analyses involved four steps:

1. division of the species range into uniform areas;
2. computation of mean values and coefficients of variation (COV, Sokal & Rohlf 1969) for each character for each area;
3. contour mapping of mean values for each character, and of the total COV for all characters for each area;

4. interpretation of the contour maps to determine OTUs whose distributions could be derived from concordant character variation, and whose boundaries were circumscribed by a zone of secondary intergradation.

Subspecies rank was awarded to any OTUs whose distributions could be derived from concordant variation in at least three characters, and which enclosed an area of relatively low total COV bounded by an area(s) of high total COV. Areas with relatively low variability (i.e. low total COV) were taken to be probable "core regions" for their associated subspecies. Areas with relatively high variability (i.e. high total COV) were taken to be regions of secondary intergradation.

The smallest uniform area that produced sample sizes that were statistically adequate, was that enclosed by a block four degrees on a side. Contour mapping was done with the assistance of a computer, using contouring programme GPCP (CALCOMP 1971). This programme fits an approximate contour surface to the data using least squares polynomial analysis.

Phylogenetic philosophy

A cladistic approach (Marx & Rabb 1970; Cracraft 1972) was used to infer phylogenetic relationships between guineafowl genera and species. Cladistic analysis involves discernment and use of derived character-states. Derived states are those which are unique or relatively restricted to the taxa under study, or which could be adaptive in a social or ecological context (Marx & Rabb 1970). Shared primitive character states, i.e. those commonly inherited from distant ancestors, cannot be used to unite more recently evolved taxa (Cracraft 1972). Other than its consistent, relatively objective methodology, the major advantage of a cladistic analysis is that a proposed phylogeny can be refuted on clearly specified grounds. A proposed phylogeny must be modified or abandoned if: derived characters used to produce it are shown to be primitive; another interpretation of the same or different combination of derived character states yields a more parsimonious phylogeny, i.e. requiring fewer convergences; a fossil form is found which possesses a character suite incompatible with the proposed phylogeny; or if it is grossly at variance with known biogeographic events (Cracraft 1972; F. Vuilleumier 1975).

Phylogenetic methodology

Since the presumed ancestor of the guineafowl is a francolin-like phasianid (Ghigi 1936), any character state common among extant francolins or guineafowl-phasianid hybrids was taken to be primitive. Ghigi (1936), Mackworth-Praed & Grant (1952, 1962, 1970) and Hall (1963) were used as sources of information on francolins. Ghigi (1936), Bourke (1967) and R. Chapin (*in litt*.) were the sources of information on the phenotypes of hybrids. Any character state unique to, or relatively common among guineafowl species was taken to be derived.

Once hypothetical primitive-derived sequences of character states were determined, a parsimonious phylogeny was produced following methods outlined by Cracraft (1972).

Speciation

There is now widespread agreement among evolutionary biologists and biogeographers that speciation, extinction and drastic distributional shifts in plants and animals have been common and world-wide during the Tertiary and Quarternary (Moreau 1966; B. Vuilleumier 1971; Axelrod & Raven in press). As mentioned in the introduction, past geological and climatic events have almost certainly helped to shape patterns of speciation and biogeography in Africa. Several authors (Chapin 1932; Cooke 1962; Howell & Bourliere 1963; Moreau 1966; Carcasson 1964; Butzer 1967; Hamilton 1976; Axelrod & Raven in press) have given maps of Africa depicting the hypothetical distribution of vegetation during relatively wetter and/or drier conditions in the past. Livingstone (1975), Hamilton (1976) and Axelrod & Raven (in press) have provided some temporal estimates for climatic and geological events which may have caused these conditions. As a preface to this study, the various hypothetical vegetation maps were compared, and compromise 'wet' and 'dry' maps (Figs. 4 & 5) were drawn which incorporated salient features of each. A hypothetical pattern and chronology for speciation in guineafowl were developed by relating the phylogeny derived herein to present-day (Fig. 6) and hypothetical past 'wet' and 'dry' vegetation maps in the light of temporal estimates given by authors mentioned above.

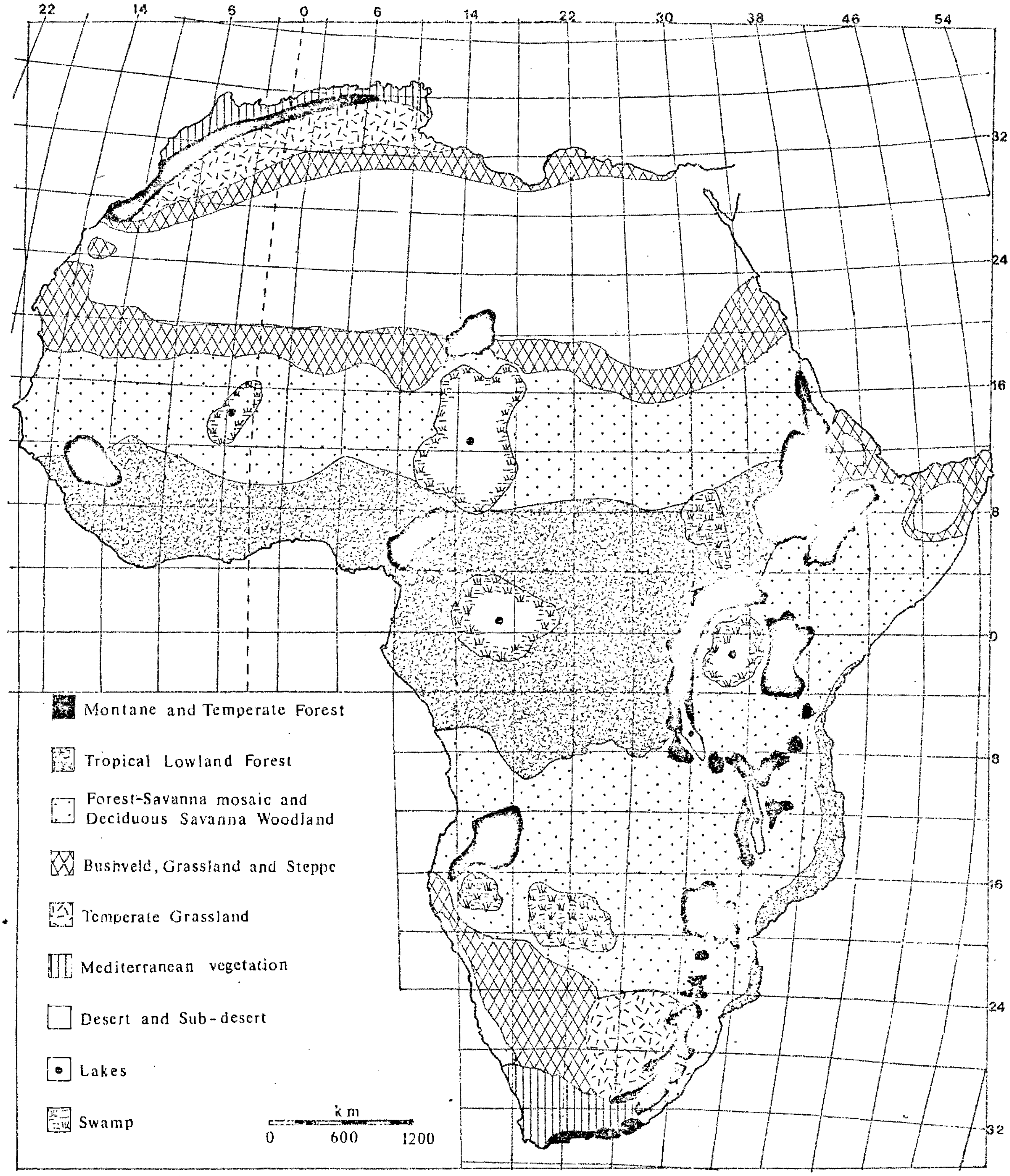

Fig. 4. Hypothetical vegetation map of Africa during a wetter period.

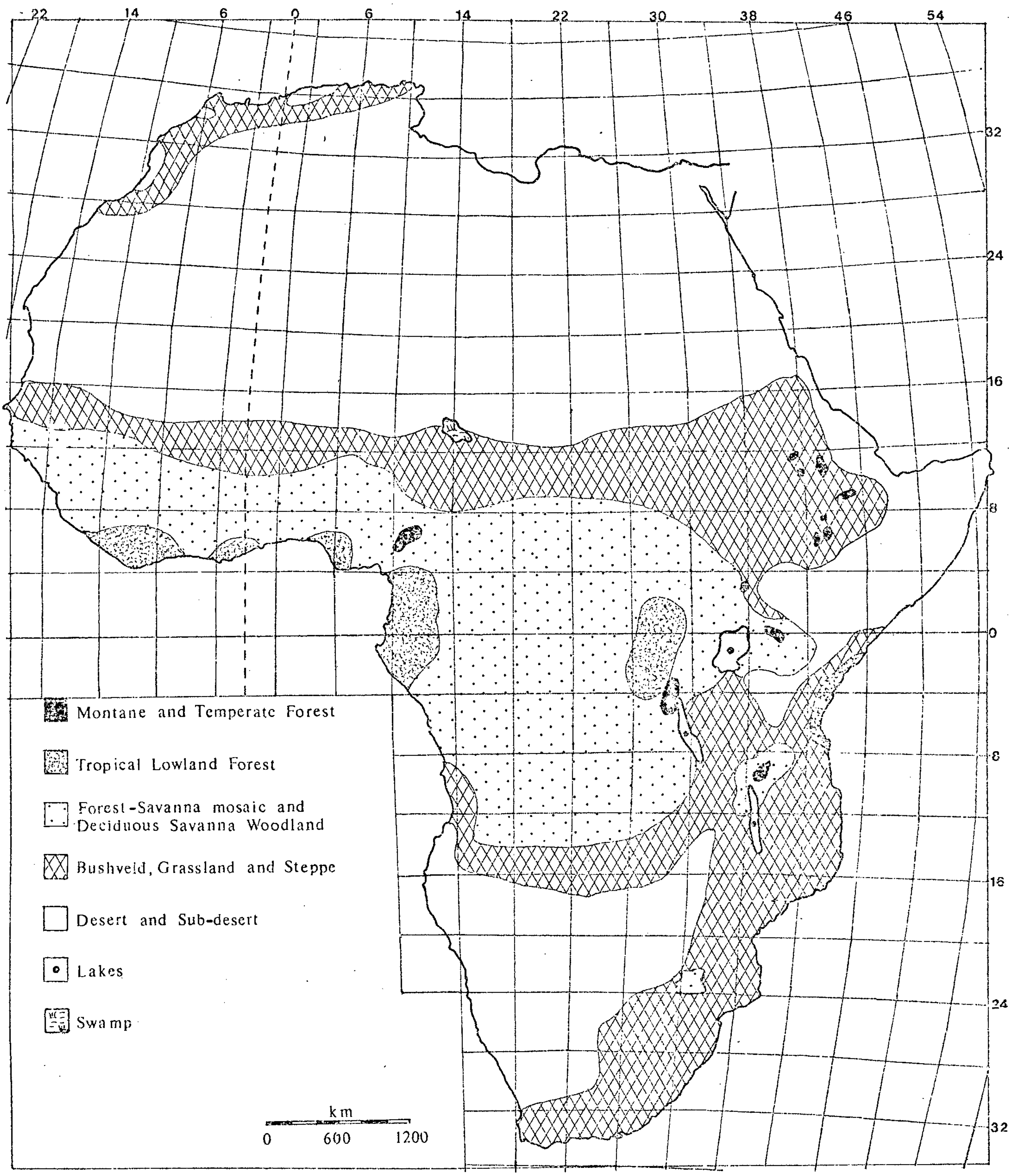

Fig. 5. Hypothetical vegetation map of Africa during a drier period.

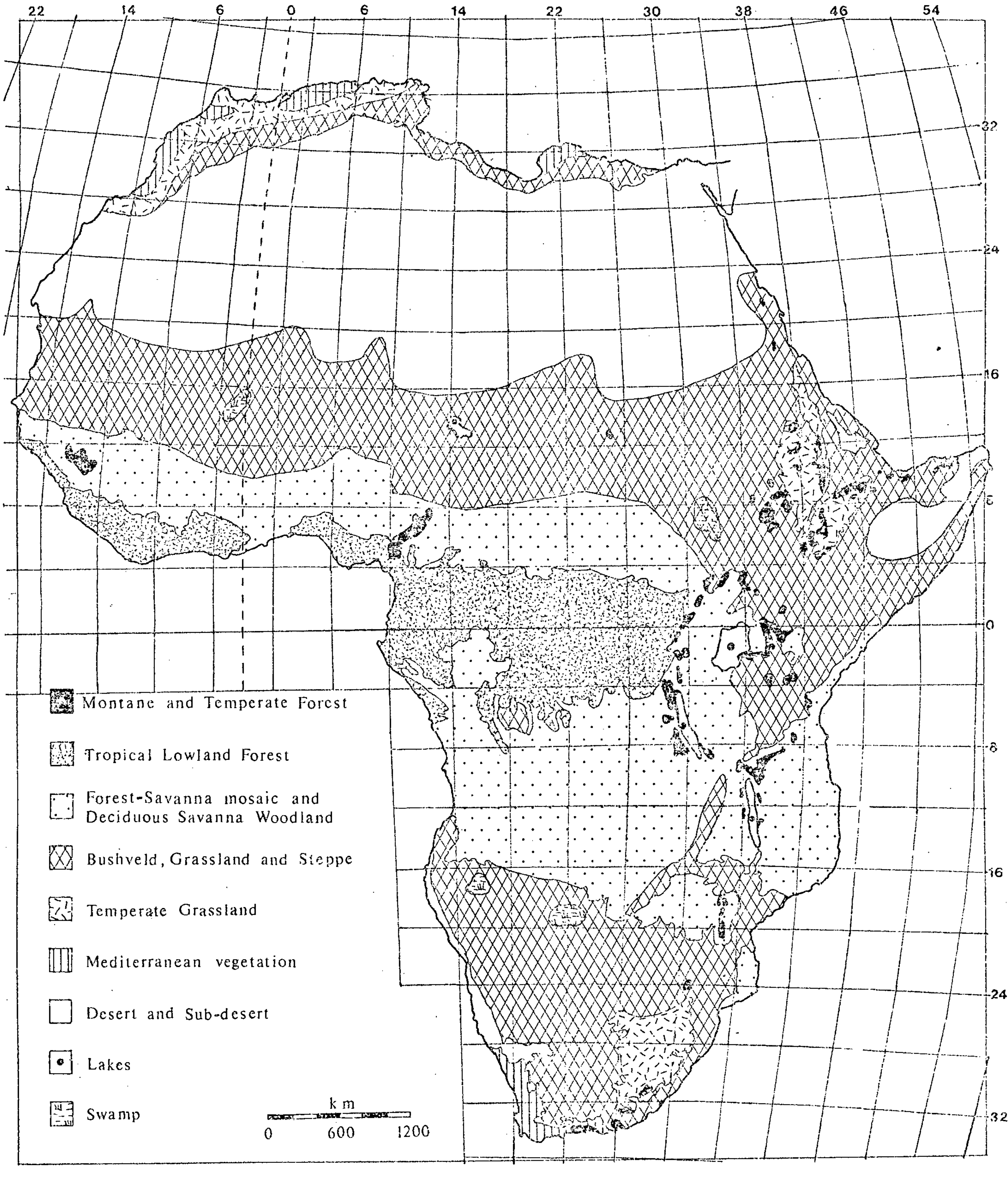

Fig. 6. Present-day vegetation map of Africa.

Biogeography

Once the taxonomy and phylogeny of a group are defined, biogeographic hypotheses based on patterns found in that group may be formulated. Since guineafowl are sedentary, stenotopic animals, the distribution of a given taxon should reflect the geographical limits and temporal stability of its associated biome. If a taxon has a vicariated distribution, it is likely that the vicars (Udvardy 1969) were isolated as a result of past partitioning of its biome. However, if a taxon shows little geographic variation, its biome probably has not been fragmented in the past. In this study, the boundaries of recognized genera, species and subspecies were used to formulate a hypothetical avifaunal map of Africa. Boundaries of taxonomically homogeneous genera (i.e. with no subspecies) were used to delimit African avian sub-regions in this map. In other words, a sub-region is any biome which has presented its assoicated guineafowl taxa with a sufficiently consistent selective regime to produce a monotypic genus, or a genus composed of monotypic species. Species boundaries were used to delimit provinces, and subspecies boundaries to delimit districts, following a similar reasoning used in defining sub-regions.

RESULTS, DISCUSSION AND CONCLUSIONS

Taxonomy

(a) Genera

There are 14 groups of guineafowl specimens (Table 2)

Table 2

Operational genera derived from analysis of qualitative character states listed in Appendix 1.

Character no.	Operational genera													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1	3	3	2	2	2	2	2	2	4	4	4	4	4
2	5	5	1	3	3	3	3	3	4	2	5	2	5	2
3	1	4	4	4	3	4	4	4	4	2	1	2	2	2
4	1	1	2	2	2	2	1	2	2	2	2	2	2	2
5	1	1	2	2	2	1	1	2	2	2	2	2	2	2
6	1	1	1	1	1	2	2	2	1	1	1	1	1	1
7	1	1	1	2	2	1	1	1	1	3	3	2	2	3
8	1	1	2	2	2	2	2	2	2	1	2	3	3	1
9	1	1	1	1	1	1	1	1	1	1	2	1	2	1
10	1	7	6	5	5	2	5	2	2	4	3	3	5	3
11	1	1	2	3	3	3	3	3	4	2	2	2	2	2
12	1	1	2	2	2	2	2	2	2	2	2	2	2	2
13	1	1	1	2	2	2	2	2	2	2	2	2	2	2
14	1	1	2	1	1	1	2	2	2	1	1	1	1	1
15	1	1	3	2	2	2	2	2	2	4	4	4	4	4
16	1	1	1	2	2	2	2	2	2	1	1	1	1	1
17	?	?	2	1	1	1	1	1	1	1	1	1	1	1
18	1	1*	2	4	4	4	4	4	4	3	3	3	3	3

* only in the juvenile bird

which possess unique combinations of the qualitative characters listed in Appendix 1. These groups are termed operational genera (OG). In the light of habitat preference information summarized by Crowe & Snow (1978), the results of a cluster analysis of the OG (Table 3; Fig. 7) suggest that there are four genera in the Numidinae. These are labelled A-D in Figure 7, and become apparent at the similarity level of 11 shared characters. In Table 1, genus A corresponds to the genera *Agelastes* Bonaparte, 1850 , and *Phasidus* Cassin, 1857, genus B to *Guttera*, genus C to *Acryllium*, and genus D to *Numida*. Genus A must be named *Agelastes*. Section (c) below consists of a taxonomic summary including: taxonomic conclusions; brief descriptions and mensural statistics; and a discussion of taxonomic conclusions when deemed necessary. All recognized genera are said to be largely restricted to broad "niches" (Crowe & Snow 1978). The genus *Agelastes* is found only in dense tropical lowland forest. The genus *Guttera* is also limited to forest areas, but inhabits riverine forest and the forest edge as well as tropical lowland forest. The genus *Acryllium* is confined to the sub-desert steppe of north-eastern Africa. The genus *Numida* can be found in virtually all areas of non-forested Africa outside of desert, mediterranean and montane vegetation.

(b) Species and subspecies

The genus *Acryllium* appears to be monotypic. A cluster analysis of 43 *Acryllium* specimens (Fig. 8) according to seven quantitative characters (nos. 1, 2, 3, 4, 5, 41, 42 in Appendix 2) yields only one OTU. Six individuals from Mt.

Table 3

Similarity matrix showing number of shared qualitative character states between OG derived and listed in Table 2.

OG no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	-	13	5	2	2	3	3	1	2	5	5	4	4	5
2		-	7	3	2	4	4	2	3	5	4	4	4	5
3			-	6	6	6	6	8	9	7	7	7	6	7
4				--	17	14	13	14	13	8	8	9	9	8
5					-	13	12	13	12	8	8	9	9	8
6						-	15	16	15	6	6	6	5	6
7							-	15	12	4	4	4	4	4
8								-	15	6	6	6	5	6
9									-	7	7	7	6	7
10										-	13	15	13	17
11											-	13	14	14
12												-	15	16
13													-	13
14														-

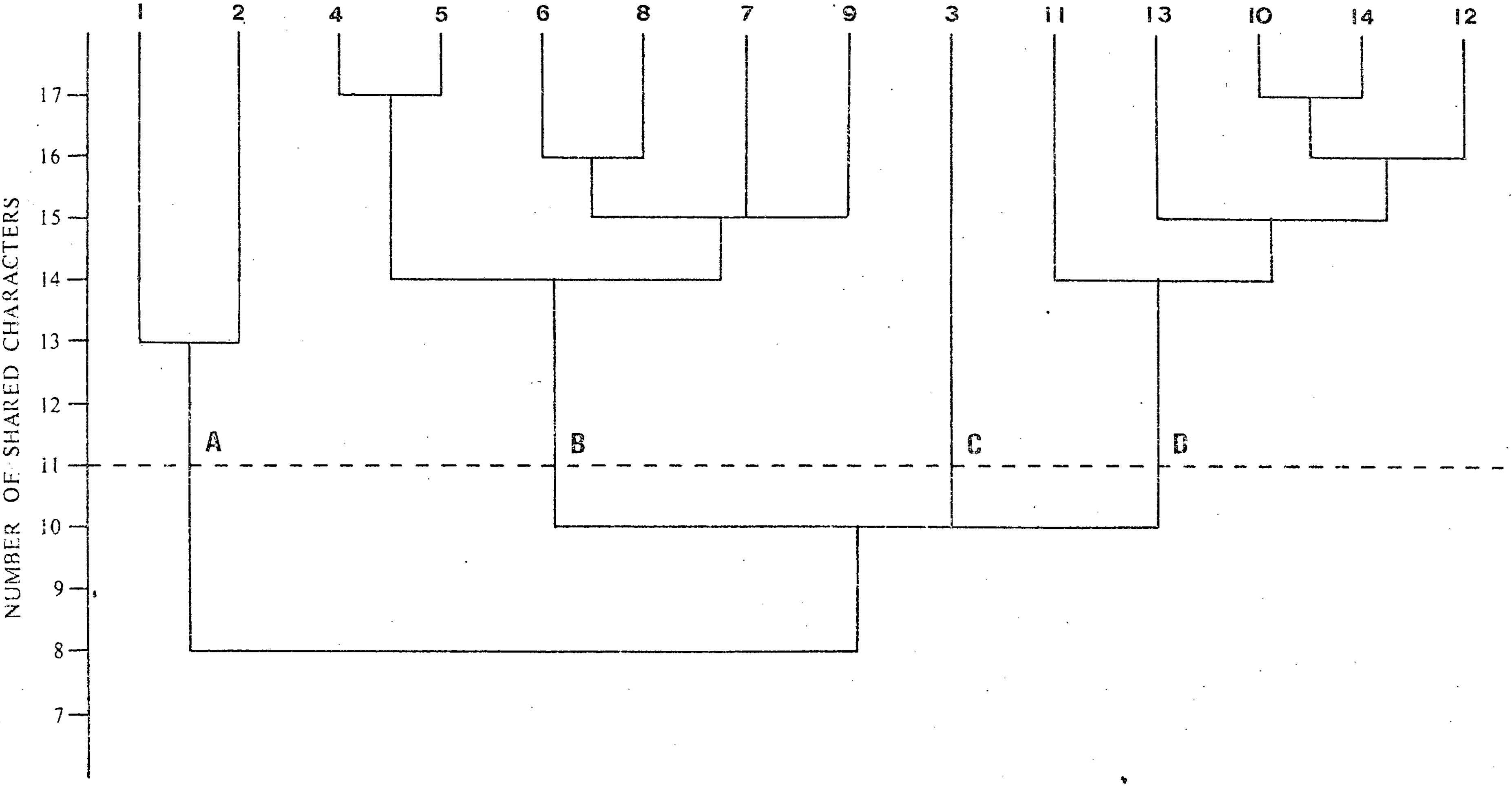

Fig. 7. The results of a cluster analysis of OG in Table 2. A. Agelastes. B. Guttera. C. Acryllium. D. Numida.

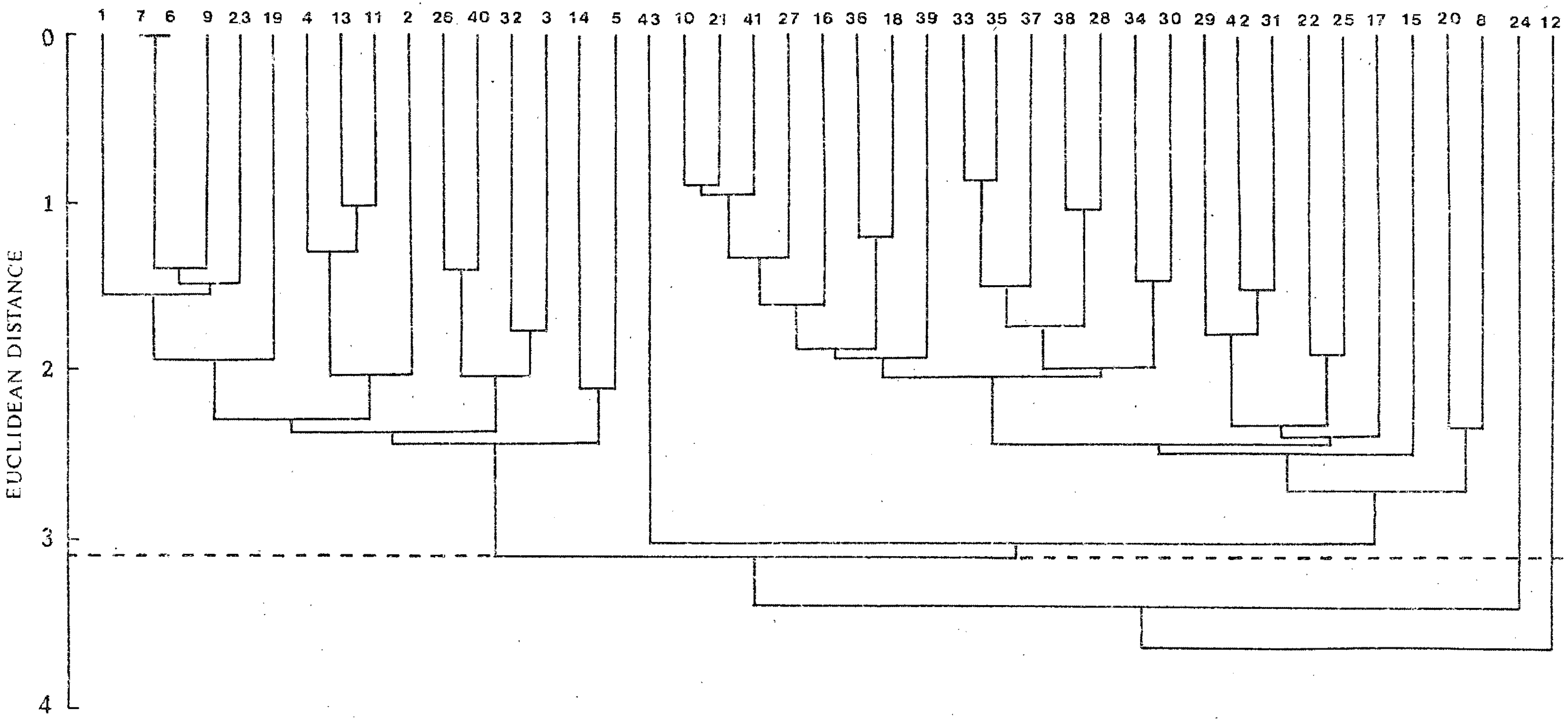

Fig. 8. The results of a cluster analysis of 43 specimens of <u>Acryllium</u>.

Kunchurro, Boran (ca. 4°30'N/38°E), Ethiopia, link to form a cluster at a level (indicated by the dashed line in Figure 8) lower than does any combination of specimens from the remainder of the distribution of the genus. Thus, for the characters investigated, variation in a single population is as great as that found throughout the range of the genus. Accordingly, in agreement with all previous studies (Table 1), one monotypic species, Acryllium vulturinum, is recognized. The distribution of this species is plotted in Figure 9.

The genus Agelastes is composed of two monotypic species. A cluster analysis of 49 specimens according to 11 quantitative characters (nos. 1, 2, 3, 4, 5, 23, 24, 41, 42, 43, 44 in Appendix 2) yields two OTUs, labelled A and B in Figure 10. The dashed line in the figure indicates the level at which eight individuals from Kribi (2°50'N/10°5'E), Cameroons, link to form a cluster. A discriminant functions analysis of the two OTUs reveals no intermediate specimens. Therefore the OTUs are recognized as species. In Table 1, OTU A corresponds to Agelastes meleagrides and OTU B to A. niger. The distributions of these species are plotted in Figure 9.

The remaining two genera are taxonomically more complex than are the first two. The results of a cluster analysis of 494 Guttera specimens according to 24 quantitative characters (nos. 1, 2, 3, 4, 5, 22 - 40 in Appendix 2) are summarized in Figure 11A. The dashed line in Figure 11A indicates the level at which 12 individuals from Ngayu (1°45'N/27°15'E), Zaire link to form a cluster. Seven OTUs are recognized.

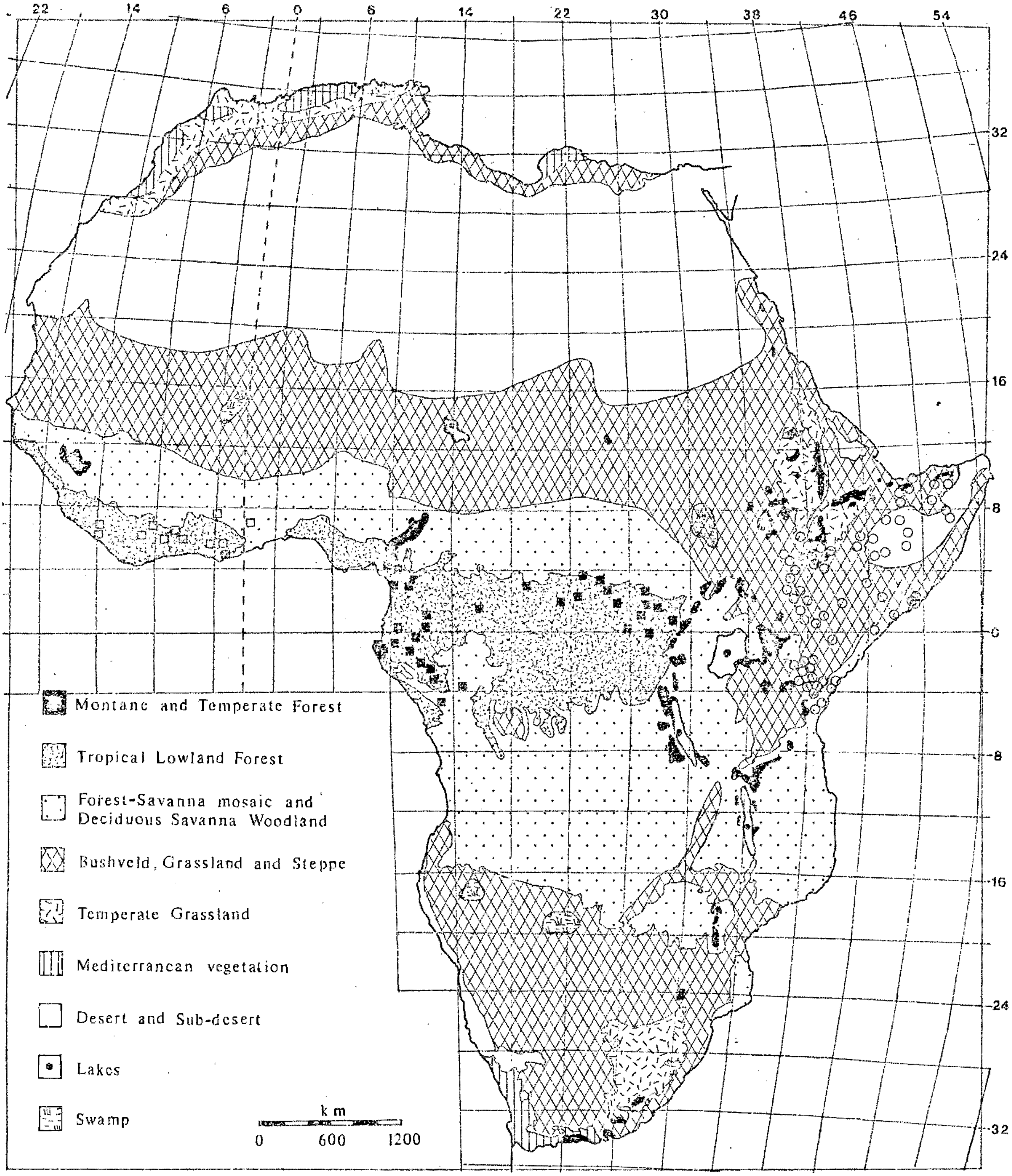

Fig. 9. The distributions of *Agelastes meleagrides* (□), *Agelastes niger* (▣), and *Acryllium vulturinum* (○).

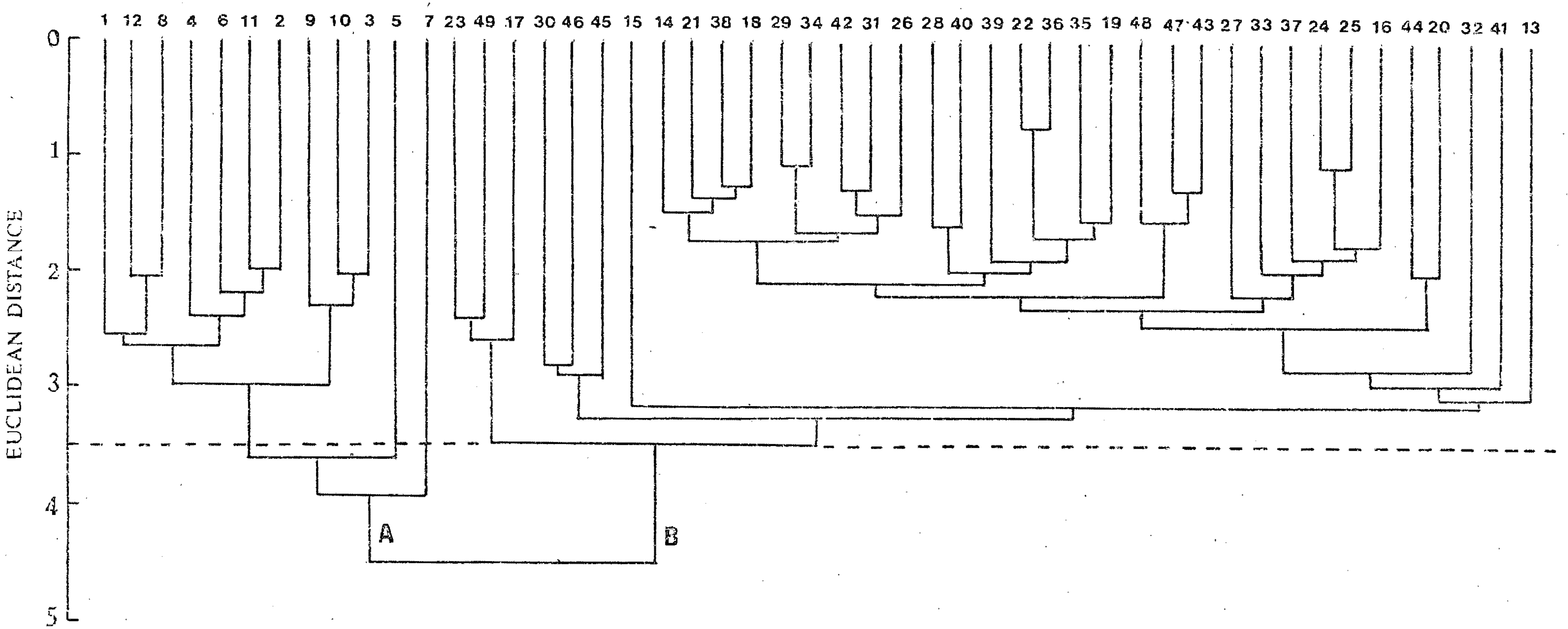

Fig. 10. The results of a cluster analysis of 49 specimens of *Agelastes*.
A. *A. meleagrides*. B. *A. niger*.

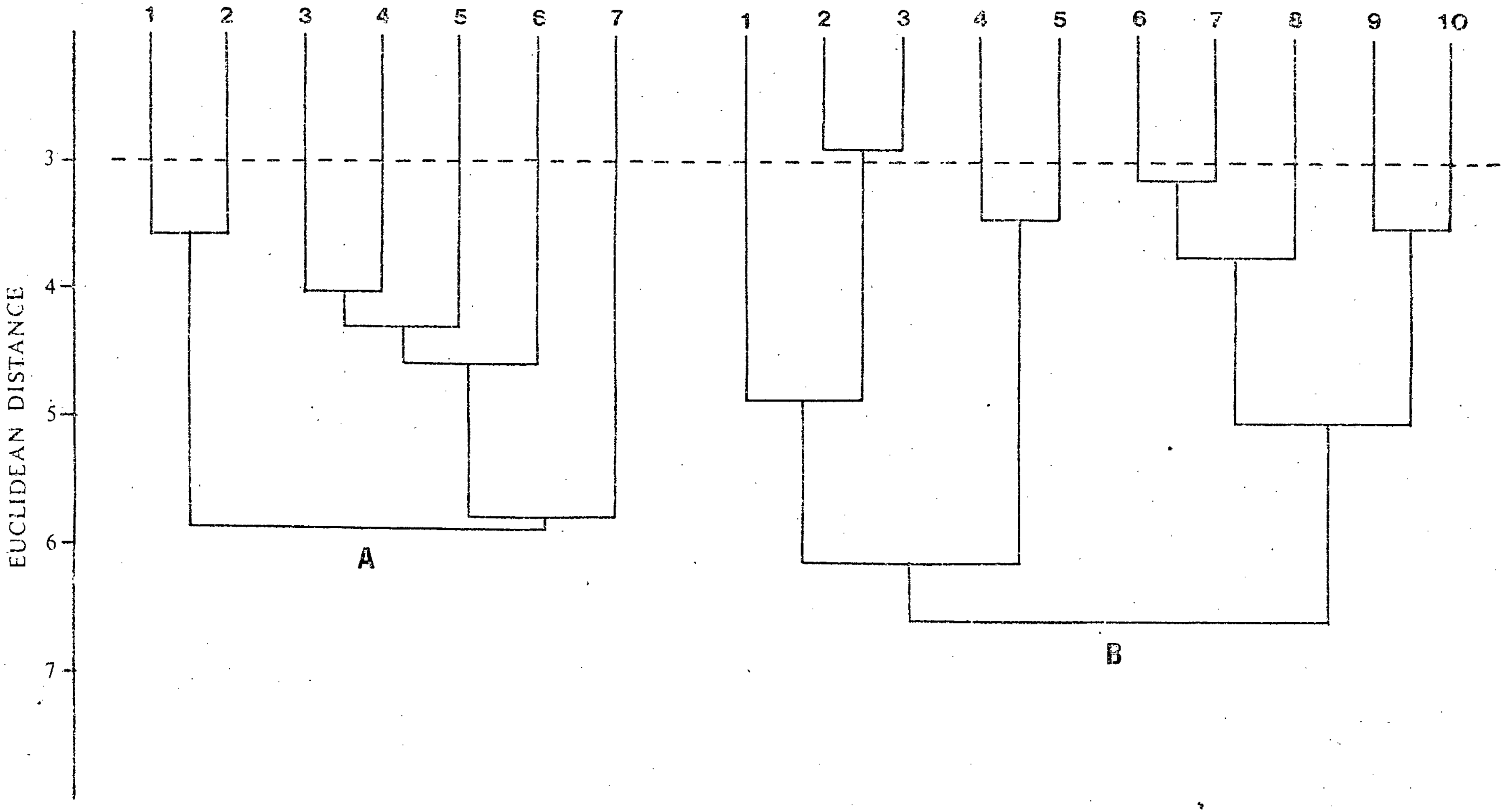

Fig. 11. The results of a cluster analysis. A. *Guttera* specimens B. *Numida* specimens.

A discriminant functions analysis (Fig. 12) suggests that there are two groups of OTUs between which there are no intermediate individuals. These OTU groups are recognized as species. The first species, comprising OTUs 1 and 2, corresponds to G. plumifera in Table 1. The second species, comprising OTUs 3-7, corresponds to two commonly recognized species, G. pucherani (Hartlaub), 1860, and G. edouardi (Hartlaub), 1867 (Table 1). Following the law of priority, this species must be named G. pucherani.

The two OTUs comprising Guttera plumifera partition the distribution of that species into eastern and western portions. The distributions of these OTUs (Fig. 13) are delineated by patterns of variation in 15 of the 16 quantitative characters which vary in G. plumifera. Contour maps of variation in these characters, and of the total COV for six areas (Fig. 14) within the distribution of G. plumifera are given in Figures 15 and 16. Two types of character variation, "mountain-valley" and clinal variation, are apparent in these contour maps. "Mountain-valley" variation occurs when eastern and western OTUs have similar values, and are separated by a transition area(s) with higher ("mountains") or lower ("valleys") values. Characters which show "mountain-valley" variation are: bill length (Fig. 15B), wing length (Fig. 15C), tarso-metatarsus length (Fig. 15D), wattle length (Fig. 15F), crest frontal length (Fig. 15G), crest basal length (Fig. 16J), dorsal spot number (Fig. 16K), total spot barbs (Fig. 16M), and total within-spot barbs (Fig. 16N). Characters which show clinal variation

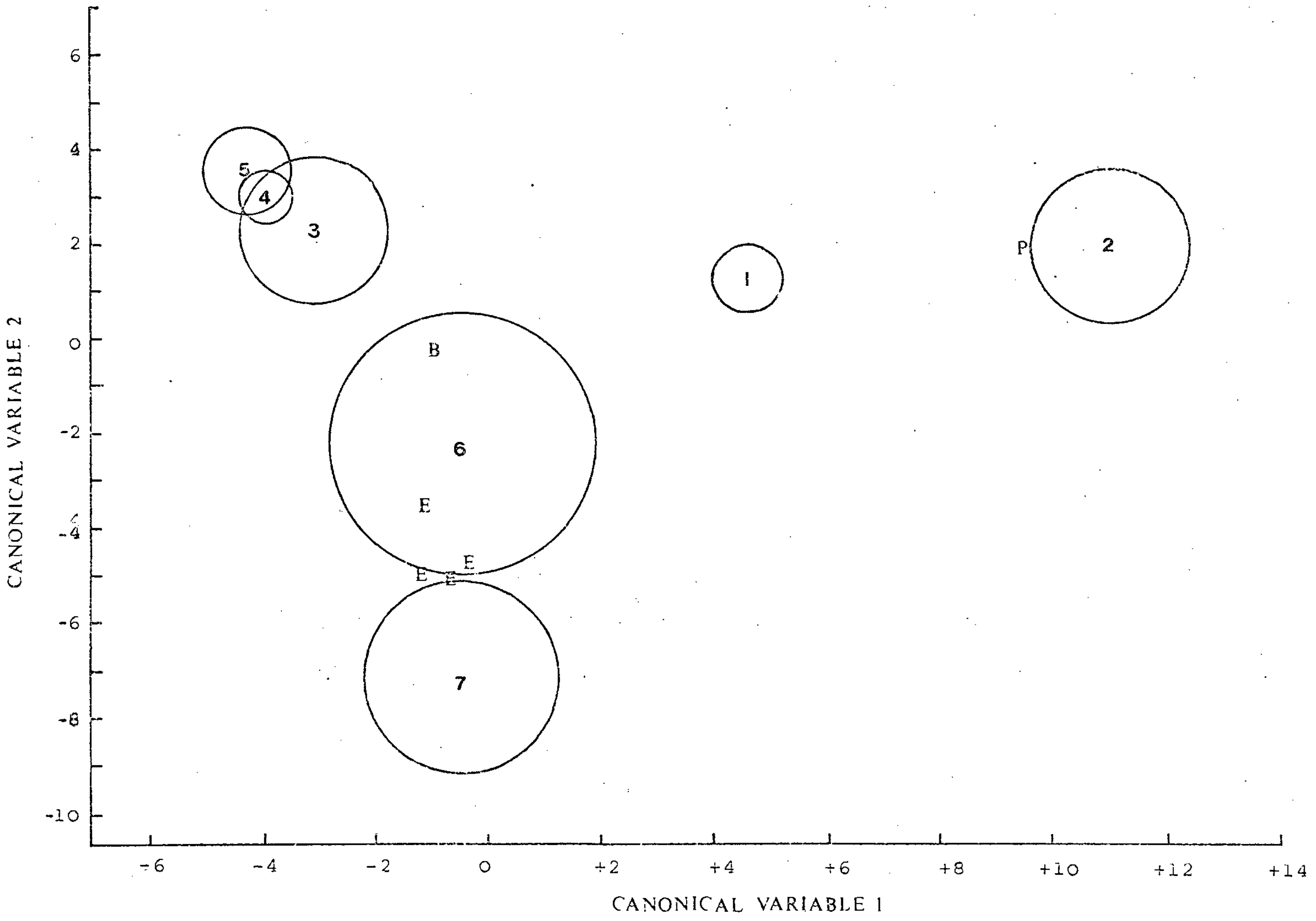

Fig. 12. A discriminant functions analysis of <u>Guttera</u> OTUs. Circles encompass 90% of the individuals assigned to each OTU. Only intermediate specimens between non-overlapping OTUs are plotted. B = intermediate between OTUs 5 and 6; E = intermediate between OTUs 6 and 7; P = intermediate between OTUs 1 and 2.

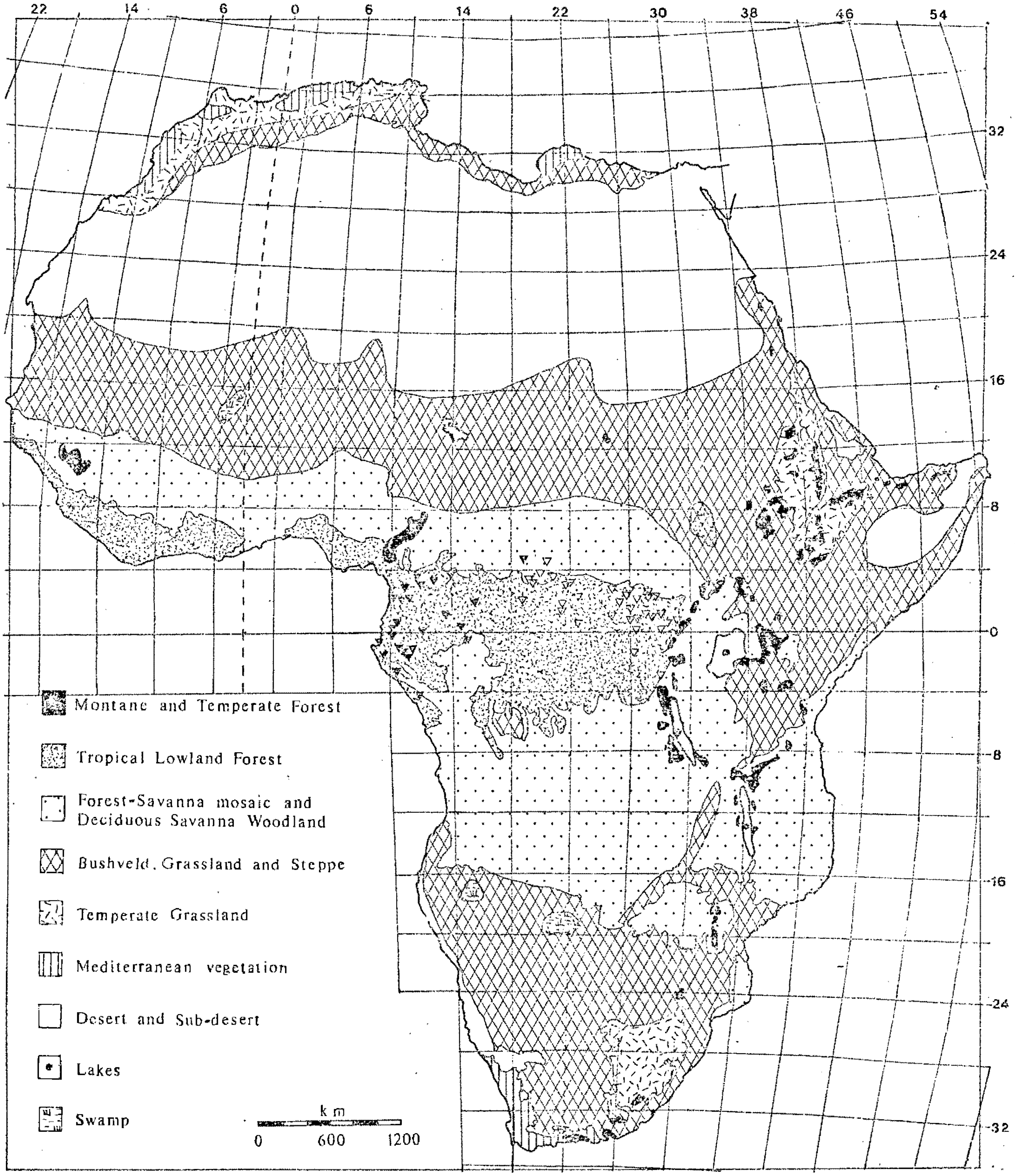

Fig. 13. The distribution of *Guttera plumifera plumifera* (▼) (=OTU 2) and *G. p. schubotzi* (▽)(=OTU 1).

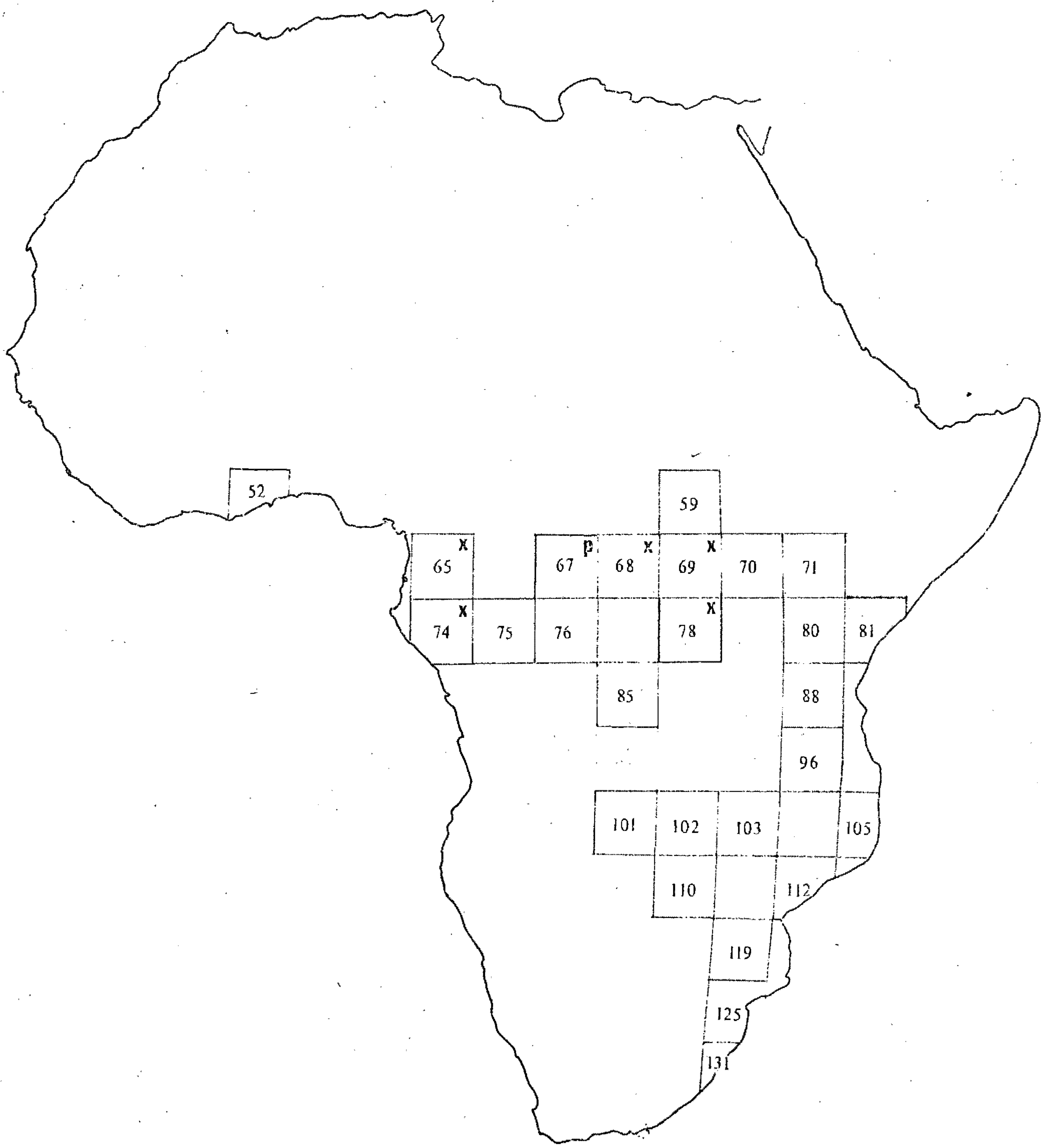

Fig. 14. Areas used in contour map analysis of Guttera spp. Those areas marked with an "X" have data for both species. Those marked with a "P" have data for G. plumifera only, and those without notation for G. pucherani only.

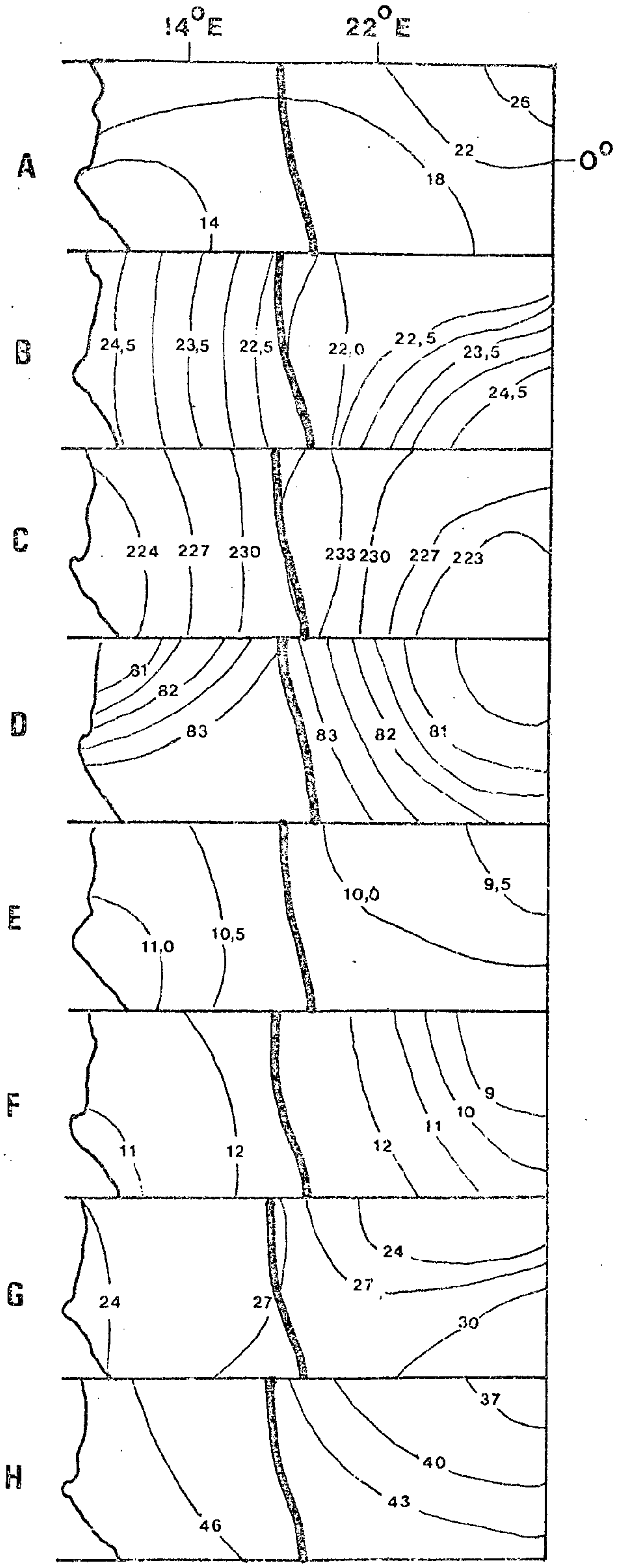

Fig. 15. Contour maps of character variation in Guttera plumifera A. Occipital fold. B. Bill length. C. Wing length. D. Tarso-metatarsus length. E. Wattle width. F. Wattle length. G. Crest frontal length. H. Crest rear length. OTU boundaries are indicated by thick lines.

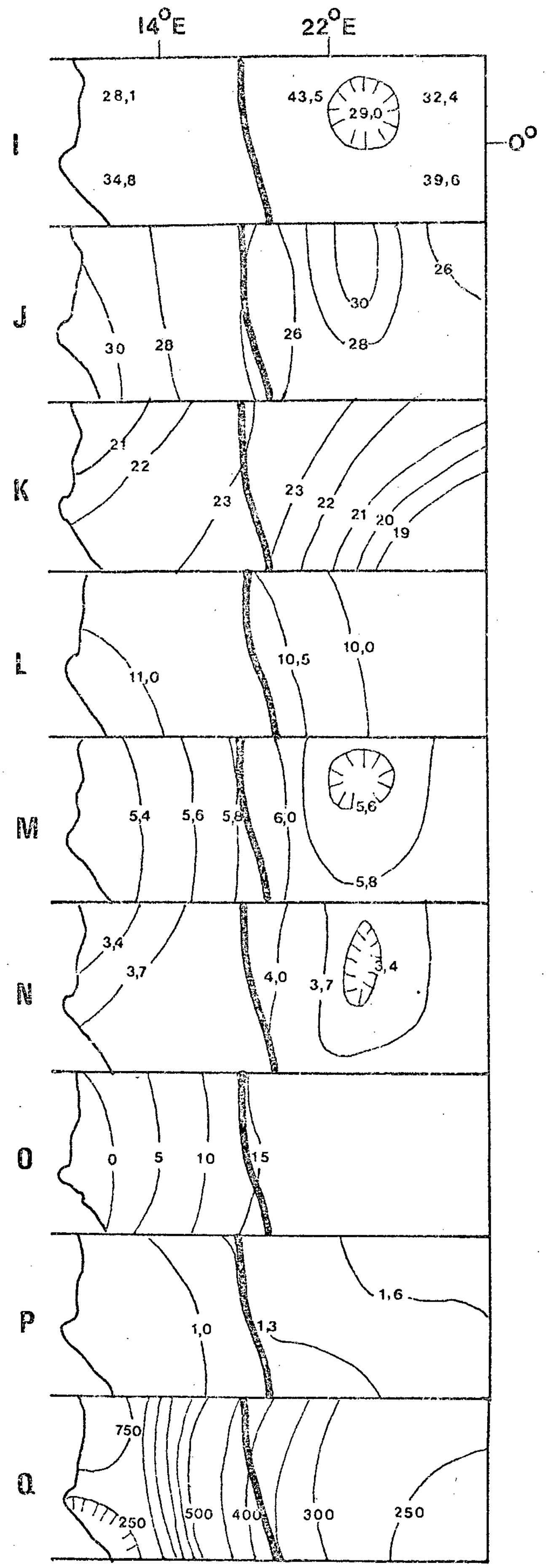

Fig. 16. Contour maps of character variation and total COV for Guttera plumifera. I. Crest central height. J. Crest basal height. K. Dorsal spot number. L. Dorsal spot size. M. Total spot barbs. N. Total within spot barbs. O. Ear patch. P. Spot barb blueness. Q. Total COV. OTU boundaries are indicated by thick lines.

are: occipital fold (Fig. 15A), wattle basal width (Fig. 15E), crest rear length (Fig. 15H), dorsal spot size (Fig. 16L), ear patch (Fig. 16O), and spot barb blueness (Fig. 16P). These well-defined OTUs each have a region of relatively low total COV (*ca* 250) within their distributions, and are separated by a transition area with a relatively high total COV (*ca* 750) (Fig. 16Q). Thus, both OTUs meet the criteria set for subspecies (see *Taxonomic methodology*). In Table 1, the western subspecies (OTU 2) corresponds to *G.p. plumifera*, and the eastern subspecies (OTU 1) to *G.p. schubotzi*. In statistical comparisons, these subspecies differ significantly ($P \leq 0,05$; *t* test) in eight characters. *Guttera plumifera plumifera* has significantly higher values for bill length, wattle basal width, wattle length, crest rear length, and crest basal length. *Guttera plumifera schubotzi* has higher values for occipital fold, ear patch, and spot barb blueness. Means and standard deviations for these and other characters are given in section (c).

Approximate geographic distributions of the five OTUs comprising *G. pucherani* are shown in Figure 17A. Contour maps of 23 characters which vary in this species (nos. 1-5, 22-31, 33-40 in Appendix 2) are given in Figures 18-29A. In these maps, the distributions of all five OTUs are delineated from those of their neighbours by statistically significant patterns of variation in 6 to 17 of the characters analyzed. The results of all possible pairwise statistical comparisons (*t* tests) between neighbouring OTUs are summarized in Tables 4 and 5. A contour map of variation

Table 4

A comparison of OTU 3 for *G. pucherani* with OTUs 4, 5 and 7. X = not significantly different ($P \leq 0,05$; *t* test); + = OTU 3 significantly greater; − = OTU 3 significantly lower; * = differences delineate OTUs in contour maps.

Character name[1]	OTU 4	 5	 7	Contour map Figure no.
Bill length	−*	−*	−*	18A
Wing length	X	−*	−*	18B
Tarso-metatarsus length	X	X	+	19A
Wattle basal width	−*	X	−*	19B
Wattle length	+*	X	+*	20A
Dorsal spot size	−*	−*	−*	20B
Crest frontal length	+*	+*	−*	21A
Crest rear length	X	+*	X	21B
Crest central height	+*	X	X	22A
Crest basal length	X	−*	−	22B
Anterior crest curliness	X	X	−*	23A
Posterior crest curliness	X	X	−*	23B
Dorsal black collar	X	+*	−*	24A
Ventral black collar	+	+*	−*	24B
Occipital fold	−	−*	−*	25A
Throat red	X	−*	+*	25B
Orbital red	X	−*	X	26A
Dorsal spot number	+	X	X	26B
Total spot barbs	X	−*	+*	27A
Total within spot barbs	X	−	+*	27B
Spot barb blueness	+	+*	+*	28A
Chestnut blotch size	X	X	−*	28B
Chestnut blotch extent	X	X	−*	29A

---

[1] see Appendix 2 for character descriptions

Table 5

A comparison of OTU 6 for *G. pucherani* with OTUs 5 and 7. X = not significantly different ($P \leq 0,05$; *t* test); + = OTU 6 significantly greater; – = OTU 6 significantly lower; * = differences delineate OTUs in contour maps.

Character name[1]	OTU 5	OTU 7	Contour map Figure no.
Bill length	X	X	18A
Wing length	X	+*	18B
Tarso-metatarsus length	X	+*	19A
Wattle basal width	X	–*	19B
Wattle length	X	+*	20A
Dorsal spot size	X	+*	20B
Crest frontal length	+*	X	21A
Crest rear length	+*	–*	21B
Crest central height	X	X	22A
Crest basal length	X	+*	22B
Anterior crest curliness	X	–*	23A
Posterior crest curliness	X	–*	23B
Dorsal black collar	+*	–*	24A
Ventral black collar	+*	–*	24B
Occipital fold	X	+*	25A
Throat red	–*	+	25B
Orbital red	–*	+	26A
Dorsal spot number	X	+*	26B
Total spot barbs	X	+	27A
Total within spot barbs	X	+*	27B
Spot barb blueness	–*	+	28A
Chestnut blotch size	+	–*	28B
Chestnut blotch extent	+	–*	29A

---

[1] see Appendix 2 for character descriptions

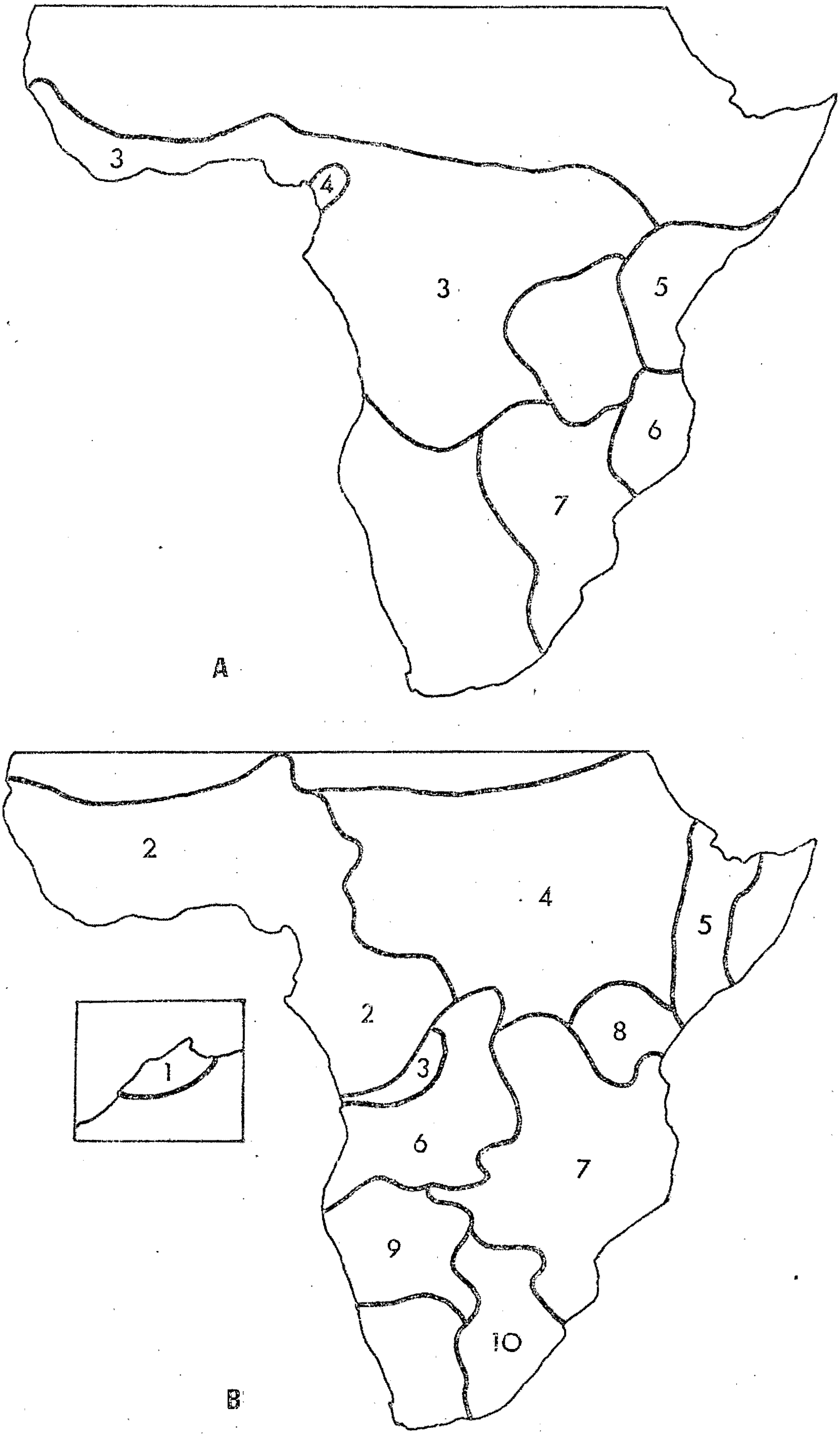

Fig. 17. The geographic distributions of OTUs comprising <u>Guttera</u> <u>pucherani</u> (A) and <u>Numida</u> <u>meleagris</u> (B).

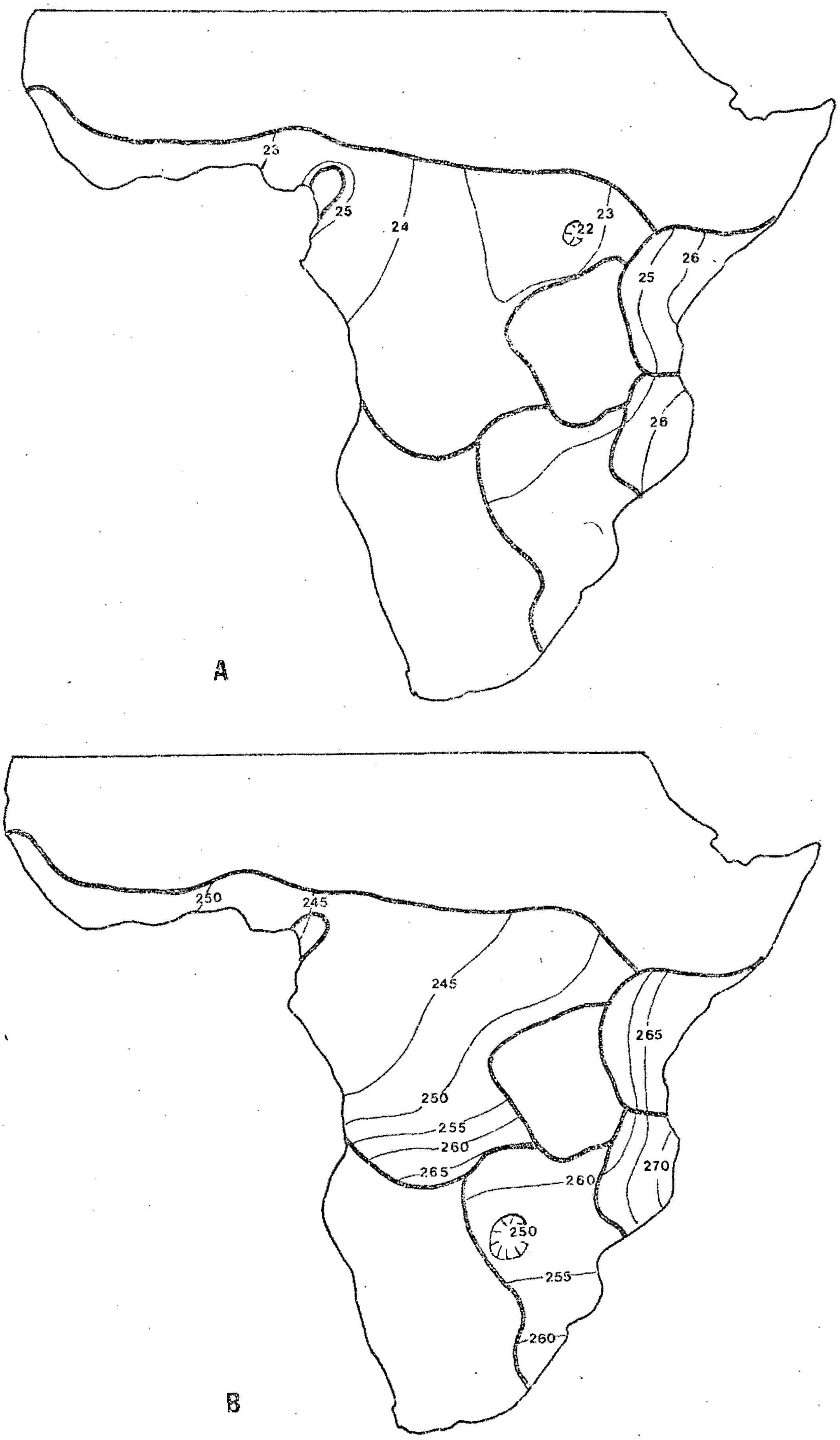

Fig. 18. Contour maps of bill length (A) and wing length (B) in *Guttera pucherani*. OTU boundaries are indicated by thick lines.

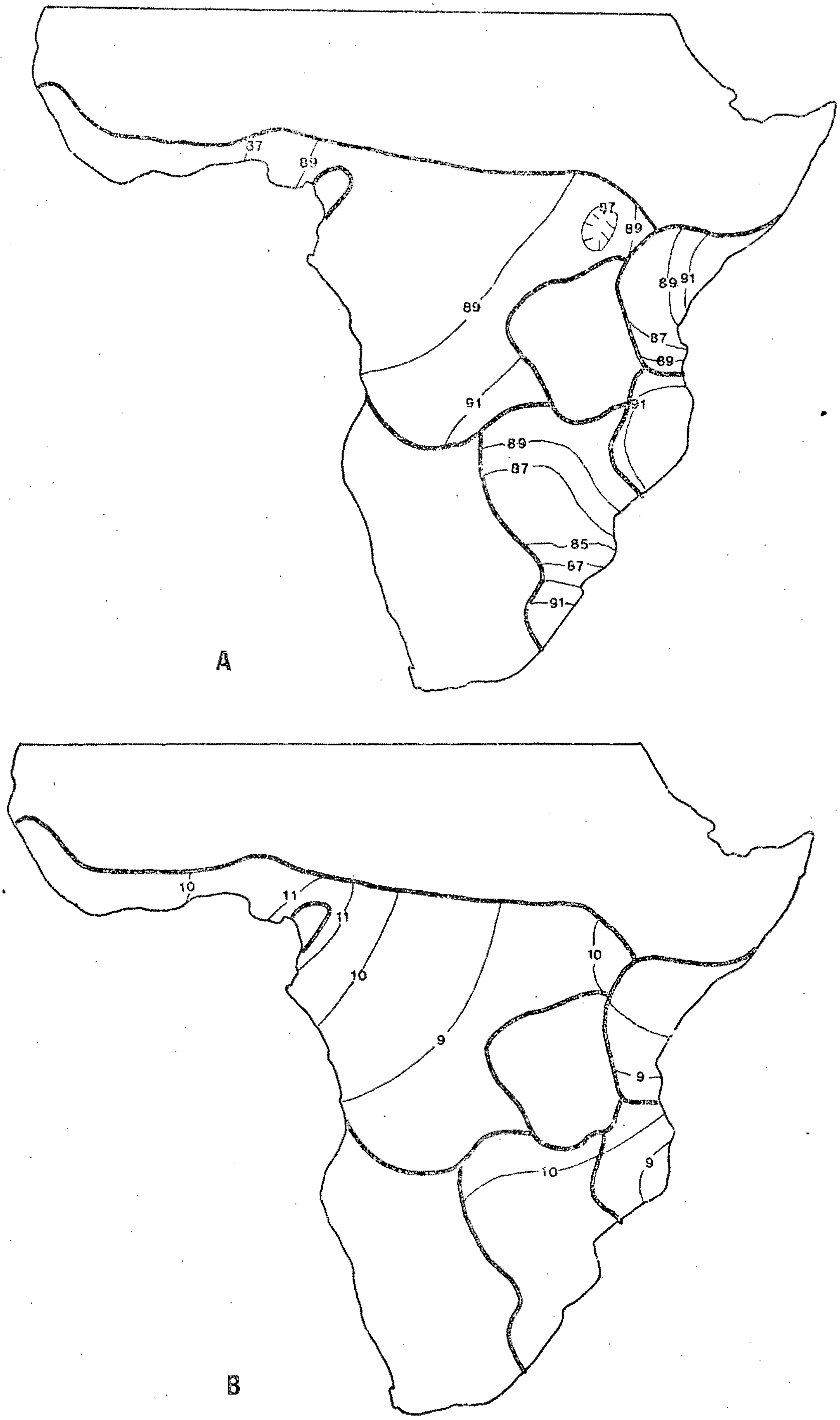

Fig. 19. Contour maps of tarso-metatarsus length (A) and wattle basal width (B) in *Guttera pucherani*. OTU boundaries are indicated by thick lines.

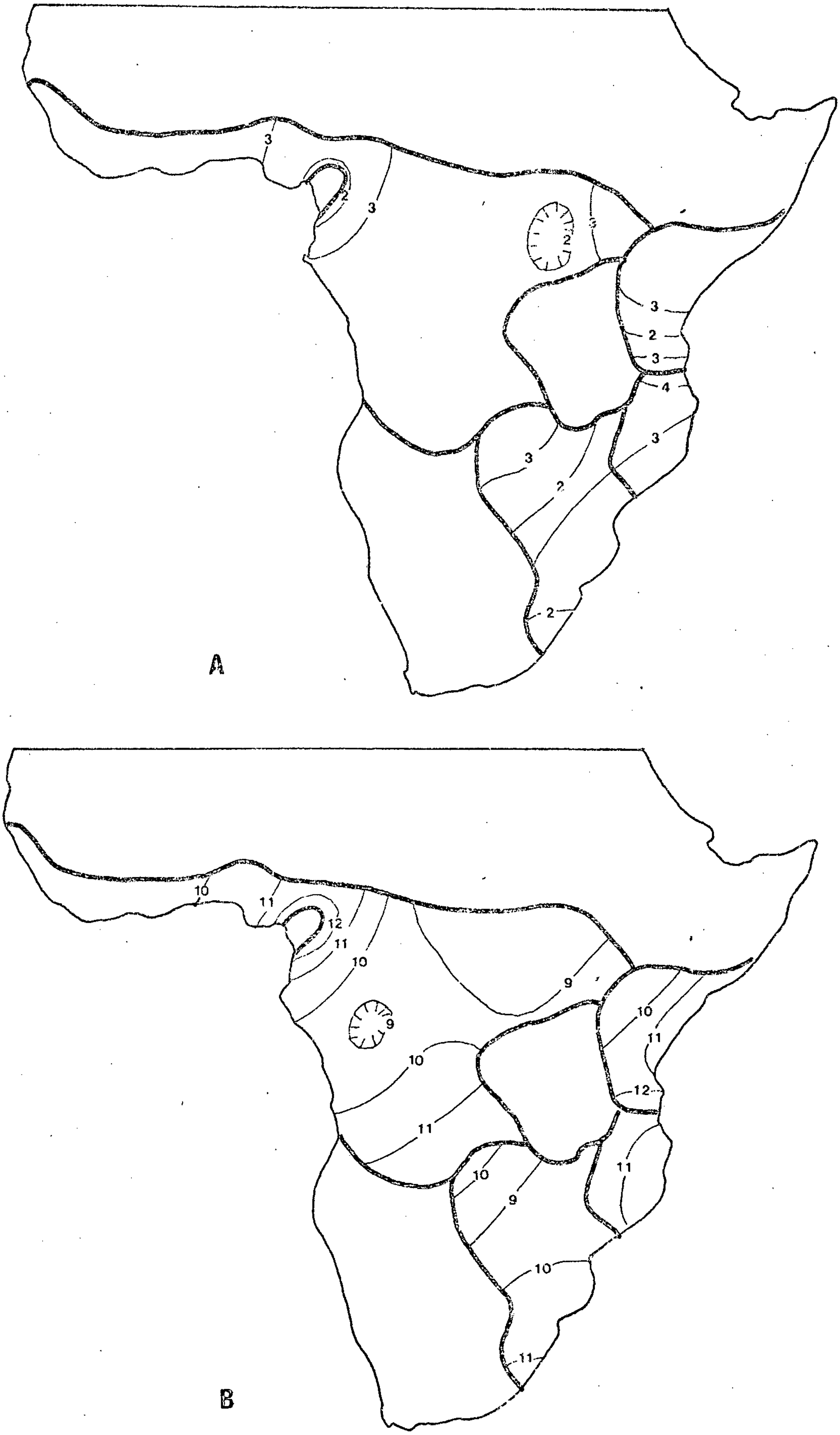

Fig. 20. Contour maps of wattle length (A) and dorsal spot size (B) in Guttera pucherani. OTU boundaries are indicated by thick lines.

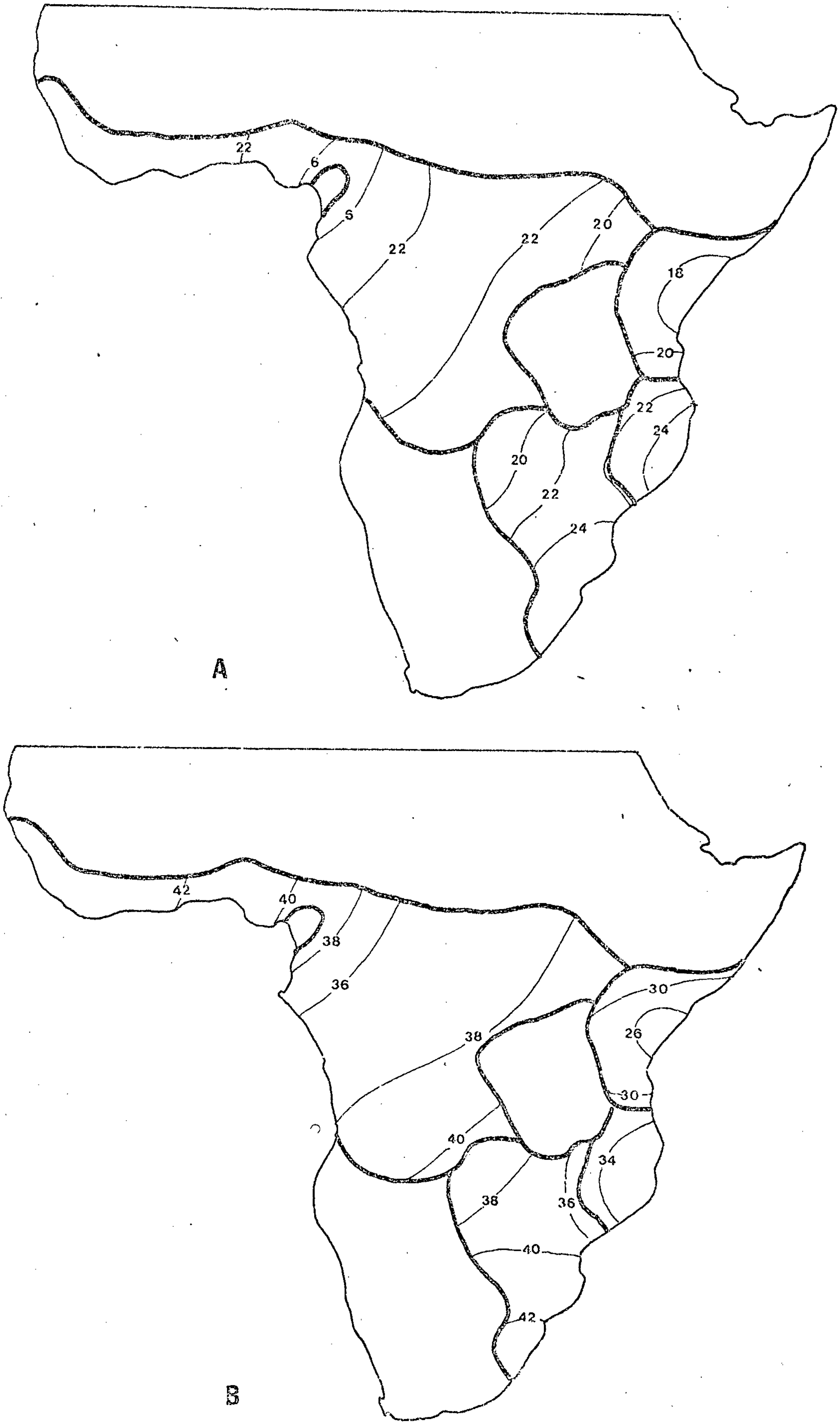

Fig. 21. Contour maps of crest frontal length (A) and crest rear length (B) in Guttera pucherani. OTU boundaries are indicated by thick lines.

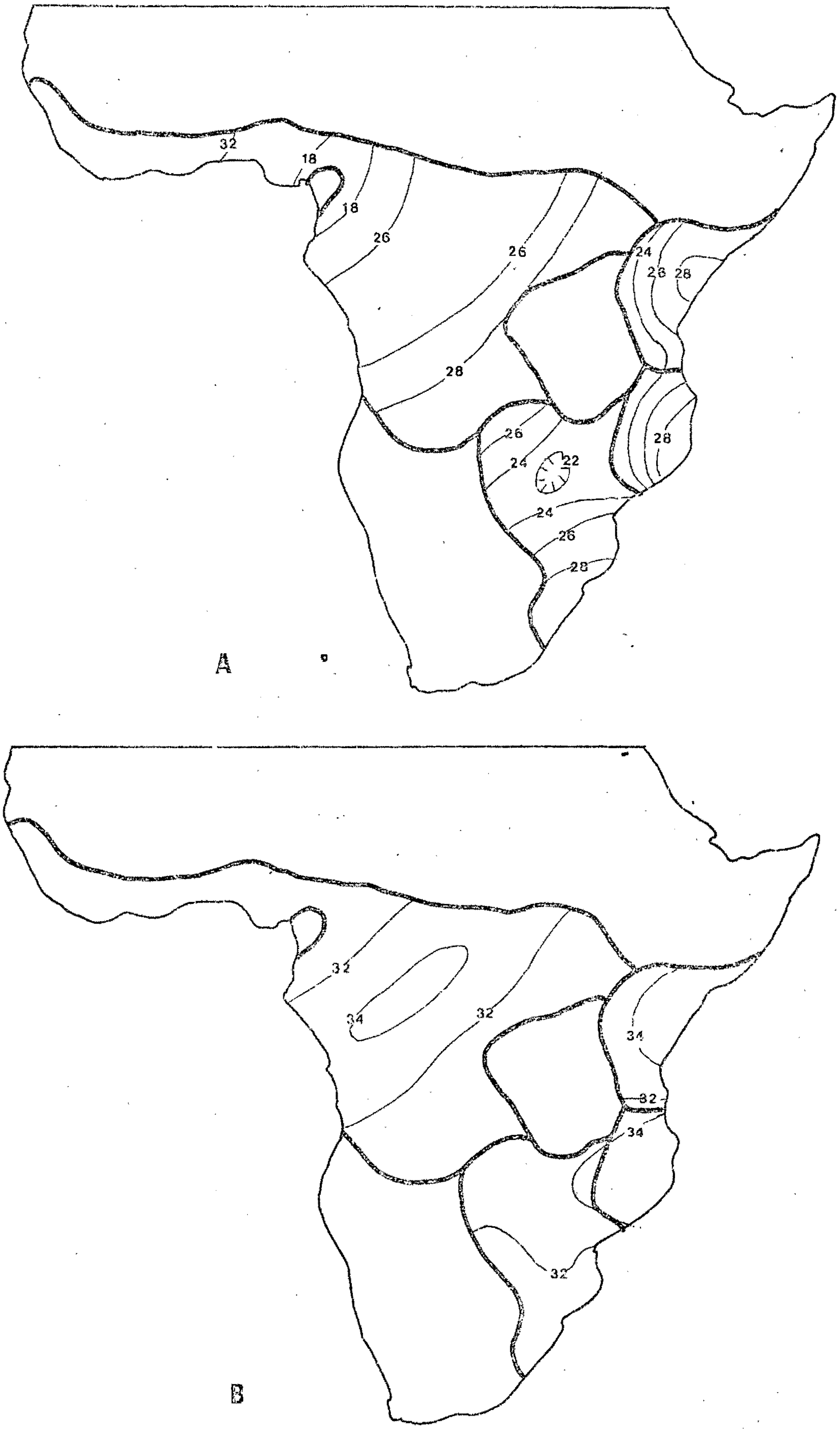

Fig. 22. Contour maps of crest central height (A) and crest basal length (B) in Guttera pucherani. OTU boundaries are indicated by thick lines.

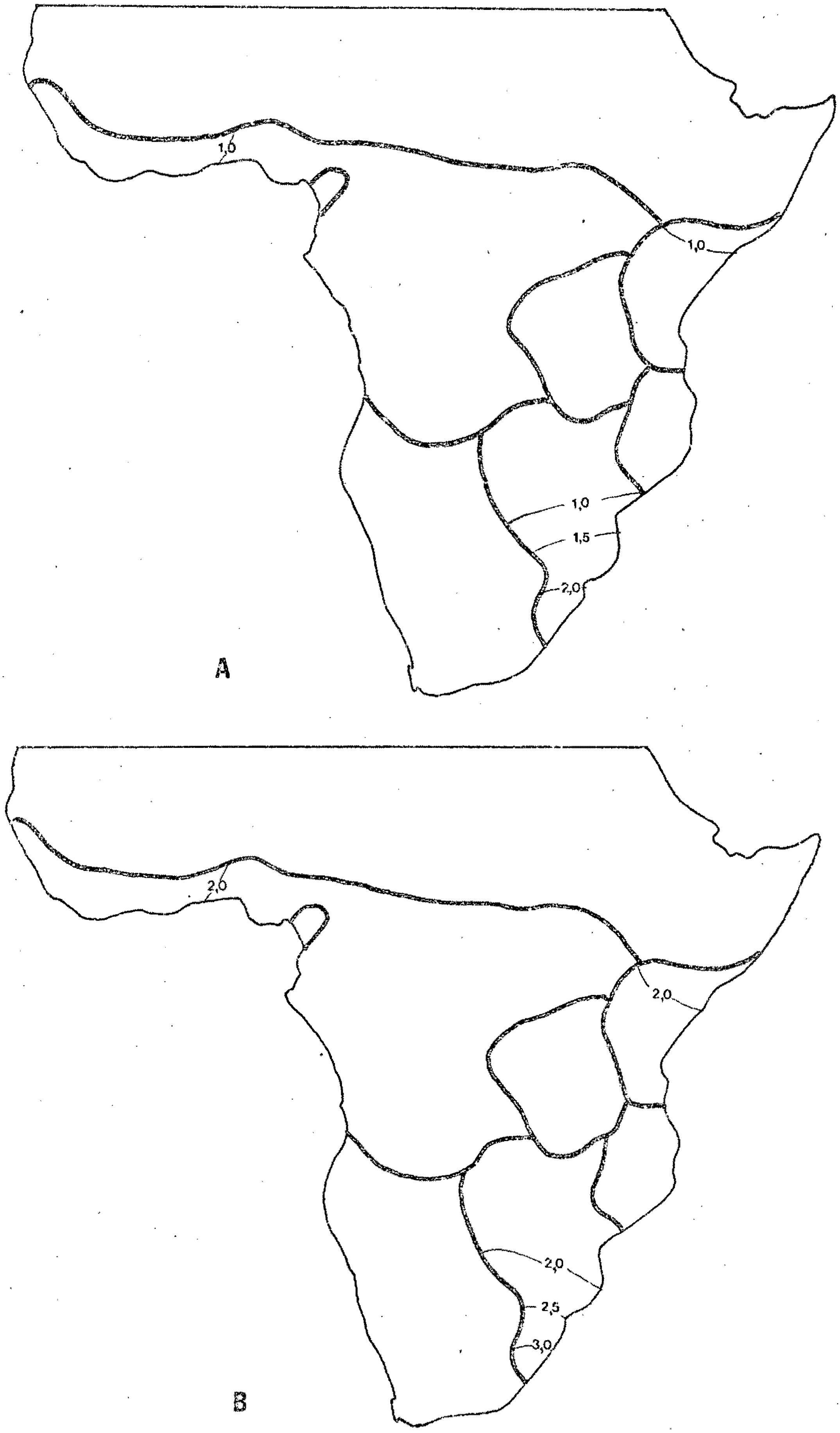

Fig. 23. Contour maps of anterior crest curliness (A) and posterior crest curliness (B) in _Guttera pucherani_. OTU boundaries are indicated by thick lines.

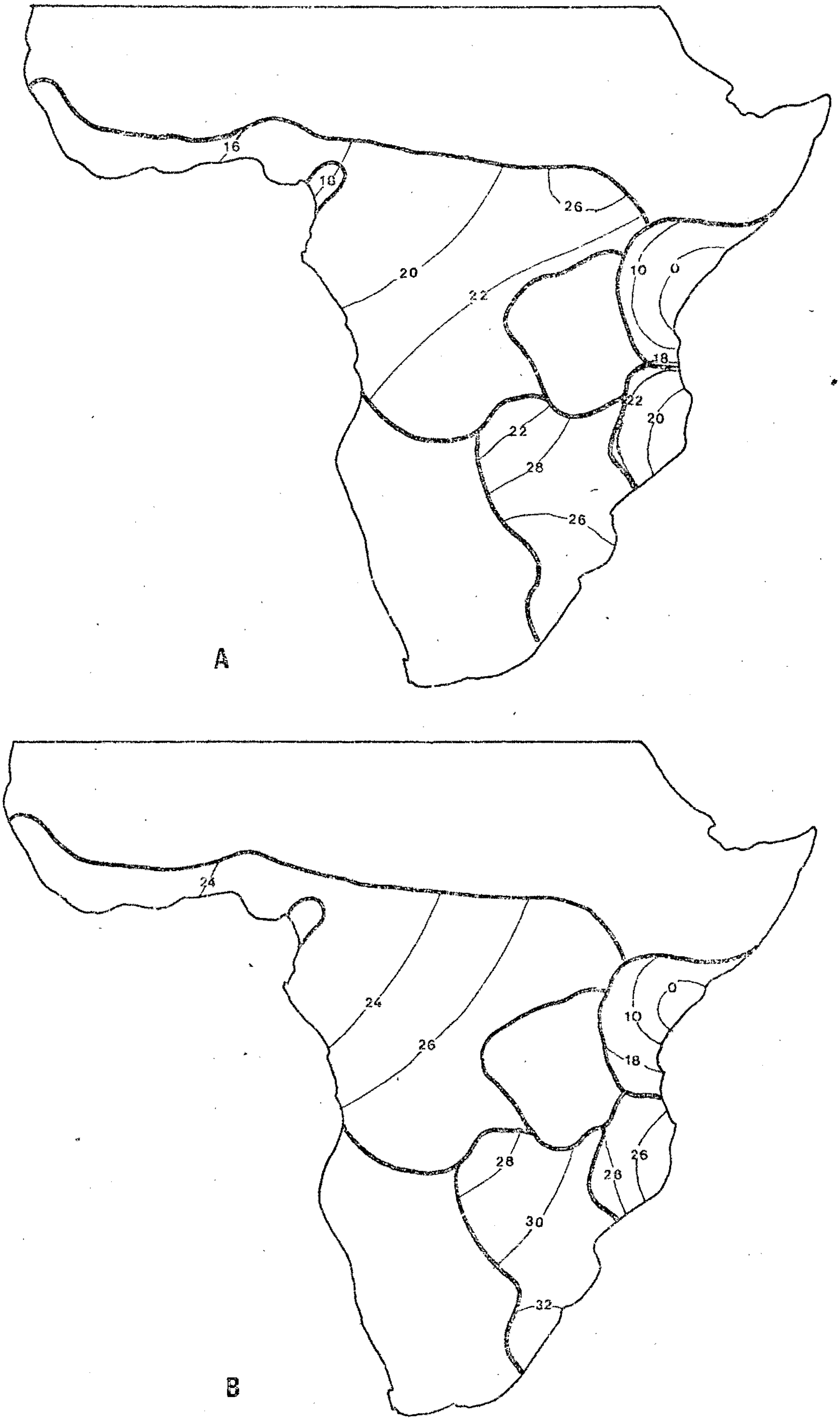

Fig. 24. Contour maps of dorsal black collar (A) and ventral black collar (B) in Guttera pucherani. OTU boundaries are indicated by thick lines.

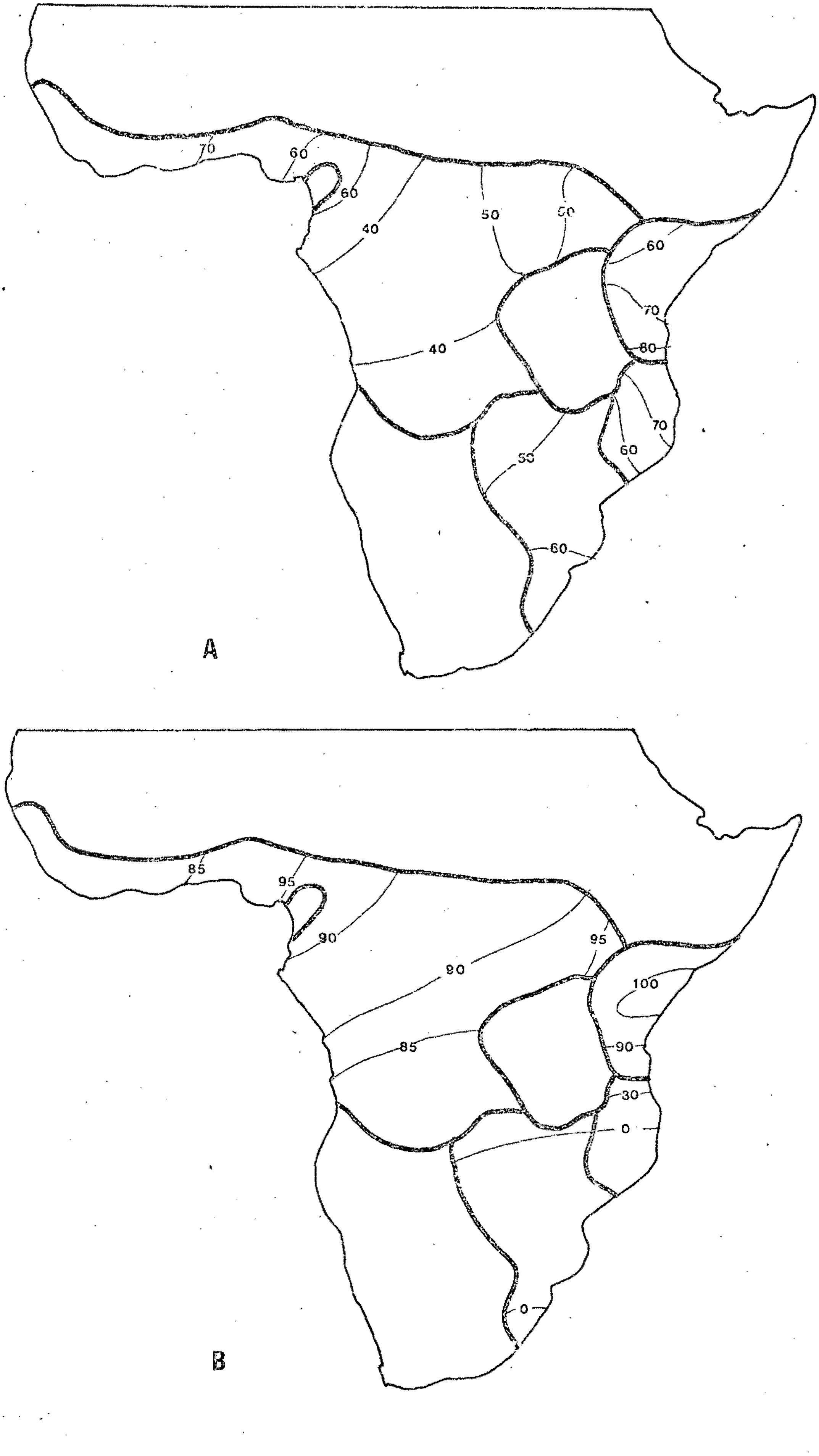

Fig. 25. Contour maps of occipital fold (A) and throat red (B) in Guttera pucherani. OTU boundaries are indicated by thick lines.

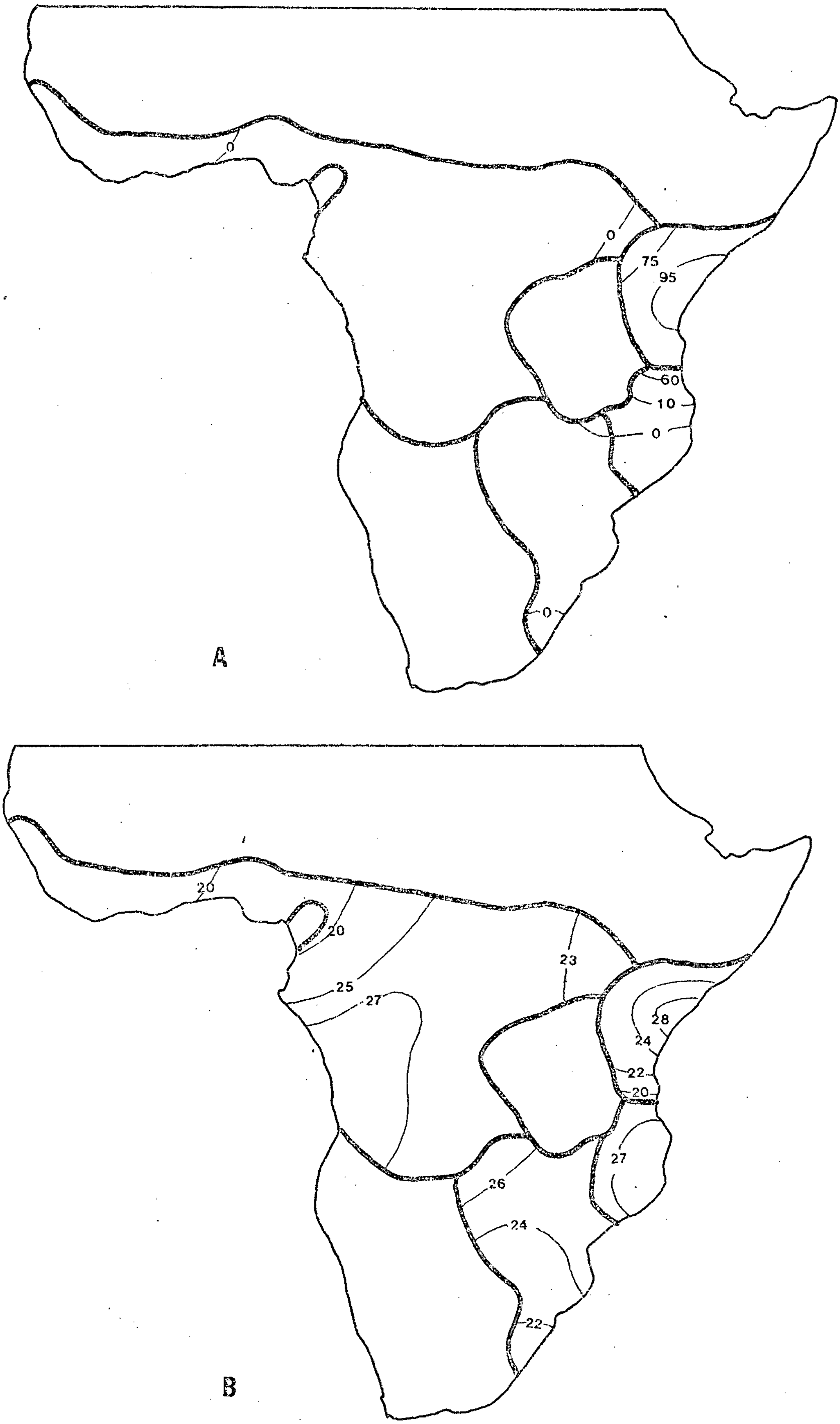

Fig. 26. Contour maps of orbital red (A) and dorsal spot number (B) in Guttera pucherani. OTU boundaries are indicated by thick lines.

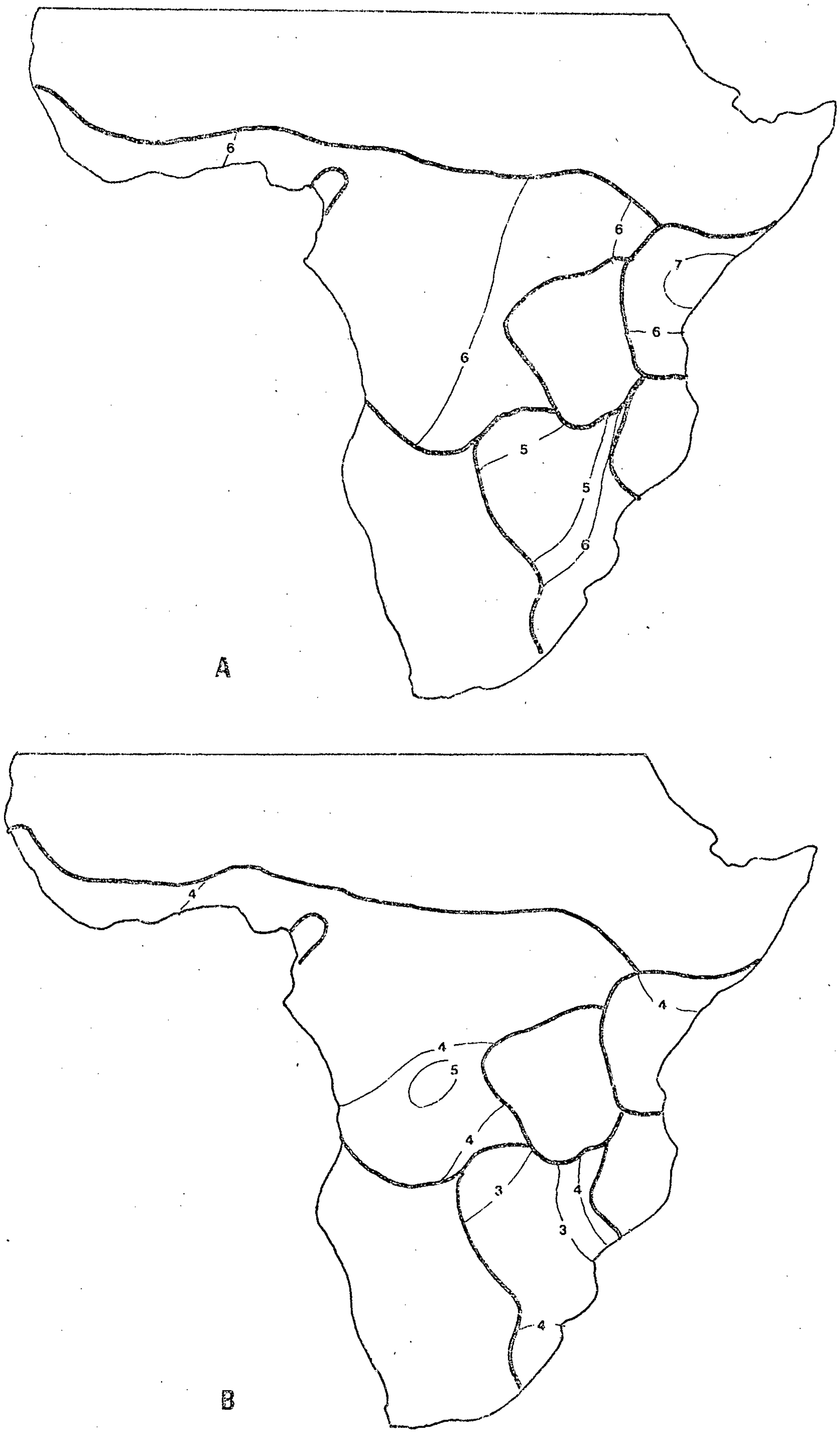

Fig. 27. Contour maps of total spot barbs (A) and total within spot barbs (B) in <u>Guttera pucherani</u>. OTU boundaries are indicated by thick lines.

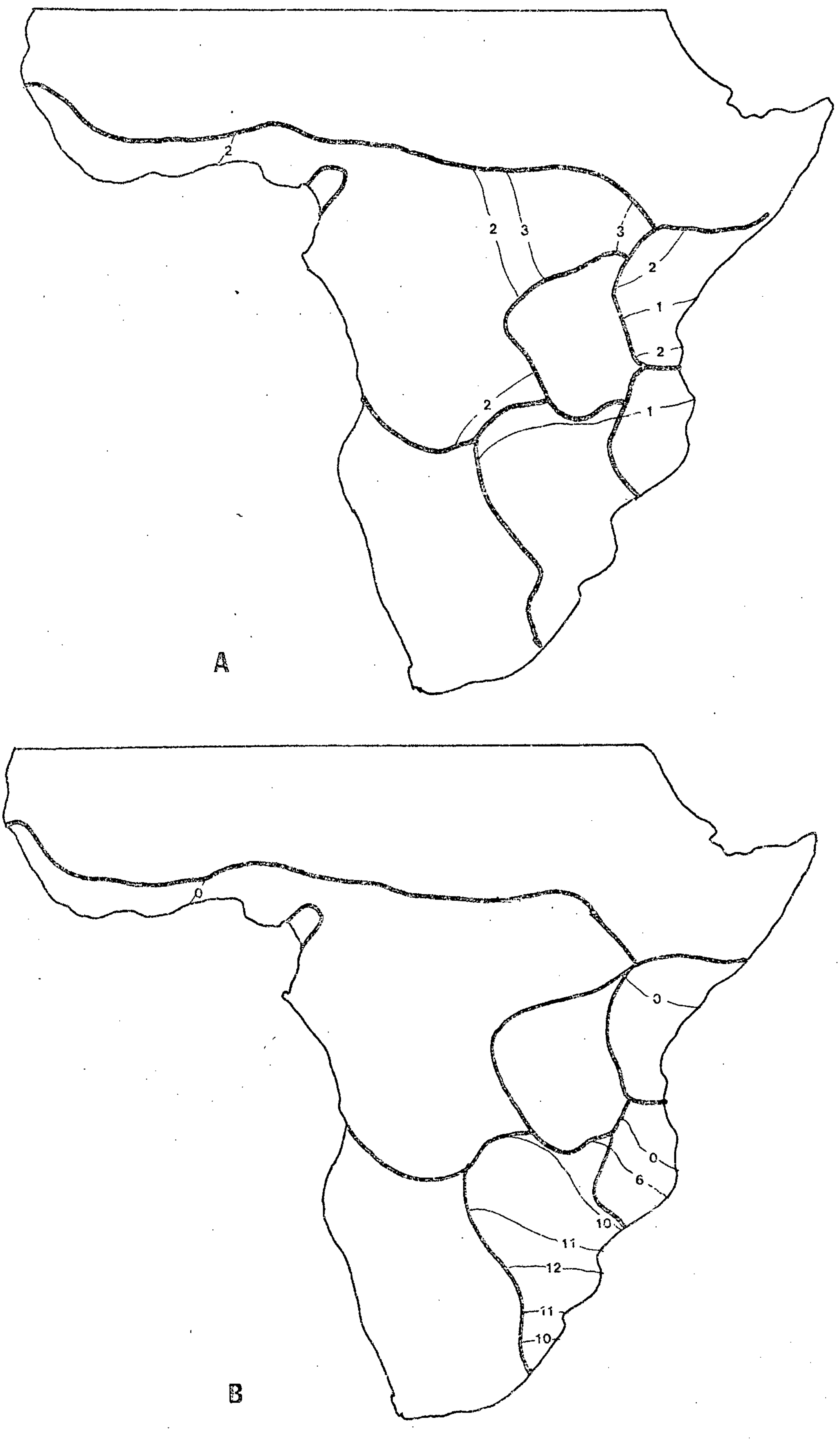

Fig. 28. Contour maps of spot barb blueness (A) and chestnut blotch size (B) in Guttera pucherani. OTU boundaries are indicated by thick lines.

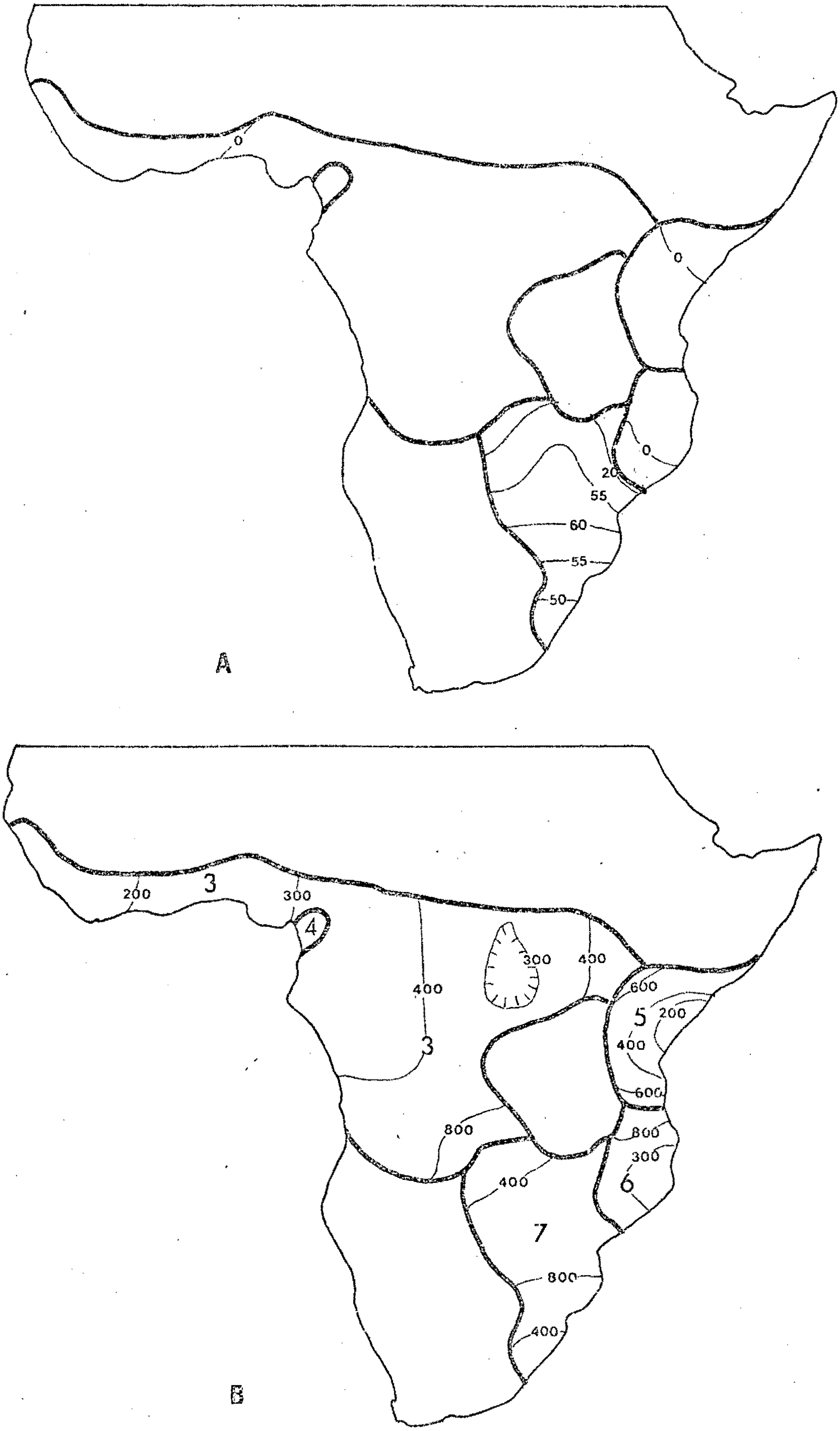

Fig. 29. Contour maps of chestnut blotch extent (A) and total COV (B) in Guttera pucherani. OTU boundaries are indicated by thick lines. Larger numbers in (B) refer to OTU numbers shown in Figure 17A.

in total COV for 24 areas (Fig. 14) within the distribution of G. pucherani is given in Figure 29B. This figure shows that the distributions of all five OTUs enclose or fall within a region of relatively low total COV (200-400). For all OTU distributions but one, that of OTU 4, the region of relatively low total COV is bordered by a region(s) of relatively high total COV (e.g. 600-800). Thus, all OTUs ascribed to G. pucherani satisfy the criteria specified for subspecies (see Taxonomic methodology). The lack of a high total COV interface between the low COV regions of OTUs 3 and 4 is attributed to poor sampling and the small geographic distribution of OTU 4. Assuming that G. edouardi is a synonym of G. pucherani in Table 1, and following the law of priority, OTU 3 corresponds to G. p. verreauxi, OTU 4 to G.p. sclateri, OTU 5 to G.p. pucherani, OTU 6 to G.p. barbata , and OTU 7 to G.p. edouardi. The geographic distributions of these subspecies, and of intermediate populations are shown in Figure 30.

The results of a cluster analysis of 704 Numida specimens according to characters 1-22 in Appendix 2 are summarized in Figure 11B. Nine well-defined, and one borderline OTU are recognized. The dashed line indicates the level at which eight individuals from the vicinity of Gassam (14°50'N/15°20'W), Senegal, link to form a cluster. Only 704 specimens could be analysed in this cluster analysis due to computer storage limitations. However, those specimens analyzed were chosen so as to ensure uniform sampling of the sexes and collection localities. A

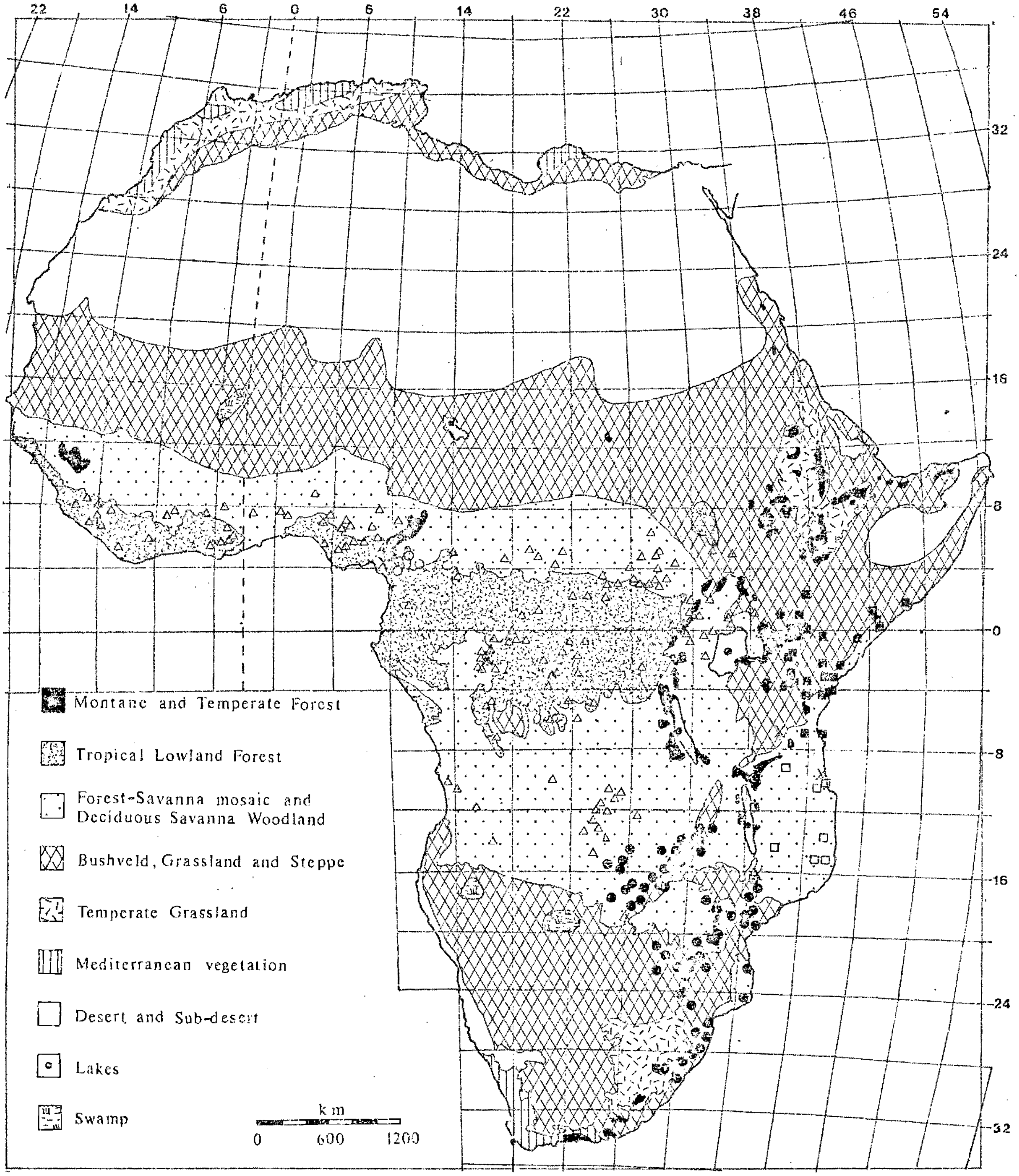

Fig. 30. The distributions of *Guttera pucherani* subspecies. *G. p. pucherani* (■). *G. p. verreauxi* (△). *G. p. sclateri* (○). *G. p. barbata* (□). *G. p. edouardi* (●). Intergrades (X).

discriminant functions analysis including all 1245 Numida specimens (Fig. 31) reveals intermediate individuals between all parapatric OTUs. Therefore only one species is recognized. Following the law of priority, this species is named Numida meleagris.

The approximate geographic distributions of the 10 OTUs comprising N. meleagris are shown in Figure 17B. Contour maps of variation in 22 quantitative characters analyzed for this species (nos. 1-22 in Appendix 2), and of the total COV for 48 areas (Fig. 32) are given in Figures 33-43. In these contour maps, the distributions of all 10 OTUs but one, that of OTU 3, are delineated from those of their neighbours by statistically significant patterns of variation in 9-17 of the 22 characters analyzed (Tables 6-11). Results of all possible pairwise statistical comparisons (t tests) between neighbouring OTUs are summarized in Tables 6-11. The distribution of OTU 3, the borderline OTU in Figure 11B, is delineated from those of its neighbours (OTUs 2 and 6) by at most two characters (Tables 7 and 9). In the contour map of total COV (Fig. 44), the distribution of all OTUs, except again OTU 3, enclose a region of relatively low total COV (ca 400-500) bordered by a region(s) of relatively high total COV (ca 700-1000). Thus, all OTUs ascribed to N. meleagris, except OTU 3, satisfy the criteria set for subspecies (see Taxonomic methodology). In Table 1, following the law of priority, OTU 1 corresponds to N.m. sabyi, OTU 2 to N.m. galeata, OTU 4 to N.m. meleagris, OTU 5 to N.m. somalienses, OTU 6 to N.m. marungensis, OTU 7

Table 6

A comparison of OTU 4 for *N. meleagris* with OTUs 2, 5, 6, 7 and 8. X = not significantly different ($P \leq 0{,}05$; *t* test); + = OTU 4 significantly greater; – = OTU 4 significantly lower; * = differences delineate OTUs in contour maps.

Character name[1]	OTU 2	OTU 5	OTU 6	OTU 7	OTU 8	Contour map Figure no.
Bill length	$+^{*}$	X	$-^{*}$	–	X	33A
Wing length	+	X	$-^{*}$	$-^{*}$	$-^{*}$	33B
Tarso-metatarsus length	$+^{*}$	X	$-^{*}$	–	$-^{*}$	34A
Wattle basal width	X	X	$+^{*}$	$+^{*}$	$+^{*}$	34B
Wattle length	–	$-^{*}$	$-^{*}$	$-^{*}$	+	35A
Wattle percent blue	$+^{*}$	$+^{*}$	$+^{*}$	$+^{*}$	$+^{*}$	35B
Helmet frontal length	$+^{*}$	X	$-^{*}$	$-^{*}$	$-^{*}$	36A
Helmet rear length	$+^{*}$	X	–	–	$-^{*}$	36B
Helmet central height	$+^{*}$	X	–	$-^{*}$	$-^{*}$	37A
Helmet basal length	X	$+^{*}$	$-^{*}$	$-^{*}$	$-^{*}$	37B
Helmet thickness	$+^{*}$	X	$-^{*}$	$-^{*}$	–	38A
Cere structure length	$+^{*}$	$-^{*}$	$+^{*}$	$+^{*}$	+	38B
Cere structure thickness	$+^{*}$	X	$+^{*}$	$+^{*}$	$+^{*}$	39A
Collar plumage	$+^{*}$	X	X	–	X	39B
Nape filoplume length	$-^{*}$	$-^{*}$	$-^{*}$	$-^{*}$	$-^{*}$	40A
Nape filoplume antero-posterior coverage	$-^{*}$	$+^{*}$	$-^{*}$	X	X	40B
Nape filoplume lateral coverage	$+^{*}$	$+^{*}$	$+^{*}$	$+^{*}$	$+^{*}$	41A
Nape filoplume density	X	X	X	+	$+^{*}$	41B
Secondary remex outer web vermiculation	$+^{*}$	+	$+^{*}$	$+^{*}$	$+^{*}$	42A
Wing covert barring	$+^{*}$	$+^{*}$	$+^{*}$	$+^{*}$	$+^{*}$	42B
Dorsal vermiculation	$-^{*}$	+	$+^{*}$	$+^{*}$	+	43A
Dorsal spot size	$+^{*}$	$-^{*}$	–	X	$-^{*}$	43B

---

[1] see Appendix 2 for character descriptions

Table 7

A comparison of OTU 2 for *N. meleagris* with OTUs 1, 3 and 6. X = not significantly different ($P \leq 0,05$; *t* test); + = OTU 2 significantly greater; - = OTU 2 significantly lower; * = differences delineate OTUs in contour maps.

Character name[1]	OTUs 1	OTUs 3	OTUs 6	Contour map Figure no.
Bill length	X	-	-*	33A
Wing length	-*	-	-*	33B
Tarso-metatarsus length	-*	-	-*	34A
Wattle basal width	X	X	+*	34B
Wattle length	X	X	-	35A
Wattle percent blue	+*	-*	-*	35B
Helmet frontal length	-*	-	-*	36A
Helmet rear length	-*	-	-	36B
Helmet central height	-*	-	-	37A
Helmet basal length	X	-	-*	37B
Helmet thickness	X	-	-*	38A
Cere structure length	X	+	X	38B
Cere structure thickness	X	+	X	39A
Collar plumage	-*	-*	-*	39B
Nape filoplume length	-*	X	-*	40A
Nape filoplume antero-posterior coverage	X	X	+	40B
Nape filoplume lateral coverage	X	+	+	41A
Nape filoplume density	X	X	X	41B
Secondary remex outer web vermiculation	X	+	+	42A
Wing covert barring	+*	+	+*	42B
Dorsal vermiculation	+*	+	+*	43A
Dorsal spot size	+*	-	-	43B

---

[1] see Appendix 2 for character descriptions

Table 8

A comparison of OTU 8 for *N. meleagris* with OTUs 5 and 7. X = not significantly different; (*P* ≤ 0,05; *t* test); + = OTU 8 significantly greater; - = OTU 8 significantly lower; * = differences delineate OTUs in contour maps.

Character name[1]	OTUs		Contour map Figure no.
	5	7	
Bill length	X	-*	33A
Wing length	+*	+*	33B
Tarso-metatarsus length	+*	+*	34A
Wattle basal width	-	+	34B
Wattle length	-	-	35A
Wattle percent blue	-*	-*	35B
Helmet frontal length	+*	+*	36A
Helmet rear length	+*	+*	36B
Helmet central height	+*	+*	37A
Helmet basal length	+*	+*	37B
Helmet thickness	+	+	38A
Cere structure length	-*	+	38B
Cere structure thickness	-	+	39A
Collar plumage	X	-	39B
Nape filoplume length	+*	-*	40A
Nape filoplume antero-posterior coverage	+	X	40B
Nape filoplume lateral coverage	-	+	41A
Nape filoplume density	-*	X	41B
Secondary remex outer web vermiculation	-*	+*	42A
Wing covert barring	-	+	42B
Dorsal vermiculation	X	+	43A
Dorsal spot size	X	+	43B

[1] see Appendix 2 for character descriptions

Table 9

A comparison of OTU 6 for *N. meleagris* with OTUs 3, 7 and 9. X = not significantly different ($P \leq 0,05$; *t* test); + = OTU 6 significantly greater; - = OTU 6 significantly lower; * = differences delineate OTUs in contour maps.

Character name[1]	OTUs			Contour map Figure no.
	3	7	9	
Bill length	+	$+^*$	$+^*$	33A
Wing length	+	$+^*$	$+^*$	33B
Tarso-metatarsus length	X	$+^*$	$+^*$	34A
Wattle basal width	-	$+^*$	+	34B
Wattle length	+	X	-	35A
Wattle percent blue	$+^*$	$+^*$	+	35B
Helmet frontal length	+	$+^*$	$+^*$	36A
Helmet rear length	+	-	$-^*$	36B
Helmet central height	+	X	-	37A
Helmet basal length	+	+	+	37B
Helmet thickness	+	$+^*$	$+^*$	38A
Cere structure length	+	X	$-^*$	38B
Cere structure thickness	+	X	$-^*$	39A
Collar plumage	+	X	$-^*$	39B
Nape filoplume length	+	$+^*$	$+^*$	40A
Nape filoplume antero-posterior coverage	-	$+^*$	$+^*$	40B
Nape filoplume lateral coverage	-	+	$+^*$	41A
Nape filoplume density	X	$+^*$	$+^*$	41B
Secondary remex outer web vermiculation	-	-	$-^*$	42A
Wing covert barring	-	X	X	42B
Dorsal vermiculation	-	-	$-^*$	43A
Dorsal spot size	+	+	X	43B

---

[1] see Appendix 2 for character descriptions

Table 10

A comparison of OTU 10 for *N. meleagris* with OTUs 7 and 9, X = not significantly different ($P \leq 0{,}05$; *t* test); + = OTU 10 significantly greater; – = OTU 10 significantly lower; * = differences delineate OTUs in contour maps.

Character name[1]	OTUs 7	OTUs 9	Contour map Figure no.
Bill length	–	+	33A
Wing length	–	–	33B
Tarso-metatarsus length	X	+	34A
Wattle basal width	X	X	34B
Wattle length	$+^*$	X	35A
Wattle percent blue	–	$-^*$	35B
Helmet frontal length	$+^*$	$+^*$	36A
Helmet rear length	$+^*$	$+^*$	36B
Helmet central height	$+^*$	$+^*$	37A
Helmet basal length	$+^*$	$+^*$	37B
Helmet thickness	+	X	38A
Cere structure length	+	$-^*$	38B
Cere structure thickness	+	$-^*$	39A
Collar featheration	$+^*$	$-^*$	39B
Nape filoplume length	$-^*$	$+^*$	40A
Nape filoplume antero-posterior coverage	–	$+^*$	40B
Nape filoplume lateral coverage	–	$+^*$	41A
Nape filoplume density	–	$+^*$	41B
Secondary remex outer web vermiculation	$+^*$	$-^*$	42A
Wing covert barring	X	X	42B
Dorsal vermiculation	$+^*$	X	43A
Dorsal spot size	+	$-^*$	43B

---

[1] see Appendix 2 for character descriptions

Table 11

A comparison of OTU 7 for N. meleagris with OTU 9. X = not significantly different ($P \leq 0,05$; t test); + = OTU 7 significantly greater; − = OTU 7 significantly lower; * = differences delineate OTUs in contour maps.

Character name[1]	OTU 9	Contour map Figure no.
Bill length	+	33A
Wing length	+	33B
Tarso-metatarsus length	+	34A
Wattle basal width	X	34B
Wattle length	−*	35A
Wattle percent blue	X	35B
Helmet frontal length	+*	36A
Helmet rear length	+*	36B
Helmet central height	−*	37A
Helmet basal length	+*	37B
Helmet thickness	−*	38A
Cere structure length	−*	38B
Cere structure thickness	−*	39A
Collar featheration	−*	39B
Nape filoplume length	+*	40A
Nape filoplume antero-posterior coverage	+*	40B
Nape filoplume lateral coverage	+*	41A
Nape filoplume density	+*	41B
Secondary remex outer web vermiculation	−*	42A
Wing covert barring	X	42B
Dorsal vermiculation	−*	43A
Dorsal spot size	−*	43B

[1] see Appendix 2 for character descriptions

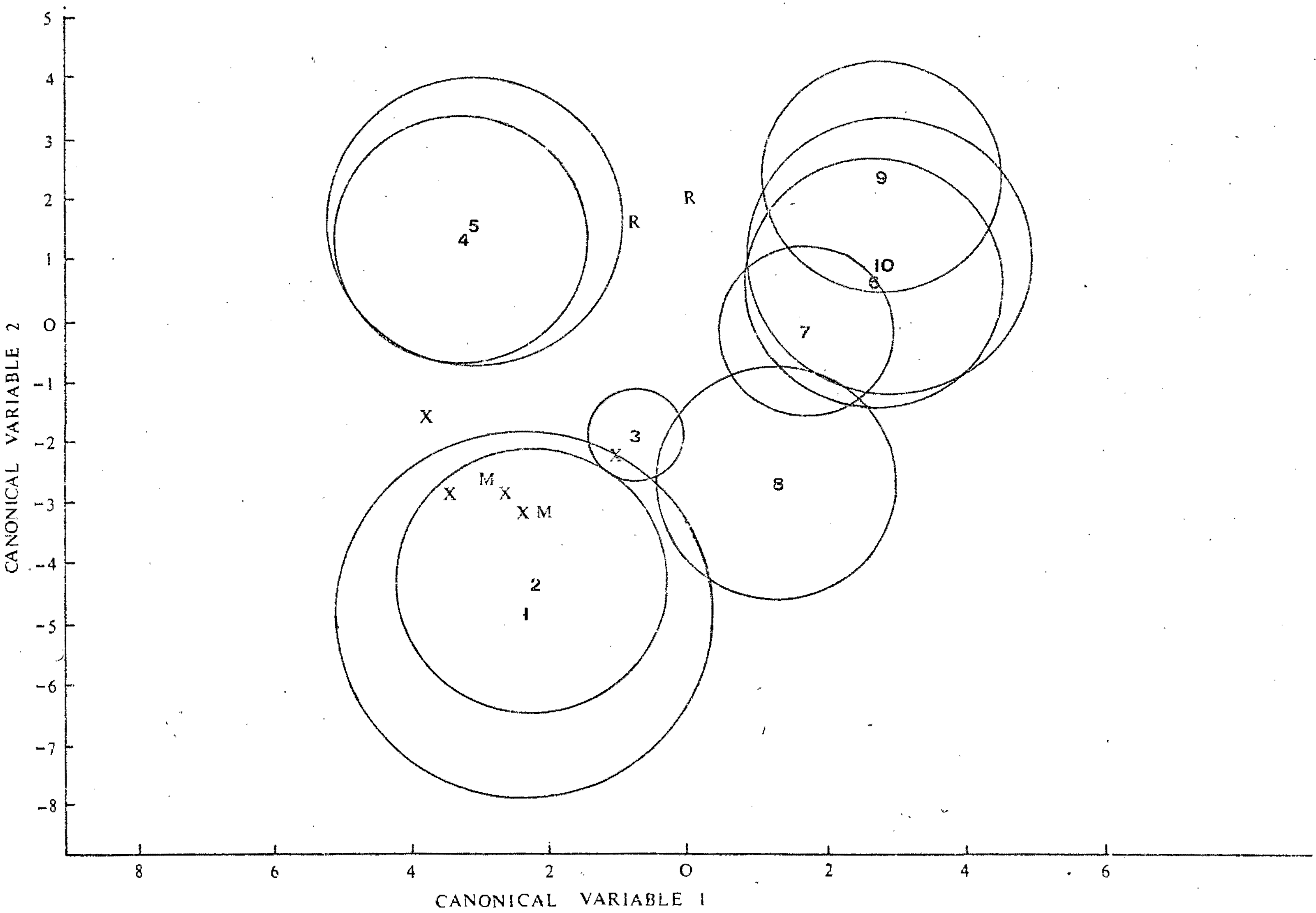

Fig. 31. A discriminant functions analysis of Numida OTUs. Circles encompass 90% of the individuals assigned to each OTU. Only intermediate specimens between non-overlapping OTUs are plotted. M= intermediate between OTUs 4 and 7; R = intermediate between OTUs 4 and 8; X = intermediate between OTUs 4 and 2.

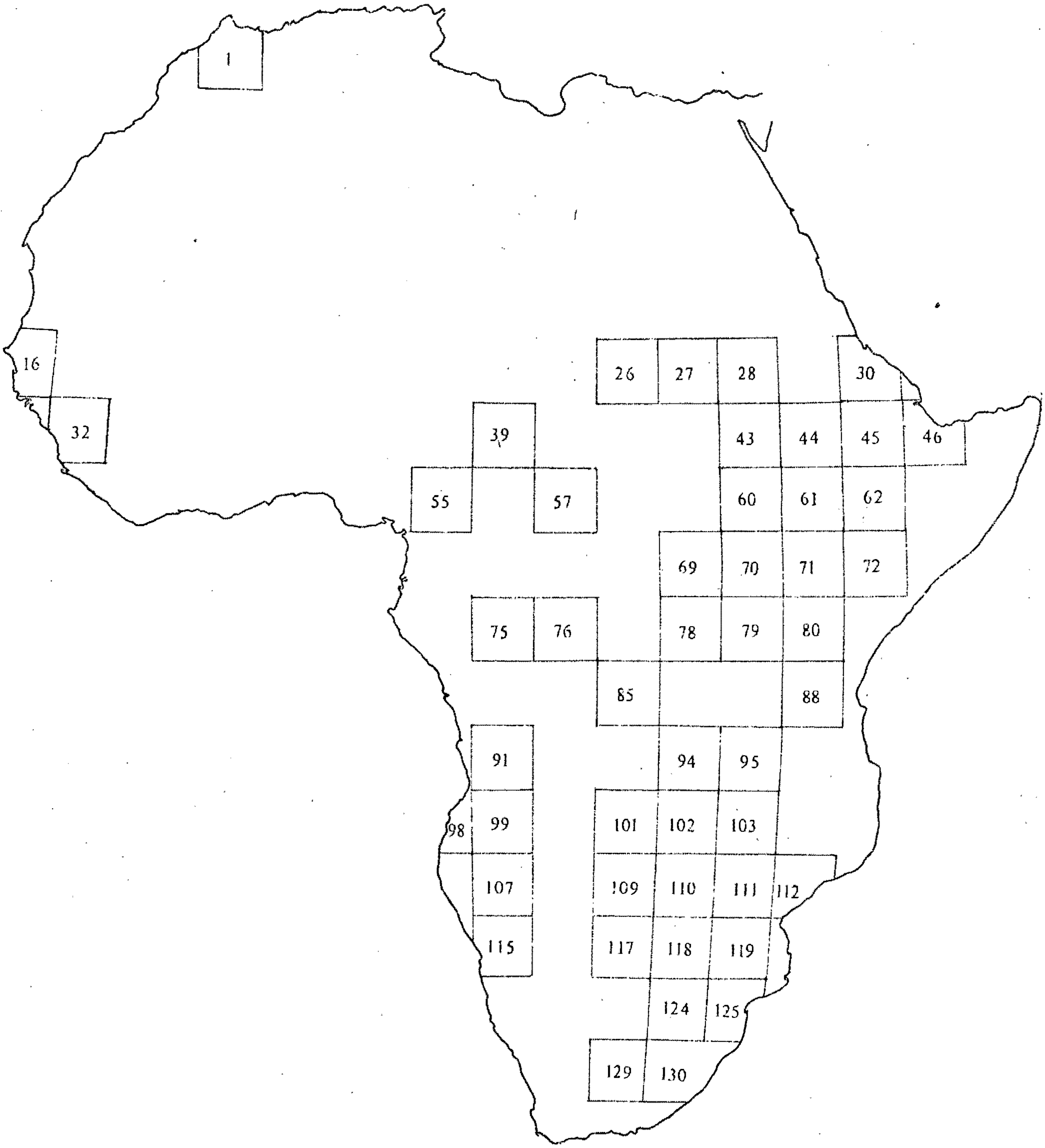

Fig. 32. Areas used in contour map analysis of Numida meleagris.

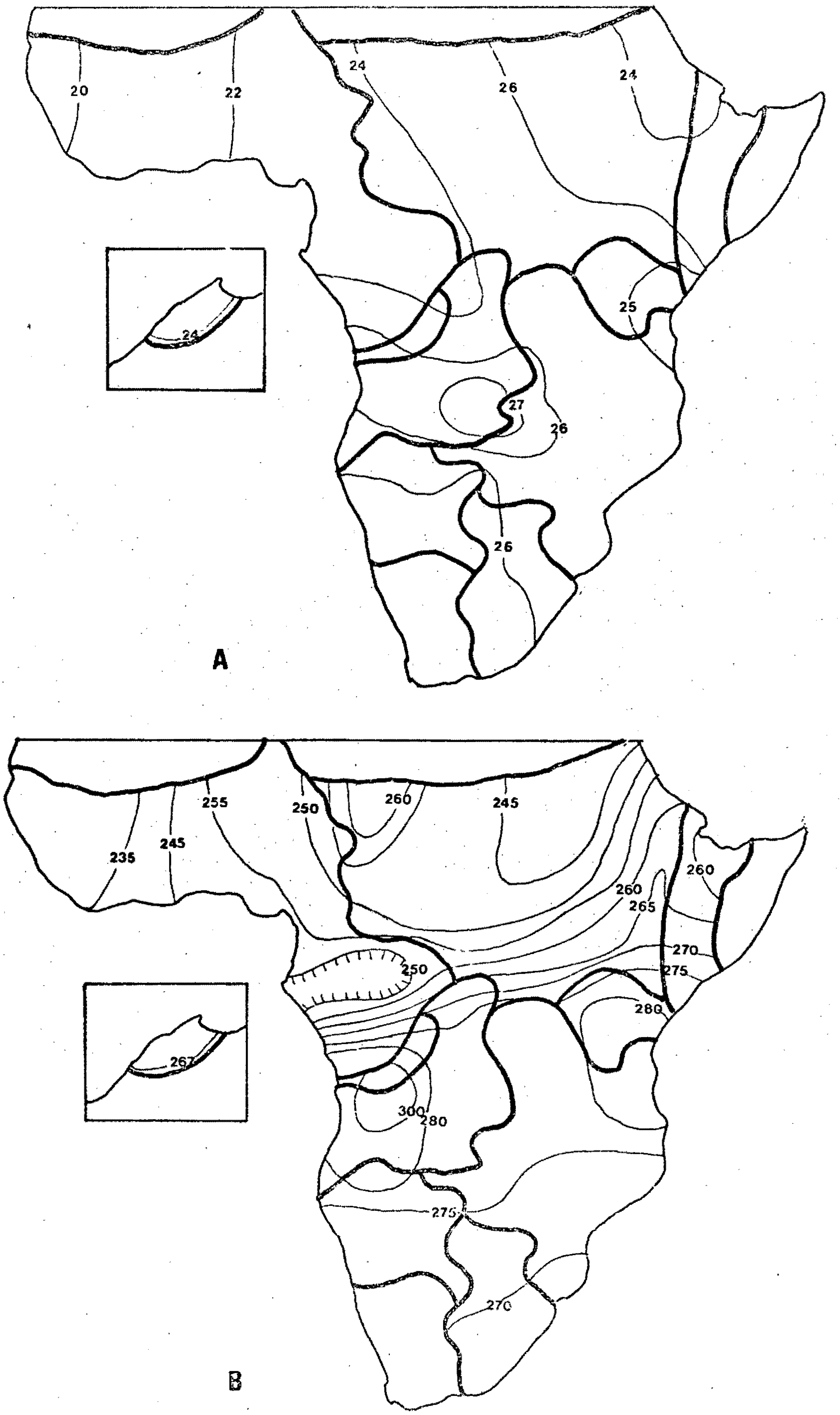

Fig. 33. Contour maps of bill length (A) and wing length (B) in *Numida meleagris*. OTU boundaries are indicated by thick lines.

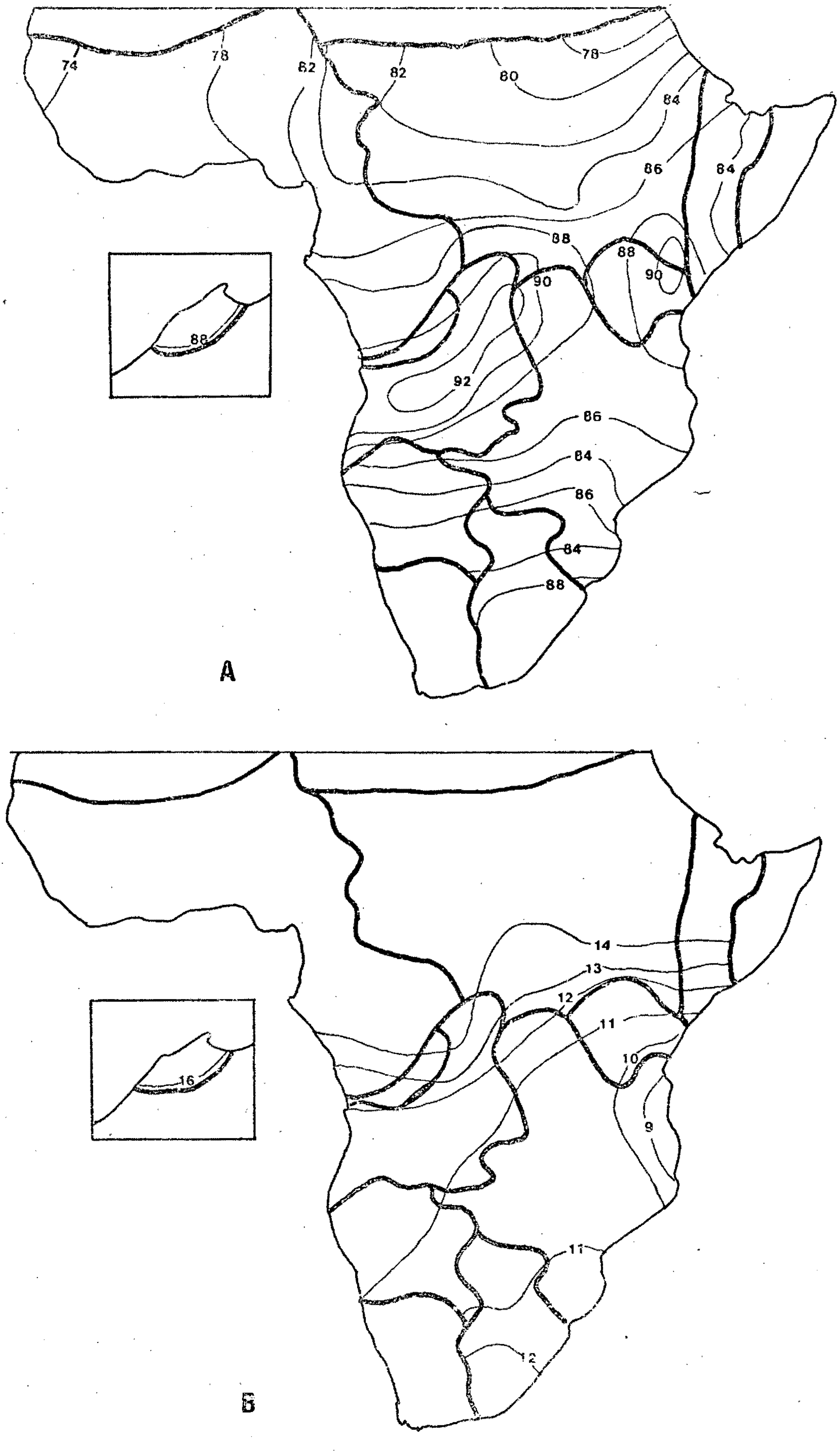

Fig. 34. Contour maps of tarso-metatarsus length (A) and wattle basal width (B) in Numida meleagris. OTU boundaries are indicated by thick lines.

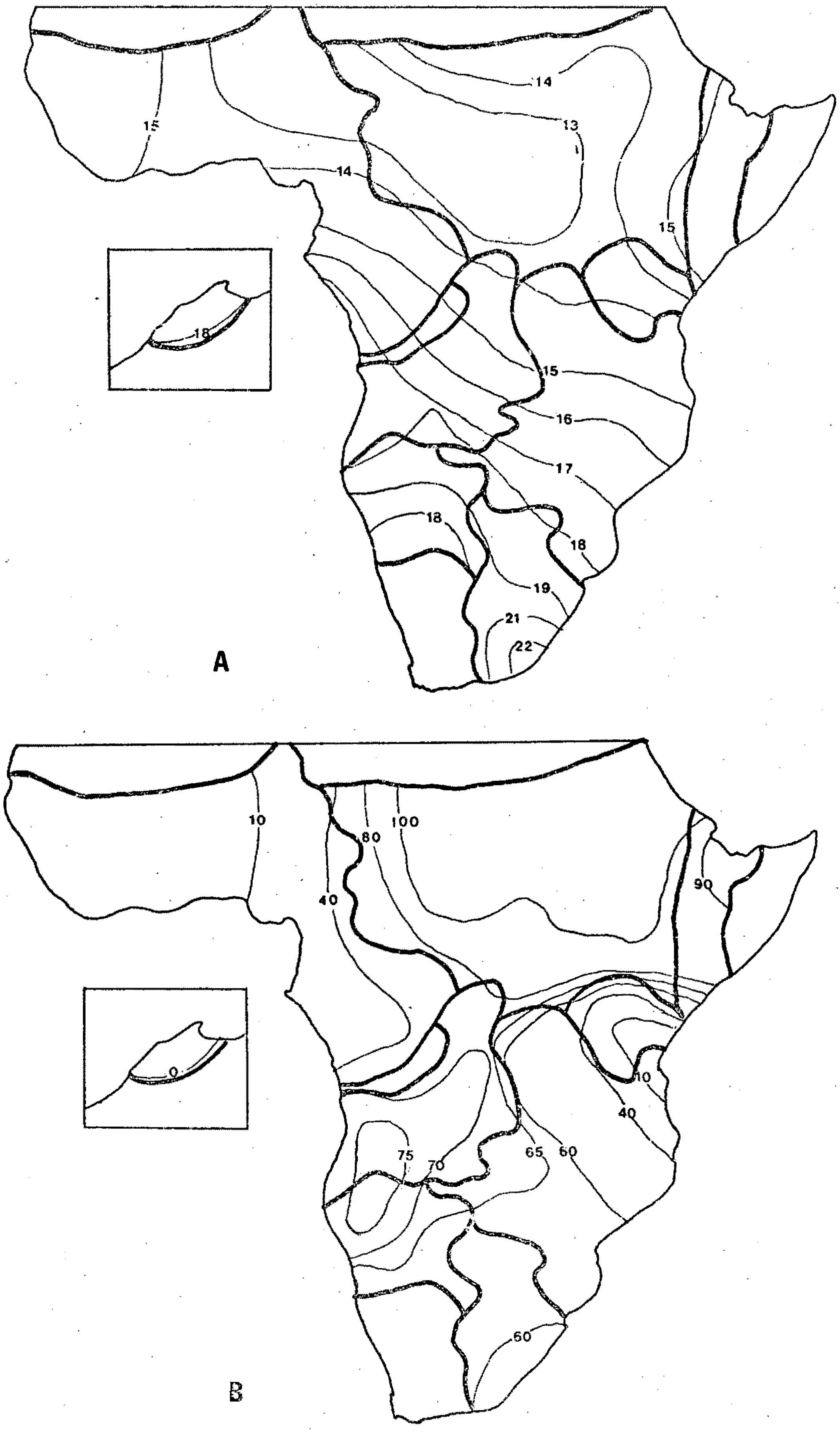

Fig. 35. Contour maps of wattle length (A) and wattle percent blue (B) in Numida meleagris. OTU boundaries are indicated by thick lines.

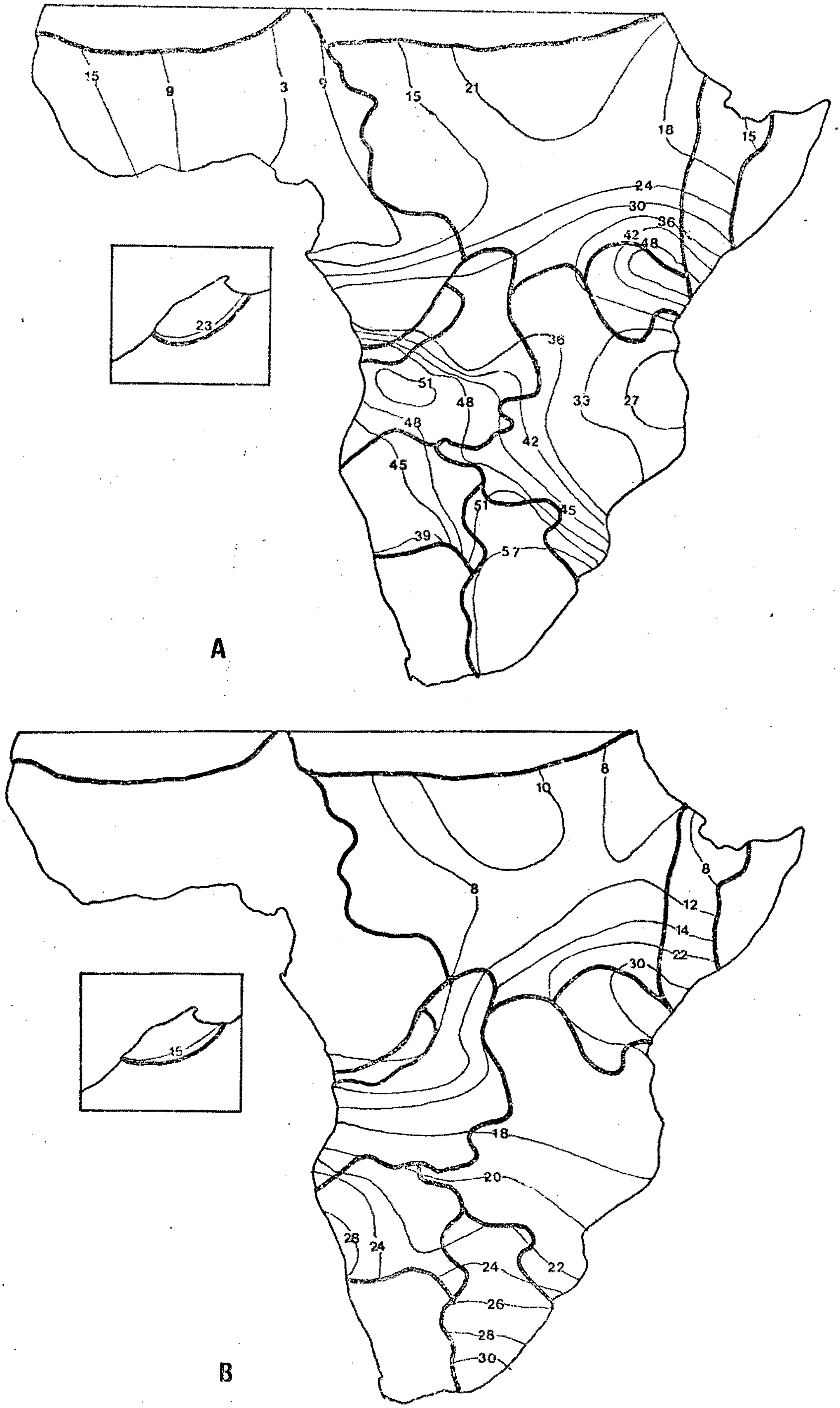

Fig. 36. Contour maps of helmet frontal length (A) and helmet rear length (B) in <u>Numida meleagris</u>. OTU boundaries are indicated by thick lines.

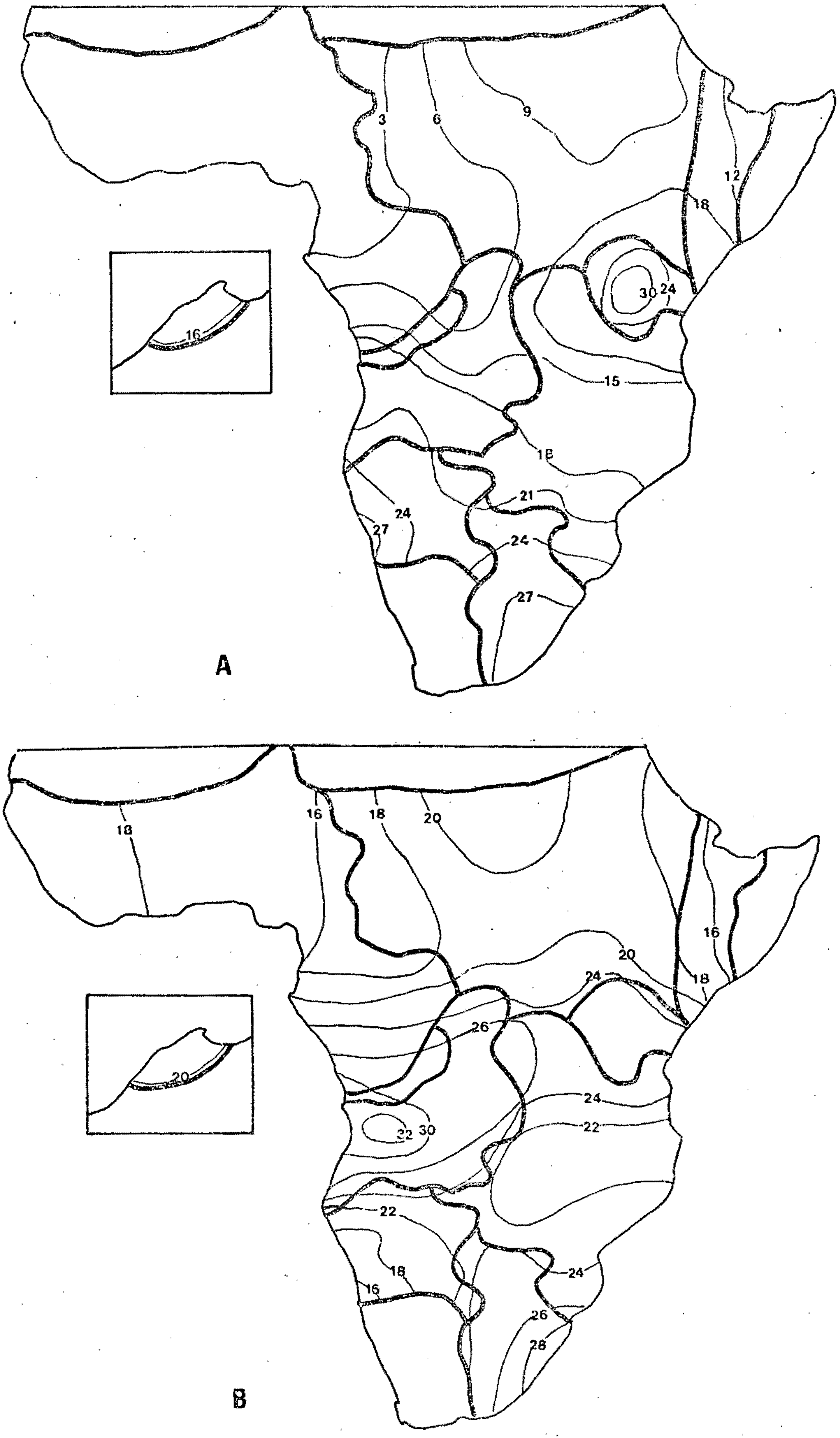

Fig. 37. Contour maps of helmet central height (A) and helmet basal length (B) in *Numida meleagris*. OTU boundaries are indicated by thick lines.

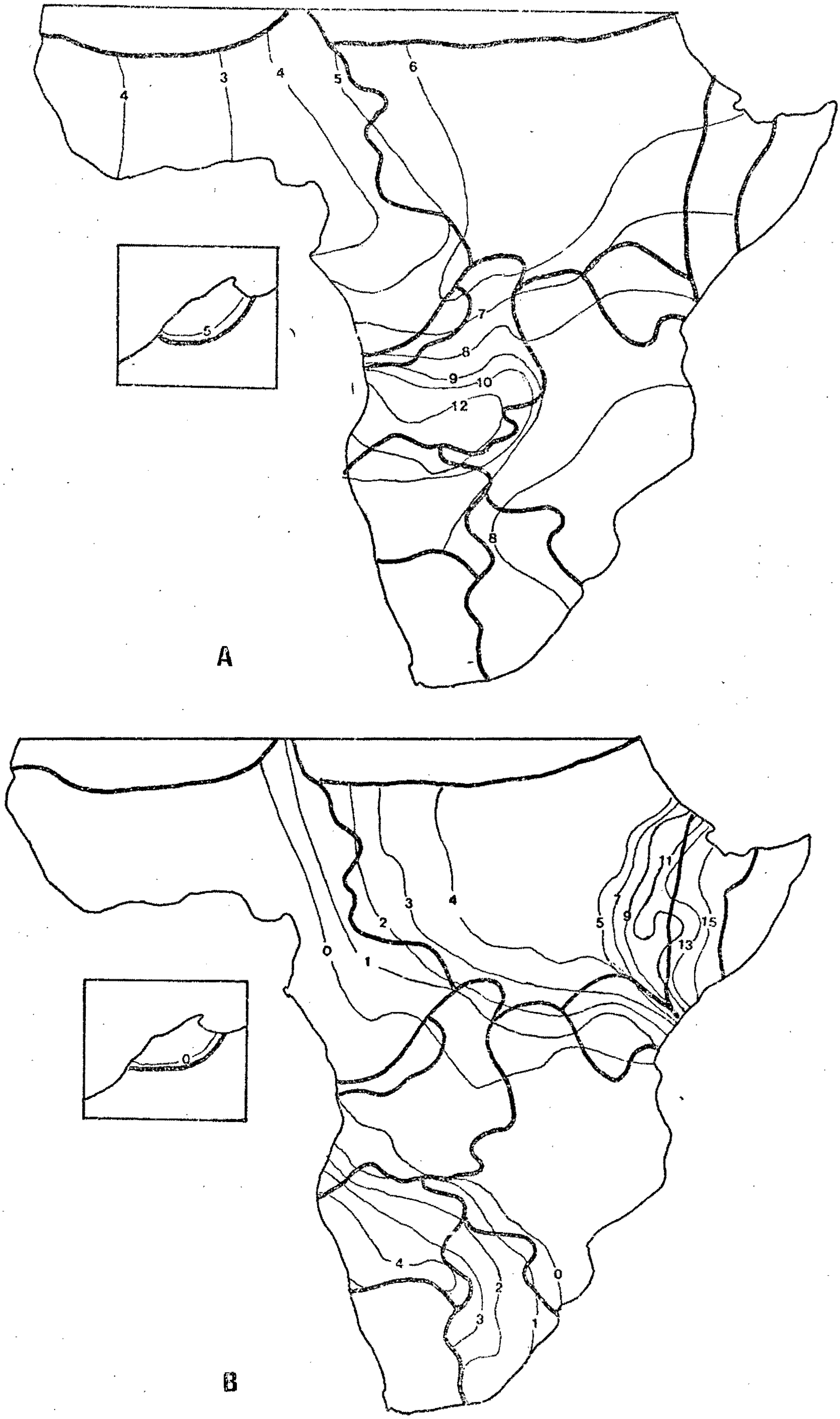

Fig. 38. Contour maps of helmet thickness (A) and cere structure length (B) in Numida meleagris. OTU boundaries are indicated by thick lines.

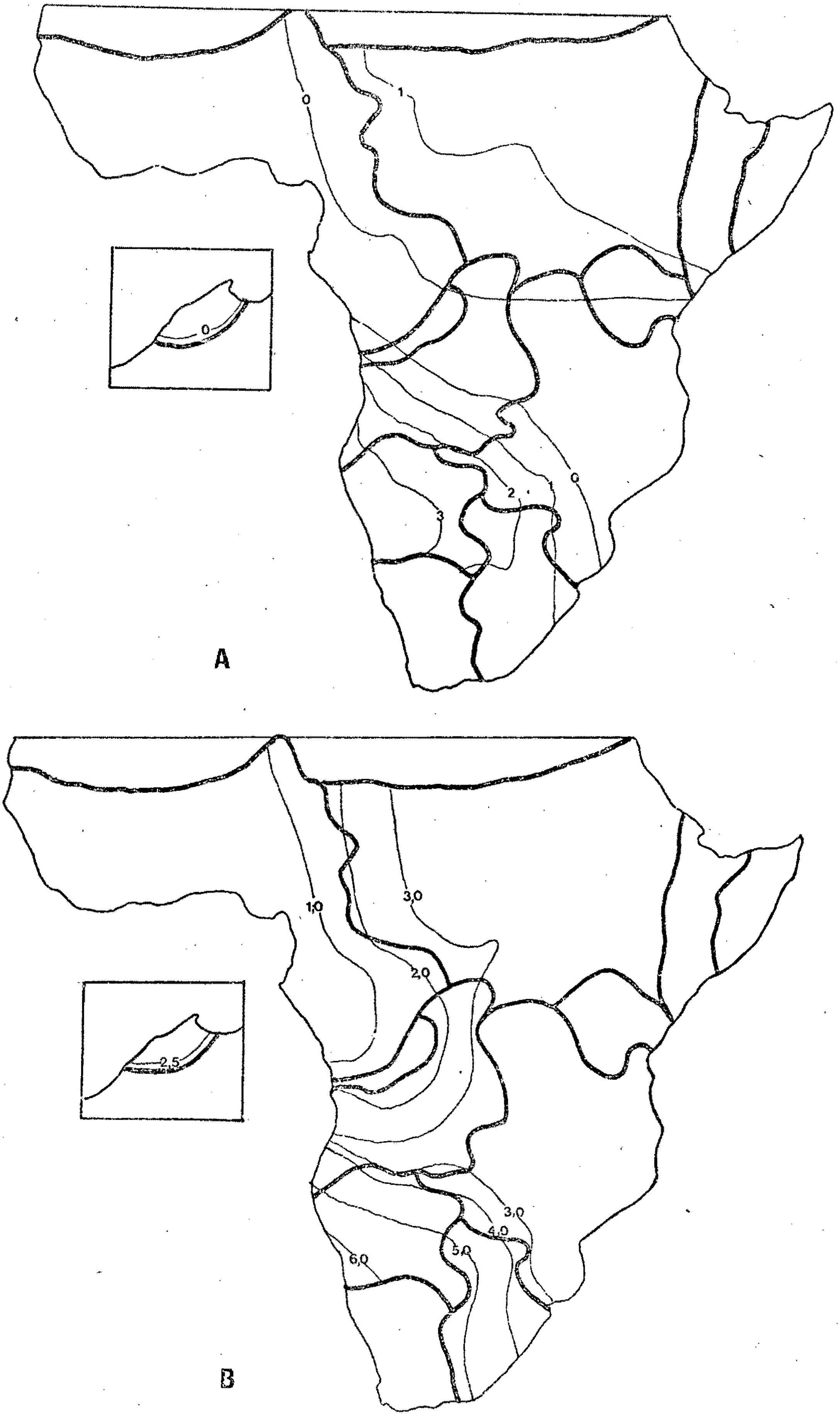

Fig. 39. Contour maps of core structure thickness (A) and collar plumage (B) in Numida meleagris. OTU boundaries are indicated by thick lines.

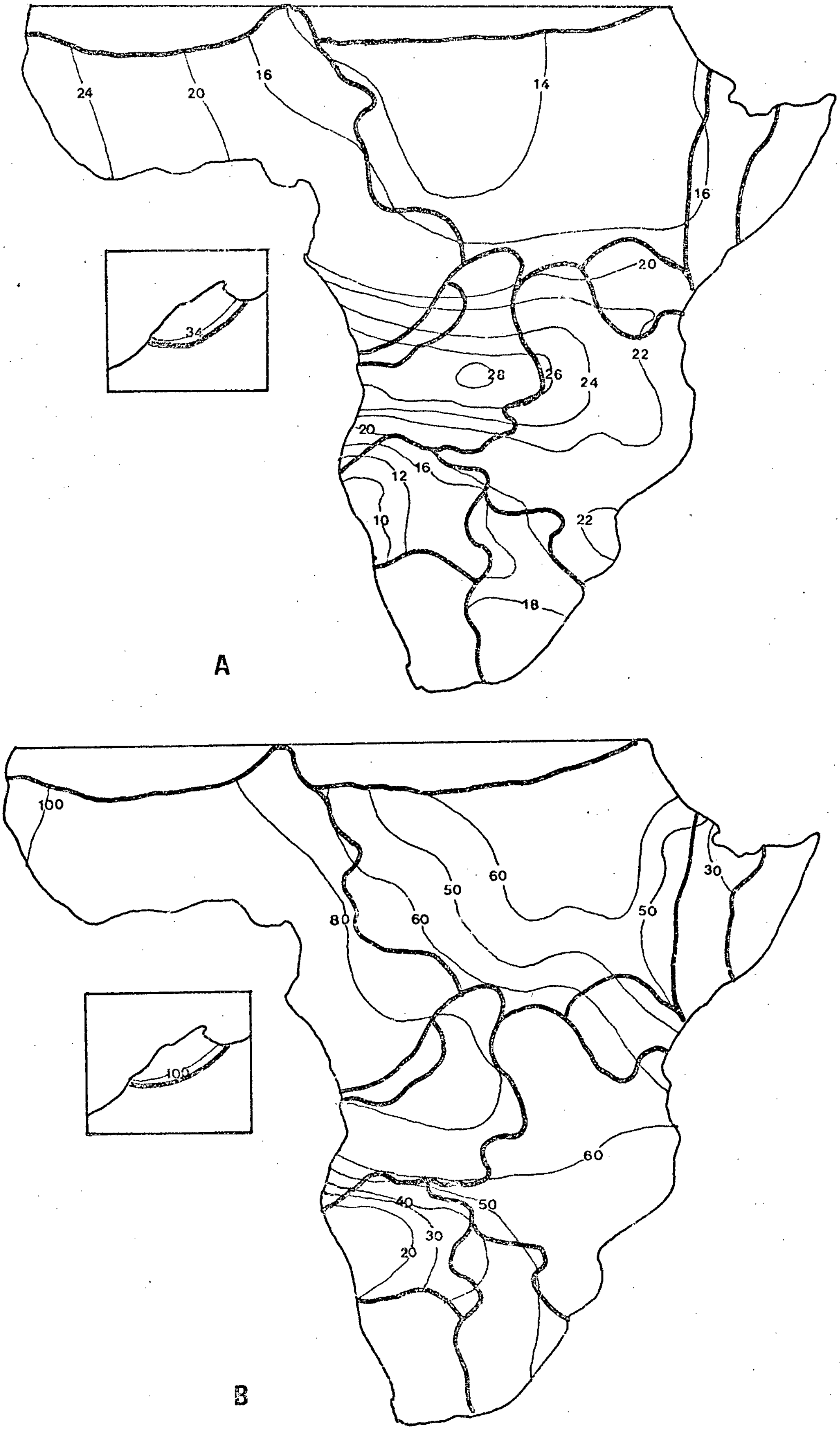

Fig. 40. Contour maps of nape filoplume length (A) and nape antero-posterior coverage (B) in <u>Numida</u> <u>meleagris</u>. OTU boundaries are indicated by thick lines.

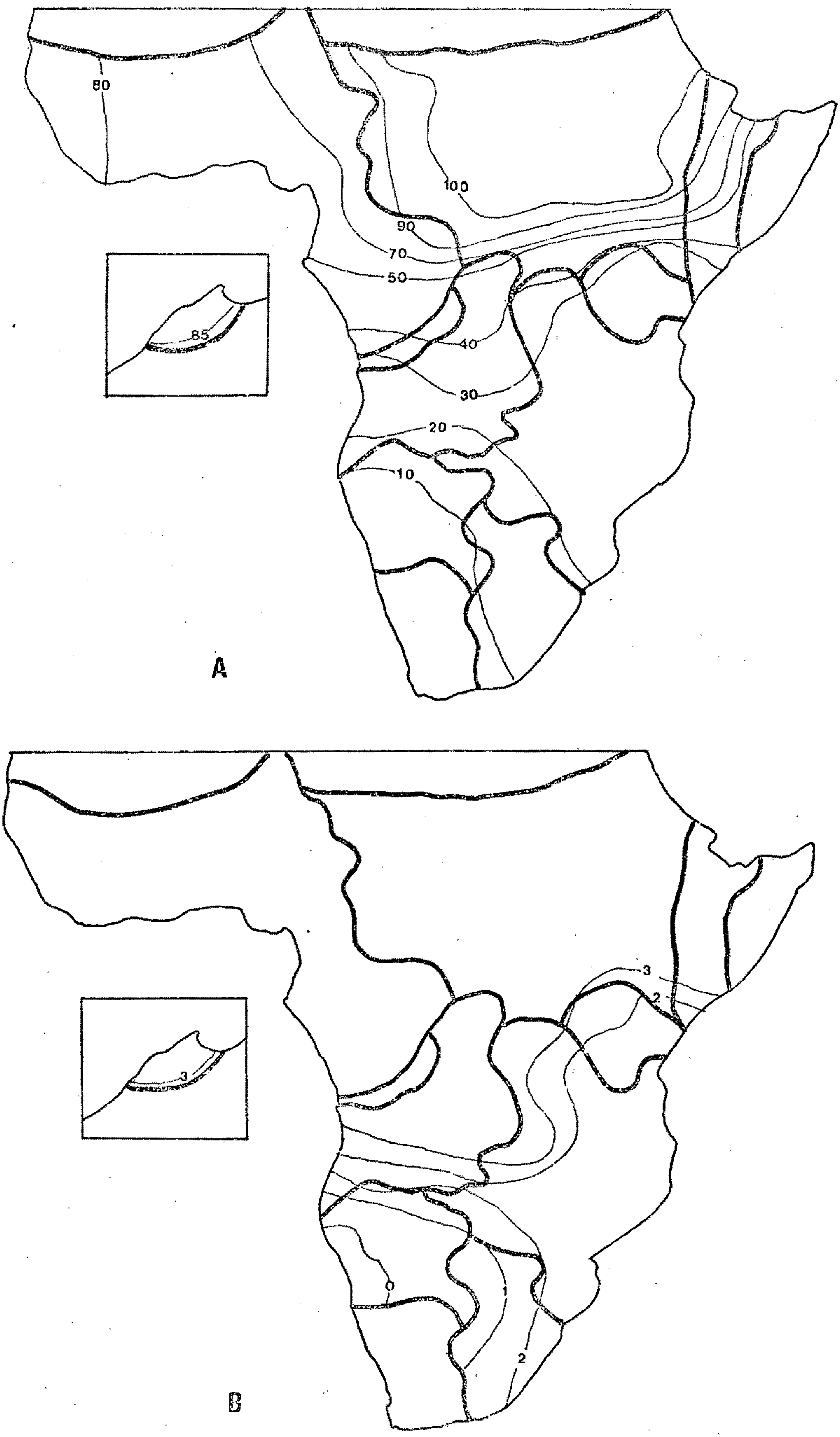

Fig. 41. Contour maps of nape filoplume lateral coverage (A) and nape filoplume density (B) in *Numida meleagris*. OTU boundaries are indicated by thick lines.

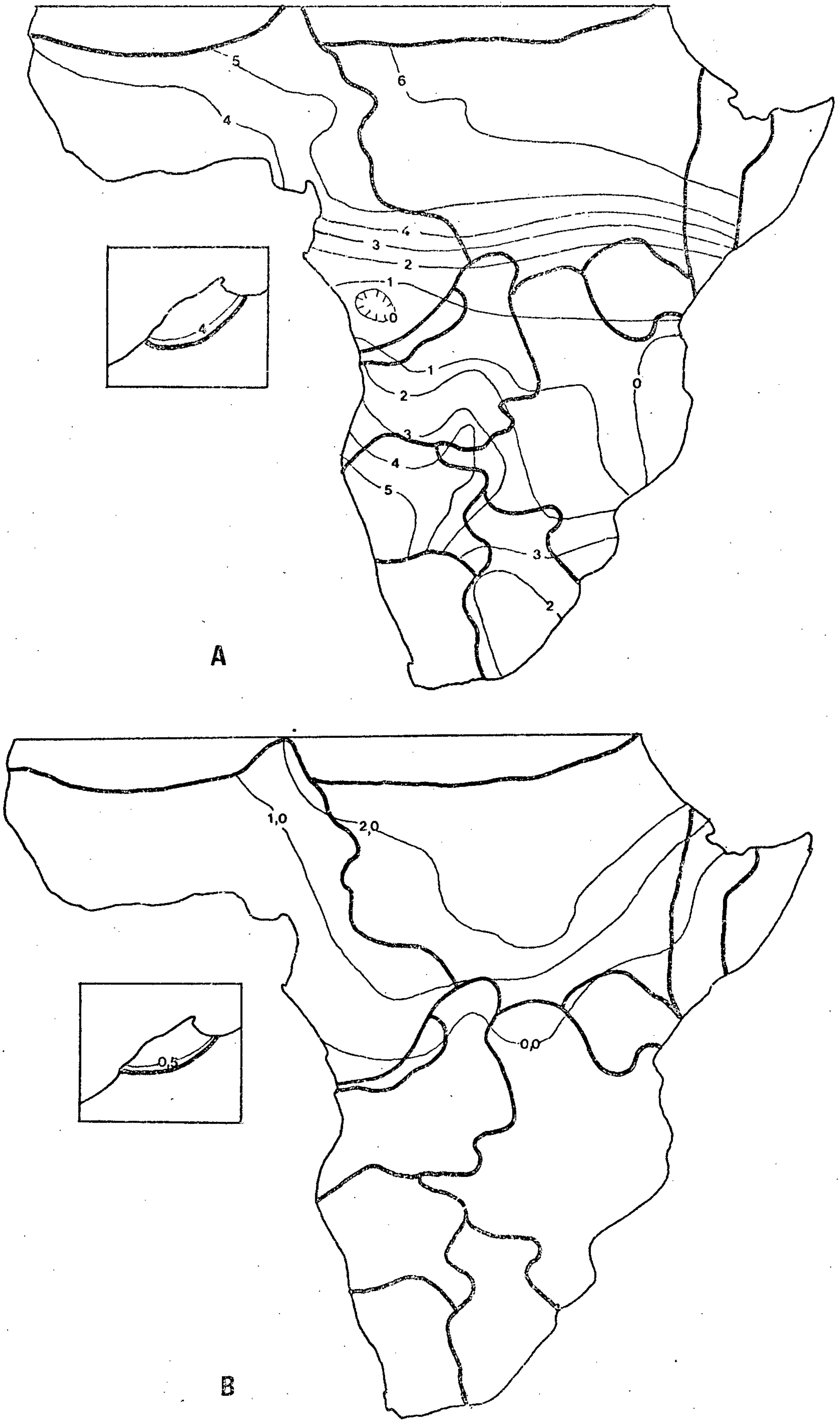

Fig. 42. Contour maps of secondary remex outer web vermiculation (A) and wing covert barring (B) in Numida meleagris. OTU boundaries are indicated by thick lines.

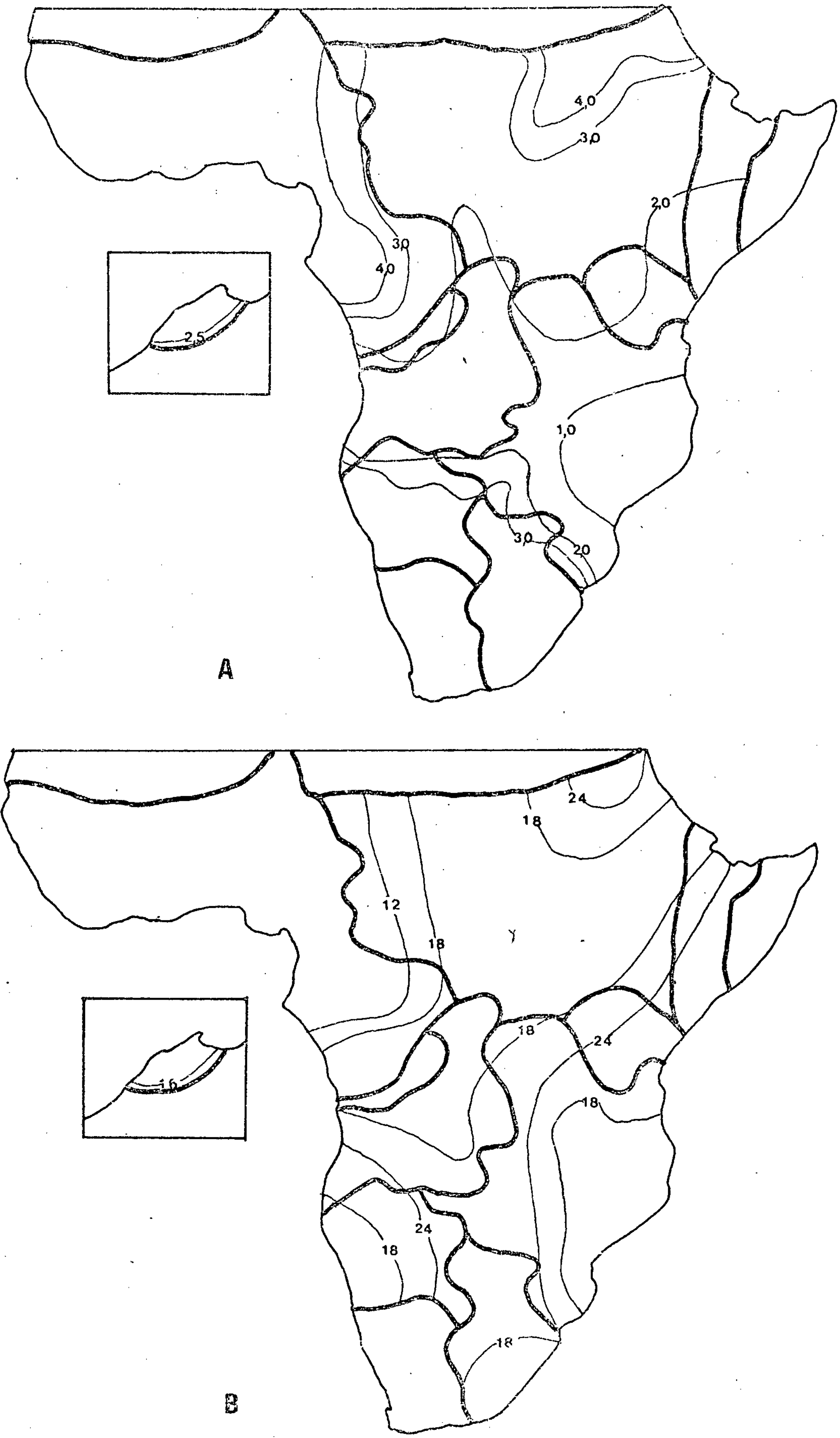

Fig. 43. Contour maps of dorsal vermiculation (A) and dorsal spot size (B) in *Numida meleagris*. OTU boundaries are indicated by thick lines.

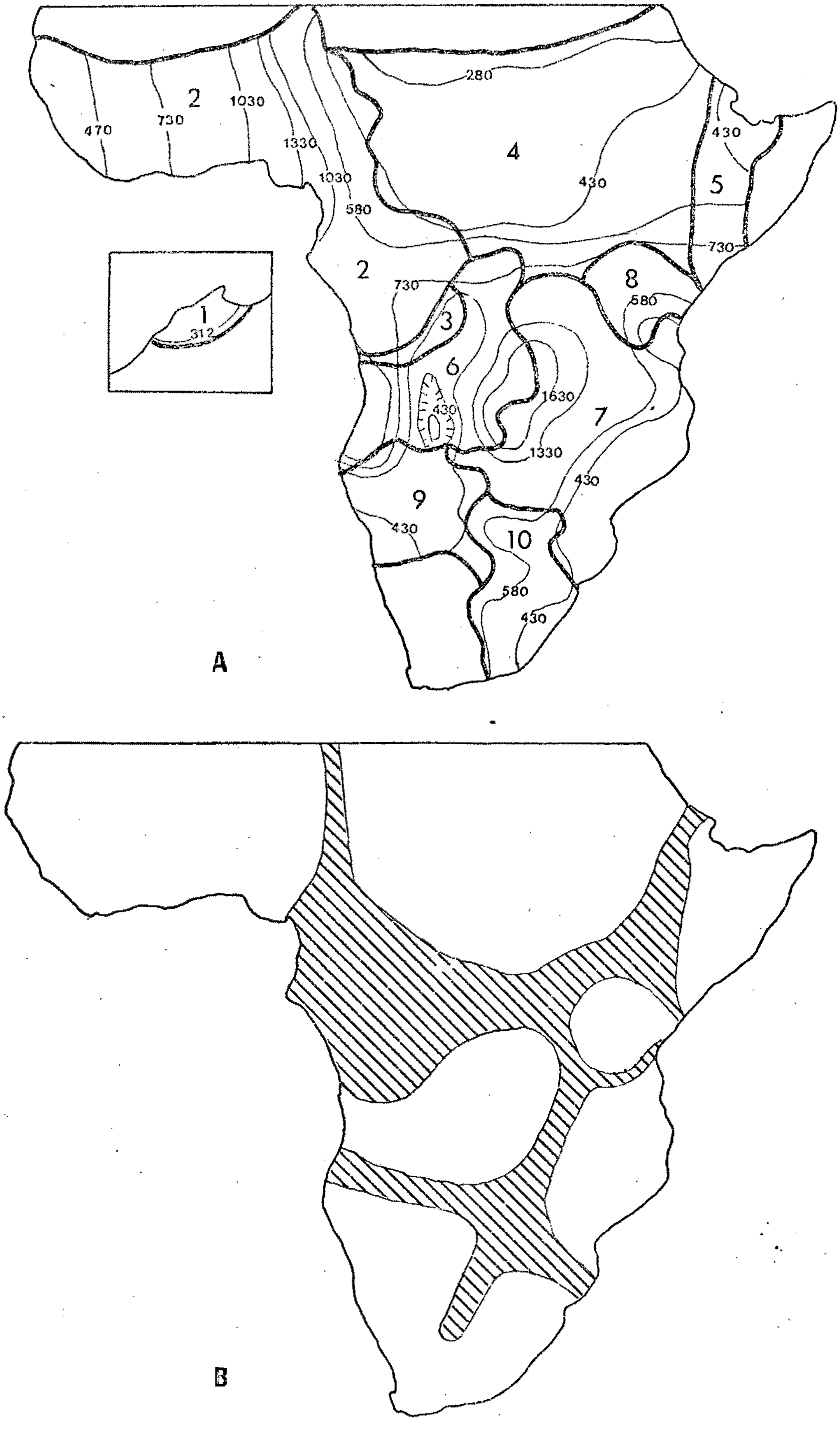

Fig. 44. A contour map of total COV in <u>Numida meleagris</u> (A) with OTU boundaries indicated by thick lines; and the approximate distribution of zones of intermediacy between <u>Numida</u> OTUs (B). Larger numbers in (A) refer to OTU numbers shown in Figure 17B.

to N.m. mitrata, OTU 8 to N.m. reichenowi, OTU 9 to N.m. damarensis, and OTU 10 to N.m. coronata. The distributions of these subspecies are plotted in Figure 45, and zones of intermediacy are shown in Figure 44B.

(c) Taxonomic summary

In the following classification, verbal descriptions are brief, focusing on more obvious differences and similarities with respect to the qualitative and quantitative characters analyzed. For each subspecies, reference is made to its OG or OTU number and the appropriate page(s), tables and figures summarizing its taxonomic relationships and quantitative comparisons with other subspecies. If a synonomized taxon is not discussed, it must be assumed that it did not emerge as an OTU in the cluster analyses. In other words, it was not taxonomically distinct above a level attributable to individual variation in a relatively homogenous population. Subspecies which are mentioned in Table 1, but are not recognized or synonomized are taken to be intergrades. Herein, an intergrade is a group of taxonomically indeterminable, phenotypically highly variable populations. A population is taken to be taxonomically indeterminable if many of its component individuals show affinities to two or more subspecies (i.e. are classed as intermediates) in discriminant analyses. A population is taken to be highly variable phenotypically if it has a high total COV. See the section on Taxonomic methodology for a detailed discussion of OTUs, discriminant analyses and total COV.

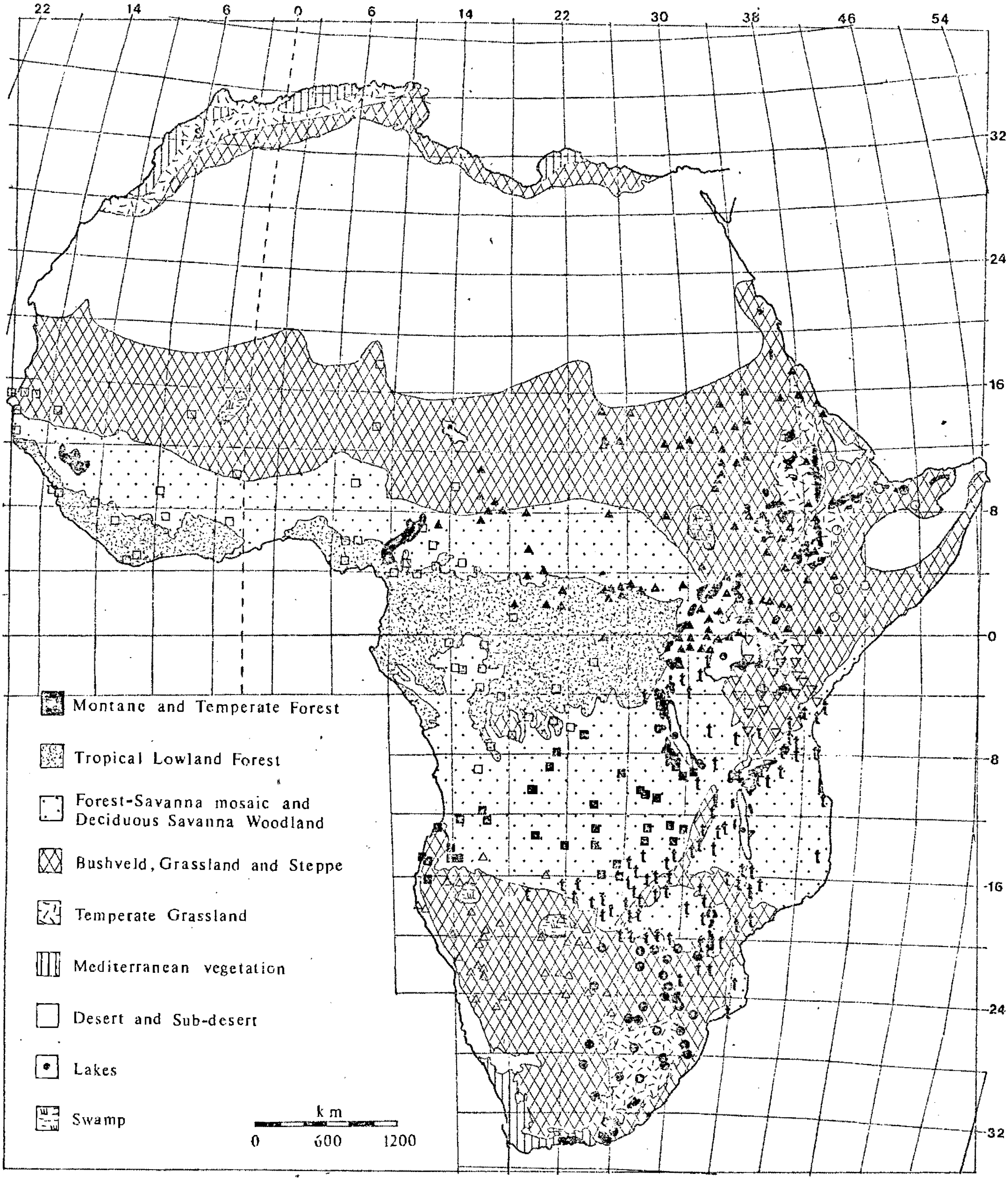

Fig. 45. The distribution of Numida meleagris. N. m. meleagris (▲). N. m. sabyi (S). N. m. galeata (□). N. m. somaliensis (○). N. m. marungensis (▣). N. m. reichenowi (▽). N. m. mitrata (t). N. m. damarensis (△). N. m. coronata (◉).

Genus Agelastes

(= OG 1 and 2 in Fig. 7)

Agelastes Bonaparte 1850, Proc. Zool. Soc. London, p.145

Agelastes meleagrides Bonaparte, 1850

Plate 1A

(= OG 1 in Fig. 7)

Agelastes meleagrides Bonaparte 1850, Proc. Zool. Soc. London, p. 145.

Description: Small overall size; no crown, occipital, cere, nape or throat adornments; rudimentary red gape wattles; no feathers on head or neck and skin colour thereof red; collar plumage white; body plumage black with faint vermiculations; tarso-metatarsus covered with imbricated scales in rows, and usually with a well-developed spur(s); iris brown; outer margins of secondaries black with faint vermiculations; furcula blade-shaped; abdominal plumage white.

Statistics for quantitative characters: (N = 12)

Character	$\overline{X}$	S.D.
Bill length	16,8 mm	1,7
Wing length	205,0 mm	4,8
Tarso-metatarsus length	80,9 mm	3,6
Wattle basal width	6,5 mm	1,2
Wattle length	2,7 mm	0,7
Tarsal structure number	0,8	0,6
Tarsal structure length	4,8 mm	3,5
White collar	100,0 %	0,0
Facial filoplumes	0,0	0,0

Distribution: Figure 9

Discussion: White collar and facial filoplumes are used as quantitative characters in cluster and discriminant analyses to demonstrate the qualitative distinctness of this taxon from *A. niger*.

Agelastes niger (Cassin) 1857

Plate 1B

(= OG 2 in Fig. 7)

Phasidus niger Cassin 1857, *Proc. Acad. Nat. Sci. Phila.*, 8: 322.

Description: As *A. meleagrides* except: crown surmounted by a short crest of feathers; nape covered by short, sparsely distributed, black downy feathers; face covered with sparsely distributed filoplumes; collar and abdominal plumage black with faint vermiculations, abdominal plumage white in juveniles.

Statistics for quantitative characters: (N = 39)

Character	$\overline{X}$	S.D.
Bill length	16,9 mm	1,5
Wing length	203,0 mm	7,3
Tarso-metatarsus length	79,2 mm	3,4
Wattle basal width	6,5 mm	1,2
Wattle length	2,4 mm	0,6
Tarsal structure number	1,1	0,7
Tarsal structure length	3,4 mm	2,4
White collar	0,0 %	0,0
Facial filoplumes	9,8	0,2

Distribution: Figure 9

Discussion: Hall (1961) also advocates the synonomy of *Phasidus* in *Agelastes*, basing her argument largely on analysis of juvenile characters.

Genus *Guttera*

Guttera Wagler 1832, Isis von Oken, col. 1225.

(= OG 4-9 in Fig. 7)

Guttera plumifera plumifera (Cassin) 1857

Plate 1C

(= OTU 2 in Figs. 11A and 12)

Numida plumifera Cassin 1857, *Proc.Acad.Nat.Sci.Phila.*,8: 321.

Description: Larger than *Agelastes* sp.; crown surmounted by a crest of long, straight, bristly feathers; small occipital fold of blue-black skin; no nape, throat or cere adornments; well-developed, pointed, blue gape wattles; orbital and throat skin blue-black; collar plumage spotted; body plumage spotted without vermiculations; tarso-metatarsus without spurs, scales pentagonal, not in rows; iris brown; outer margin of secondaries white; furcula blade-shaped; caecum up to 150 mm; abdominal plumage spotted bluish-white without vermiculations.

Statistics for quantitative characters: (N = 26)

(See p. 16 for statistical comparisons with *G.p. schubotzi*)

Character	$\overline{X}$	S.D.
Bill length	24,5 mm	1,7
Wing length	225,6 mm	5,9

Character	$\overline{X}$	S.D.
Tarso-metatarsus length	81,7 mm	3,1
Wattle basal width	10,7 mm	1,2
Wattle length	11,6 mm	2,2
Dorsal spot size	10,7 units	1,0
Crest frontal length	24,6 mm	3,7
Crest rear length	46,9 mm	5,6
Crest central height	31,8 mm	6,7
Crest basal length	30,0 mm	2,6
Anterior crest curliness	1,0	0,0
Posterior crest curliness	1,0	0,0
Dorsal black collar	0,0 %	0,0
Ventral black collar	0,0 %	0,0
Occipital fold	18,3 %	7,5
Ear patch	0,4 mm	0,6
Throat red	0,0 %	0,0
Orbital red	0,0 %	0,0
Dorsal spot number	21,3	3,7
Total spot barbs	5,4	0,6
Total within spot barbs	3,5	0,6
Spot barb blueness	0,8	0,6
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution: Figure 13

Guttera plumifera schubotzi Reichenow, 1912

Plate 1D

(= OTU 1 in Figs. 11A and 12)

Guttera plumifera schubotzi Reichenow 1912, _Journ. f. Orn._, 60: 320.

Description: As _G.p. plumifera_ except that the base of the nape and an area anterior to the ear are covered by patches of orange-yellow skin.

Statistics for quantitative characters: (N = 71)

(See p. 16 for statistical comparisons with _G.p. plumifera_)

Character	$\overline{X}$	S.D.
Bill length	22,8 mm	1,4
Wing length	227,2 mm	8,2
Tarso-metatarsus length	80,7 mm	3,4
Wattle basal width	9,6 mm	1,5
Wattle length	8,9 mm	2,4
Dorsal spot size	10,0 units	1,4
Crest frontal length	24,3 mm	5,9
Crest rear length	38,4 mm	4,8
Crest central height	32,4 mm	6,4
Crest basal length	25,9 mm	2,4
Anterior crest curliness	1,0	0,0
Posterior crest curliness	1,0	0,0
Dorsal black collar	0,0 %	0,0
Ventral black collar	0,0 %	0,0
Occipital fold	24,0 %	8,5
Ear patch	15,1 mm	2,8
Throat red	0,0 %	0,0
Orbital red	0,0 %	0,0
Dorsal spot number	21,2	2,9
Total spot barbs	5,7	0,6

Character	$\overline{X}$	S.D.
Total within-spot barbs	3,7	0,5
Spot barb blueness	1,6	0,6
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution: Figure 13

Discussion: The one intermediate specimen between G.p. schubotzi and G.p. plumifera is more schubotzi in appearance, but the patches of orange on the nape and ear are much reduced in extent.

Guttera pucherani pucherani (Hartlaub) 1860

Plate 1E

(= OTU 5 in Figs. 11A and 12, and in Tables 4 and 5)

Numida pucherani Hartlaub 1860, Journ. f. Orn., 8: 341.

Description: Larger than G. plumifera; crown surmounted by a long crest of relatively curly, downy feathers; well-developed occipital fold of blue-black skin; no nape and cere adornments; orbital and throat skin red; throat skin folded; rudimentary, relatively short blue wattles at gape; collar plumage spotted; body plumage spotted without vermiculations; tarso-metatarsus without spurs, scales pentagonal, not in rows; iris red; outer margin of secondaries white; furcula hollow; caecum length up to 150 mm; abdominal plumage spotted bluish-white without vermiculations.

Statistics for quantitative characters: (N = 64)

(See Tables 4 and 5 for statistical comparisons with other subspecies)

Character	$\overline{X}$	S.D.
Bill length	25,5 mm	1,8
Wing length	261,6 mm	14,8
Tarso-metatarsus length	90,2 mm	6,9
Wattle basal width	9,2 mm	1,5
Wattle length	2,7 mm	0,7
Dorsal spot size	11,3 units	1,3
Crest frontal length	19,4 mm	3,9
Crest rear length	29,5 mm	3,7
Crest central height	26,4 mm	6,6
Crest basal length	34,7 mm	3,2
Anterior crest curliness	1,0	0,2
Posterior crest curliness	2,0	0,2
Dorsal black collar	5,3 %	7,5
Ventral black collar	7,4 %	10,4
Occipital fold	74,6 %	19,5
Ear patch	0,0 mm	0,0
Throat red	98,0 %	12,7
Orbital red	95,4 %	2,4
Dorsal spot number	26,0	4,3
Total spot barbs	6,3	1,3
Total within spot barbs	4,3	0,7
Spot barb blueness	1,9	0,9
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

<u>Distribution</u>: Figure 30

<u>Discussion</u>: From breeding experiments with captive birds, Ghigi (1936) demonstrated complete interfertility between

individuals ascribed to *G. edouardi* and *G. pucherani*. He also found that red throat and orbital skin, characters used to distinguish *G. pucherani*, were invaribaly absent among F1 hybrids. This suggests that these character-states may be recessive. Ghigi (1936) further hypothesized that *Guttera edouardi suahelica* (Neumann 1908, *Bull. Brit. Orn. Cl.*,23: 14) and *G.e. granti* (Elliot 1871, *Proc. Zool. Soc. London*, p. 584), subspecies described from specimens collected in southern Tanzania, are in fact intergrades between *G.p. pucherani* and *G.p. barbata*. The results of this study support that hypothesis, since *pucherani*-*barbata* intermediates in discriminant analysis (Fig. 12) almost invariably fit descriptions of these taxa, and the distribution attributed to them falls in the high total COV region between the suggested parental subspecies (Fig. 29B).

Guttera pucherani verreauxi (Elliot) 1870

Plate 1F

(= OTU 3 in Fig. 11A and 12, and Table 4)

Numida verreauxi Elliot 1870, *Ibis*, p. 300.

Guttera cristata sethsmithi Neumann 1908, *Bull. Brit. Orn. Cl.*, 23: 13.

Guttera pallasi Stone 1912, *Auk*, 29: 208.

Guttera edouardi schoutedeni Chapin 1923, *Rev. Zool. Afr.*, 11: 73.

Guttera edouardi chapini Frade 1926, *Bul. Soc. Port. Sci. Nat. Lisbonne*, 9: 139.

Guttera edouardi kathleenae White 1943, *Bull. Brit. Orn. Cl.*, 64: 19.

Description: As G.p. pucherani except crest longer; less well developed occipital fold; orbital skin colour blue; collar plumage black with no vermiculations; spotting with stronger blue hue; iris brown.

Statistics for quantitative characters: (N = 159)

(See Table 4 for statistical comparisons with other subspecies)

Character	$\bar{X}$	S.D.
Bill length	23,8 mm	1,6
Wing length	249,2 mm	11,2
Tarso-metatarsus length	89,2 mm	4,2
Wattle basal width	9,2 mm	1,2
Wattle length	2,7 mm	0,8
Dorsal spot size	9,5 units	1,5
Crest frontal length	21,1 mm	4,2
Crest rear length	37,4 mm	6,0
Crest central height	26,5 mm	5,8
Crest basal length	31,9 mm	2,6
Anterior crest curliness	1,1	0,3
Posterior crest curliness	2,0	0,2
Dorsal black collar	21,1 %	6,6
Ventral black collar	27,5 %	6,8
Occipital fold	47,1 %	18,4
Ear patch	0,0 mm	0,0
Throat red	91,7 %	13,3
Orbital red	0,0 %	0,0
Dorsal spot number	24,1	3,8
Total spot barbs	6,0	0,7

Total within-spot barbs	3,9	0,7
Spot barb blueness	2,3	0,6
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution: Figure 30

Guttera pucherani sclateri Reichenow, 1898

Plate 1G

(= OTU 4 in Figs. 11A and 12 and Table 4)

Guttera sclateri Reichenow 1898, *Orn. Monatsb.*, 6: 115.

Description: As *G.p. verreauxi*, except anterior crest much shorter.

Statistics for quantitative characters: (N = 12)

Character	$\overline{X}$	S.D.
Bill length	25,2 mm	2,2
Wing length	245,6 mm	10,4
Tarso-metatarsus length	89,9 mm	4,5
Wattle basal width	10,4 mm	1,2
Wattle length	2,3 mm	0,5
Dorsal spot size	11,5 units	1,5
Crest frontal length	5,8 mm	2,7
Crest rear length	40,8 mm	7,2
Crest central height	18,5 mm	4,2
Crest basal length	32,1 mm	4,1
Anterior crest curliness	1,1	0,3
Posterior crest curliness	2,1	0,3
Dorsal black collar	18,0 %	2,7
Ventral black collar	23,5 %	5,1

Occipital fold	62,5 %	17,6
Ear patch	0,0 mm	0,0
Throat red	95,3 %	6,6
Orbital red	0,0 %	0,0
Dorsal spot number	21,3	2,1
Total spot barbs	6,3	0,8
Total within-spot barbs	4,3	0,8
Spot barb blueness	1,8	0,5
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution: Figure 30

Guttera pucherani barbata Ghigi, 1905

Plate 1H

(= OTU 6 in Figs. 11A and 12 and Table 5)

Guttera barbata Ghigi 1905, *Mem. R. Accad. Sci. Inst. Bologna*, 2: 194.

Description: As *G.p. pucherani* except: crest longer; throat and orbital skin blue; collar plumage black with no vermiculation; body plumage spots occasionally interspersed with chestnut blotches.

Statistics for quantitative characters: (N = 28)

Character	$\overline{X}$	S.D.
Bill length	25,3 mm	1,3
Wing length	264,7 mm	11,0
Tarso-metatarsus length	90,2 mm	4,5
Wattle basal width	9,4 mm	1,3

Wattle length	2,8 mm	0,8
Dorsal spot size	10,9 units	1,2
Crest frontal length	23,3 mm	3,7
Crest rear length	32,2 mm	3,9
Crest central height	26,9 mm	8,5
Crest basal length	34,6 mm	2,9
Anterior crest curliness	1,1	0,3
Posterior crest curliness	1,9	0,3
Dorsal black collar	21,4 %	4,5
Ventral black collar	26,5 %	5,5
Occipital fold	76,4 %	11,3
Ear patch	0,0 mm	0,0
Throat red	6,9	25,8
Orbital red	0,3	3,9
Dorsal spot number	25,9	4,9
Total spot barbs	5,9	0,7
Total within-spot barbs	4,0	0,5
Spot barb blueness	1,5	0,7
Chestnut blotch size	2,7 units	1,1
Chestnut blotch extent	4,8 %	2,6

Distribution: Figure 30

Discussion: Ghigi (1936) mentions *G.p. barbata* specimens with brown irides. This is further evidence of gene flow between the brown-eyed western and red-eyed eastern subspecies of *G. pucherani*.

Guttera pucherani edouardi (Hartlaub) 1867

Plate II

(= OTU 7 in Figs. 11A and 12 and Tables 4 and 5)

Numida edouardi Hartlaub 1867, Journ. f. Orn., 15: 36.

Guttera lividicollis Ghigi 1905, Mem. R. Accad. Sci. Inst. Bologna, 2: 195.

Guttera edouardi symonsi Roberts 1917, Ann. Transv. Mus., 6: 3.

Description: As G.p. barbata except: crest curlier; occipital fold is of whitish skin; no throat fold; black collar plumage extensively covered with chestnut blotching.

Statistics for quantitative characters: (N = 34)

Character	$\overline{X}$	S.D.
Bill length	25,6 mm	4,9
Wing length	255,8 mm	7,4
Tarso-metatarsus length	86,9 mm	4,8
Wattle basal width	9,9 mm	1,0
Wattle length	2,5 mm	0,6
Dorsal spot size	9,9 units	1,0
Crest frontal length	22,6 mm	4,7
Crest rear length	38,0 mm	4,1
Crest central height	25,9 mm	5,3
Crest basal length	32,8 mm	2,4
Anterior crest curliness	1,5	0,7
Posterior crest curliness	2,1	0,3
Dorsal black collar	27,4 %	4,8
Ventral black collar	32,8 %	4,7
Occipital fold	55,8 %	9,6

Character	$\overline{X}$	S.D.
Ear patch	0,0 mm	0,0
Throat red	0,0 %	0,0
Orbital red	0,0 %	0,0
Dorsal spot number	23,7	4,2
Total spot barbs	5,2	0,7
Total within-spot barbs	3,5	0,6
Spot barb blueness	0,8	0,5
Chestnut blotch size	10,8 units	3,4
Chestnut blotch extent	54,2 %	19,7

Distribution: Figure 30

Genus Acryllium

Acryllium Gray 1840, List Gen. Bds., p.61.

Acryllium vulturinum (Hardwicke) 1834

(= OG 3 in Fig. 7)

Plate 1J

Numida vulturina Hardwicke 1834. Proc. Zool. Soc. London, p. 52.

Description: The largest guineafowl species; no crown, nape, throat or cere adornments; occiput covered by short, dense, downy chestnut-coloured feathers; rudimentary blue-grey wattles at gape; orbital and throat skin blue-grey; well-developed collar hackle; body plumage spotted with vermiculations; tarso-metatarsus usually with bump(s), scales pentagonal, not in rows; iris red; outer margins of secondaries lavender; furcula blade-shaped; caecum longer than 200 mm; abdominal plumage blue.

Statistics for quantitative characters: (N = 43)

Character	$\overline{X}$	S.D.
Bill length	28,5 mm	2,0
Wing length	293,3 mm	10,1
Tarso-metatarsus length	106,0 mm	6,9
Wattle basal width	7,2 mm	1,1
Wattle length	2,2 mm	0,6
Tarsal structure number	1,8	1,4
Tarsal structure length	2,6 mm	1,9

Distribution: Figure 9

Genus *Numida*

Numida Linne' 1766, *Syst*. *Nat*. ed. 12, 1: 273.

(= OG 10-14 in Fig. 7)

Numida meleagris meleagris (Linne') 1758

Plate 1K

(= OTU 4 in Figs. 11B and 31, and Table 6)

Phasianus meleagris Linne' 1758, *Syst*. *Nat*., ed. 10, p. 158.

Numida ptilorhyncha var. *major* Hartlaub 1884, *Abh*. *naturwiss*. *Ver*. *Bremen*, 8: 217.

Numida ptilorhyncha omoensis Neumann 1904, *Journ*. *f*. *Orn*., 52: 407.

Numida ptilorhyncha toruensis Neumann 1904, *Journ*. *f*. *Orn*., 52: 410.

Numida ptilorhyncha macroceras Erlanger 1904, *Orn*. *Monatsb*., 12: 97.

Numida ptilorhyncha neumanni Erlanger 1904, *Orn*. *Monatsb*., 12: 97.

Numida ptilorhyncha var. *inermis* DuBois 1915, *Ann*. *Mus*. *Congo*., *Zool*., 1: 18, 27.

Description: Larger than Guttera sp.; crown surmounted by a bony helmet; no occipital or throat adornments; well-developed, rounded, blue gape wattles; nape covered by short downy feathers; orbital and throat skin blue; cere surmounted by a tuft of cartilaginous bristles; collar black, finely barred with white; body plumage spotted with vermiculations; tarso-metatarsus lacks spurs, scales pentagonal, not in rows; iris brown; outer margins of secondaries banded black and white with vermiculations; furcula blade-shaped; caecum less than 150 mm; abdominal plumage spotted with faint vermiculations.

Statistics for quantitative characters: (N = 311)

(See Table 6 for statistical comparisons with neighboring subspecies)

Character	$\overline{X}$	S.D.
Bill length	25,0 mm	1,7
Wing length	262,2 mm	12,2
Tarso-metatarsus length	84,3 mm	5,2
Wattle basal width	14,1 mm	1,7
Wattle length	13,5 mm	3,0
Wattle percent blue	97,1 %	12,1
Helmet frontal length	22,6 mm	10,2
Helmet rear length	11,8 mm	7,5
Helmet central height	11,7 mm	8,0
Helmet basal length	19,2 mm	3,0
Helmet thickness	6,4 mm	1,7
Cere structure length	6,0 mm	3,6
Cere structure thickness	1,1 mm	0,4
Collar plumage	2,9	0,6
Nape filoplume length	14,9 mm	2,7
Nape filoplume antero-posterior coverage	58,3 %	17,4

Character	$\bar{X}$	S.D.
Nape filoplume lateral coverage	95,6 %	15,7
Nape filoplume density	2,9	0,3
Secondary remex outer web vermiculation	5,8	0,7
Wing covert barring	1,5	0,7
Dorsal vermiculation	3,0	0,7
Dorsal spot size	18,8 units	5,7

Distribution: Figure 45

Discussion: Two taxa *N.m. strasseni* (Reichenow 1911, *Orn. Monatsb.*, 19: 82) and *N.m. blancoui* (Grote 1936, *Orn. Monatsb.*, 44: 158) have been described from the region in which *N.m. galeata* and *N.m. meleagris* meet. Specimens attributed to these taxa are invariably intermediate between *galeata* and *meleagris* in discriminant analysis, and their collection sites fall in the region of high total COV between the parental forms (Fig. 44A). They are treated as intergrades.

Numida meleagris sabyi Hartert

Plate 1L

(= OTU 1 in Figs. 11B and 31, and in Table 7)

Numida sabyi Hartert 1919, *Bull. Brit. Orn. Cl.*, 39: 69.

Description: As *N.m. meleagris* except: gape wattles red; nape featheration long filoplumes restricted to the mid-dorsal line; no cere adornment.

Statistics for quantitative characters: (N = 4)

(See Table 7 for statistical comparisons with neighboring subspecies)

Character	$\overline{X}$	S.D.
Bill length	24,0 mm	0,8
Wing length	267,3 mm	10,3
Tarso-metatarsus length	88,3 mm	3,1
Wattle basal width	15,5 mm	1,0
Wattle length	17,8 mm	1,7
Wattle percent blue	0,0 %	0,0
Helmet frontal length	22,5 mm	3,0
Helmet rear length	15,0 mm	6,5
Helmet central height	16,3 mm	2,6
Helmet basal length	20,0 mm	3,4
Helmet thickness	5,3 mm	0,5
Cere structure length	0,0 mm	0,0
Cere structure thickness	0,0 mm	0,0
Collar plumage	2,5	0,6
Nape filoplume length	34,0 mm	7,1
Nape filoplume antero-posterior coverage	100,0 %	0,0
Nape filoplume lateral coverage	85,0 %	17,9
Nape filoplume density	3,0	0,0
Secondary remex outer web vermiculation	3,8	1,5
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,5	0,6
Dorsal spot size	7,2	0,5

Distribution: Figure 45

Discussion: Although this taxon is represented by only four specimens, its validity was upheld owing to its isolation and correspondence with criteria set for subspecies.

Numida meleagris galeata Pallas, 1767

Plate 1M

(= OTU 2 in Figs. 11B and 31, and Tables 6 and 7)

Numida galeata Pallas 1767, Spic. Zool., 1: 13, 15.

Numida marchei Oustalet 1882, Ann. Sci. Nat., Zool., 13: 1.

Description: As N.m. sabyi except smaller with collar plumage grey-to blue-grey.

Statistics for quantitative characters: (N = 137)

(See Tables 6 and 7 for statistical comparisons with neighboring subspecies)

Character	$\overline{X}$	S.D.
Bill length	22,3 mm	1,8
Wing length	251,4 mm	14,6
Tarso-metatarsus length	81,8 mm	6,4
Wattle basal width	14,2 mm	1,9
Wattle length	15,5 mm	2,9
Wattle percent blue	8,3 %	4,3
Helmet frontal length	15,5 mm	5,8
Helmet rear length	7,0 mm	2,5
Helmet central height	5,8 mm	2,9
Helmet basal length	18,6 mm	3,3
Helmet thickness	4,9 mm	1,5

Character	$\overline{X}$	S.D.
Cere structure length	0,3	0,9
Cere structure thickness	0,3 mm	1,6
Collar plumage	0,1	0,3
Nape filoplume length	20,4 mm	4,3
Nape filoplume antero-posterior coverage	90,9 %	16,0
Nape filoplume lateral coverage	70,8 %	33,3
Nape filoplume density	2,8	0,4
Secondary remex outer web vermiculation	4,4	1,3
Wing covert barring	0,6	0,2
Dorsal vermiculation	3,6	0,6
Dorsal spot size	12,2 units	3,8

Distribution: Figure 45

Numida meleagris somaliensis Neumann, 1899

Plate 1N

(= OTU 5 in Figs. 11B and 31, and Tables 6 and 8)

Numida somaliensis Neumann 1899, *Orn. Monatsb.*, 7: 25.

Description: As *N.m. meleagris* except: gape wattles blue with red tips; cere tufts much longer and more numerous; and nape featheration long filoplumes restricted to the mid-dorsal line.

Statistics for quantitative characters: (N = 44)

(See Tables 6 and 8 for statistical comparisons with neighboring subspecies)

Character	$\overline{X}$	S.D.
Bill length	25,1 mm	1,4
Wing length	265,5 mm	11,0
Tarso-metatarsus length	84,2 mm	4,2
Wattle basal width	13,6 mm	2,4
Wattle length	14,6 mm	3,3
Wattle percent blue	87,5 %	14,9
Helmet frontal length	20,0 mm	7,6
Helmet rear length	10,3 mm	6,0
Helmet central height	12,9 mm	12,3
Helmet basal length	17,4 mm	3,9
Helmet thickness	6,6 mm	1,3
Cere structure length	13,3 mm	7,6
Cere structure thickness	1,0 mm	0,5
Collar plumage	3,0	0,7
Nape filoplume length	15,8 mm	3,1
Nape filoplume antero-posterior coverage	41,5 %	20,7
Nape filoplume lateral coverage	53,3 %	34,0
Nape filoplume density	2,8	0,5
Secondary remex outer web vermiculation	5,2	2,0
Wing covert barring	0,8	0,6
Dorsal vermiculation	2,4	0,9
Dorsal spot size	23,6 units	6,5

Distribution: Figure 45

Numida meleagris marungensis Schalow, 1884

Plate 10

(= OTU 6 in Figs. 11B and 31, and Tables 7 and 9)

Numida coronata marungensis Schalow 1884, *Zeitschr. ges. Orn.*, 1: 105.

Numida marungensis maxima Neumann 1898, *Orn. Monatsb.*, 6: 21.

Description: The largest subspecies; helmet characteristically thicker and longer basally; long gape wattles, blue with red tips; no cere adornment, and wattles pointed.

Statistics for quantitative characters: (N = 97)

(See Tables 7 and 9 for statistical comparisons with neighboring subspecies)

Character	$\overline{X}$	S.D.
Bill length	26,7 mm	1,4
Wing length	283,5 mm	11,1
Tarso-metatarsus length	90,2 mm	4,7
Wattle basal width	11,8 mm	1,5
Wattle length	16,6 mm	3,1
Wattle percent blue	73,6 %	8,5
Helmet frontal length	47,7 mm	8,5
Helmet rear length	13,4 mm	5,1
Helmet central height	18,7 mm	3,8
Helmet basal length	39,2 mm	3,7
Helmet thickness	12,4 mm	2,6
Cere structure length	0,3 mm	0,7
Cere structure thickness	0,3 mm	0,9
Collar plumage	2,9	0,7
Nape filoplume length	26,3 mm	3,3

Character	$\bar{X}$	S.D.
Nape filoplume antero-posterior coverage	77,3 %	17,5
Nape filoplume lateral coverage	29,6 %	17,5
Nape filoplume density	2,9	0,4
Secondary remex outer web vermiculation	0,9	1,0
Wing covert barring	0,0	0,0
Dorsal vermiculation	1,5	0,8
Dorsal spot size	23,5 units	4,5

Distribution: Figure 45

Discussion: *N.m. frommi* (Kothe 1911, *Orn. Monatsb.*, 19: 13) and *N.m. rikwae* (Reichenow 1900, *Orn. Monatsb.*, 8: 40) have been described from the region between *N.m. marungensis* and *N.m. mitrata*, and *N.m. callewaerti* (Chapin 1932, *Am. Mus. Novit.*, p. 1) from the region between *N.m. galeata* and *N.m. marungensis*. Specimens attributed to these three forms are invariably intermediate between two subspecies in discriminant analyses, and their collection localities fall within regions of high total COV (Fig. 44A). They are treated as intergrades.

Numida meleagris reichenowi Ogilvie-Grant, 1894

Plate 1P

(= OTU 8 in Figs. 11B and 31, and Tables 6 and 8)

Numida reichenowi Ogilvie-Grant 1894, *Ibis*, p. 536.

Description: Similar to, and nearly as large as *N.m. marungensis*; except wattles rounded and red, helmet taller and sabre-shaped, and nape featheration less dense.

Statistics for quantitative characters: (N = 121)

(See Tables 6 and 8 for statistical comparisons with neighboring subspecies)

Character	$\bar{X}$	S.D.
Bill length	24,7 mm	1,6
Wing length	282,2 mm	9,1
Tarso-metatarsus length	90,7 mm	11,4
Wattle basal width	11,9 mm	1,4
Wattle length	12,8 mm	2,5
Wattle percent blue	12,9 %	29,2
Helmet frontal length	44,2 mm	10,9
Helmet rear length	29,5 mm	9,8
Helmet central height	29,5 mm	9,0
Helmet basal length	24,9 mm	2,9
Helmet thickness	8,3 mm	1,7
Cere structure length	0,7 mm	1,8
Cere structure thickness	0,4 mm	0,8
Collar plumage	2,9	0,5
Nape filoplume length	20,5 mm	3,6
Nape filoplume antero-posterior coverage	63,8 %	49,2
Nape filoplume lateral coverage	30,0 %	21,3
Nape filoplume density	2,5	0,6
Secondary remex outer web vermiculation	2,3	1,3
Wing covert barring	0,2	0,5
Dorsal vermiculation	2,4	0,7
Dorsal spot size	23,2 units	3,5

Distribution: Figure 45

Discussion: N.m. intermedia (Neumann 1898, Orn. Monatsb., 6: 21), and N.m. ansorgei (Hartert 1899, In Ansorge's Under the African Sun, p. 331) has been described from the transition area between N.m. meleagris and N.m. reichenowi. N.m. uhehensis (Reichenow 1898, Orn. Monatsb., 6: 88) has been described from the transition area between N.m. mitrata and N.m. reichenowi. For reasons given in other such instances, these forms are treated as intergrades.

Numida meleagris mitrata Pallas, 1767

Plate 1Q

(= OTU 7 in Figs. 11B and 31, and Tables 6, 8-10)

Numida mitrata Pallas 1767, Spic. Zool., 1: 18.

Description: Smaller than the last two subspecies; phenotype as N.m. marungensis except that helmet less well developed.

Statistics for quantitative characters: (N = 293)

(See Tables 6, 8, 9 and 10 for statistical comparisons with neighboring subspecies)

Character	$\overline{X}$	S.D.
Bill length	25,7 mm	1,3
Wing length	275,4 mm	8,2
Tarso-metatarsus length	86,1 mm	4,2
Wattle basal width	10,9 mm	1,5
Wattle length	16,8 mm	3,0
Wattle percent blue	64,6 %	9,3
Helmet frontal length	38,3 mm	9,5
Helmet rear length	18,8 mm	5,1

Character	X̄	S.D.
Helmet central height	19,4 mm	7,9
Helmet basal length	23,3 mm	3,8
Helmet thickness	8,3 mm	2,0
Cere structure length	0,2 mm	0,8
Cere structure thickness	0,2 mm	0,7
Collar plumage	3,1	0,6
Nape filoplume length	23,0 mm	3,9
Nape filoplume antero-posterior coverage	59,1 %	19,7
Nape filoplume lateral coverage	23,0 %	8,3
Nape filoplume density	2,5	0,7
Secondary remex outer web vermiculation	1,5	1,3
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,2	0,7
Dorsal spot size	19,4 units	4,5

Distribution: Figure 45

Numida meleagris coronata Gurney, 1868

Plate 1R

(= OTU 10 in Figs. 11B and 31, and Table 10)

Numida coronata Gurney 1868, *Ibis*, p.253.

Numida transvaalensis Neumann 1899, *Orn. Monatsb.*, 7: 26.

Numida papillosa limpopoensis Roberts 1924, *Ann. Transv. Mus.*, 10: 77.

Description: As *N.m. marungensis* except: smaller overall size; decidedly thinner and taller helmet, collar plumage more streaked than barred with white.

Statistics for quantitative characters: (N = 136)

(See Table 10 for statistical comparisons with neighbouring subspecies)

Character	$\overline{X}$	S.D.
Bill length	25,1 mm	1,7
Wing length	270,9 mm	7,0
Tarso-metatarsus length	85,6 mm	5,2
Wattle basal width	11,0 mm	1,5
Wattle length	18,7 mm	3,2
Wattle percent blue	61,5 %	10,0
Helmet frontal length	54,8 mm	9,6
Helmet rear length	25,1 mm	5,8
Helmet central height	24,7 mm	5,3
Helmet basal length	25,8 mm	2,9
Helmet thickness	8,8 mm	2,1
Cere structure length	0,4 mm	0,7
Cere structure thickness	0,3 mm	0,4
Collar plumage	4,2	1,1
Nape filoplume length	18,5 mm	4,6
Nape filoplume antero-posterior coverage	40,0 %	22,8
Nape filoplume lateral coverage	15,3 %	4,9
Nape filoplume density	1,2	0,8
Secondary remex outer web vermiculation	2,5	1,4
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,6	0,6
Dorsal spot size	20,4 units	5,6

Distribution: Figure 45

Discussion: Numida meleagris papillosa (Reichenow 1894, Orn. Monatsb., 2: 145) has been described from the region south of Lake Ngami, i.e. the transition area between N.m. damarensis and N.m. coronata. For reasons given in other instances this form is taken to be an intergrade.

Numida meleagris damarensis Roberts, 1917

Plate 1S

(= OTU 9 in Figs. 11B and 31, and Tables 9-11)

Numida papillosa damarensis Roberts 1917, Ann. Transv. Mus., 6: 2.

Description: As N.m. coronata except: well developed papilli at cere; collar spotted; helmet less well developed.

Statistics for quantitative characters: (N = 102)

(See Tables 9, 10 and 11 for statistical comparisons with neighbouring subspecies)

Character	$\overline{X}$	S.D.
Bill length	24,6 mm	1,6
Wing length	273,2 mm	7,6
Tarso-metatarsus length	83,4 mm	3,9
Wattle basal width	11,1 mm	1,3
Wattle length	18,9 mm	2,8
Wattle percent blue	64,4 %	8,5
Helmet frontal length	45,2 mm	7,5
Helmet rear length	22,9 mm	4,6
Helmet central height	22,3 mm	4,3
Helmet basal length	19,7 mm	3,1

Character	$\overline{X}$	S.D.
Helmet thickness	9,2 mm	1,3
Cere structure length	3,7 mm	1,5
Cere structure thickness	2,9 mm	0,3
Collar plumage	4,9	1,0
Nape filoplume length	12,3 mm	8,5
Nape filoplume antero-posterior coverage	24,7 %	27,2
Nape filoplume lateral coverage	9,7 %	8,0
Nape filoplume density	0,5	0,7
Secondary remex outer web vermiculation	3,8	1,4
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,6	0,5
Dorsal spot size	22,5 units	8,5

Distribution: Figure 45

Phylogeny

(a) Primitive and derived character-states

The following hypothetical primitive-derived sequences are postulated for the characters listed in Appendix 1. The number in parentheses following each character name is its number in Appendix 1.

Crown (1), occipital (2), nape (3) and throat (6) adornments

All francolins and guineafowl-phasianid hybrids have feathered crowns, occiputs and napes. Very few francolins have crests, and then only rudimentary ones. No francolin has a throat fold. Therefore, a naked crown, nape or occiput is taken to be derived relative to the feathered condition. Among guineafowl with feathered crowns, a well-developed crest of downy feathers is taken to be derived relative to a short crest of downy feathers, and a well-developed crest of bristly, erect filoplumes derived relative to a well-developed crest of downy feathers. The latter assumption is based on the idea that a modification of a downy, drooping crest to an erect bristly crest allows species or individual recognition in social encounters. Also, among guineafowl which have these regions unfeathered, any likely secondary elaboration of the unfeathered condition (e.g. a helmet, long filoplumes, patches of skin of contrasting colour, folds of skin) is taken to be derived, since these structures may be adaptive in a social (individual and species identification) or physio-ecological (thermoregulation, crypsis) contexts (Brown 1963; Reynolds 1977). Finally, folded throat skin is taken to be derived relative to the unfolded condition.

Orbital (4), throat (5), and gape wattle (8) skin colour

In nearly all francolins, areas of naked skin on the head and throat are red. Therefore, red is taken to be the primitive condition relative to any other colour for the above characters.

Gape adornment (7)

No francolin has a gape wattle, and guineafowl-phasianid hybrids have at most rudimentary wattles. Therefore, well-developed gape wattles are taken to be derived.

Cere adornment(9)

No francolin or guineafowl-phasianid hybrid has an adornment at the cere. Therefore, any cere adornment is taken to be derived.

Collar(10), body(11) and abdominal(18) plumage

The plumage of francolins and guineafowl-phasianid hybrids is usually dark, often streaked, barred or vermiculated with lighter colours. Moreover, none of the above possess an elaborate collar-hackle. Therefore, among guineafowl, white or blue plumage is taken to be derived relative to dark plumage, and spotted plumage derived relative to barred, streaked or vermiculated plumage. Among guineafowl with spotted plumage, spotted plumage without peripheral vermiculation is taken to be derived relative to that with vermiculation. Also, regardless of plumage pattern, an elaborate collar hackle is taken to be derived relative to an undifferentiated collar.

Tarso-metatarsal scales(12) and adornment(13)

All francolins have their posterior tarso-metatarsus covered by small imbricated scales in rows. In nearly all francolins, the male at least possesses spurs. Therefore, among guineafowl any modification of the spurred condition (e.g. naked tarsi or tarsal bumps), and any scalation pattern other than that described above are taken to be derived conditions.

Iris colour(14)

Nearly all francolins have brown eyes. Therefore, among guineafowl, a red iris is taken to be derived.

Outer margins of secondaries(15)

In most francolins the secondaries are brown to grey, sometimes faintly streaked or vermiculated with white. In only a few francolins do the outer margins of these feathers appear to be strikingly different from the general body plumage. Therefore, among guineafowl, secondaries that contrast with the general body plumage pattern, i.e. character states 2-4, are taken to be derived.

Furcula(16)

All francolins have blade-shaped furculas. Therefore, a hollow furcula is taken to be derived.

Caecum length(17)

In francolin and guineafowl of the genera Numida and Guttera caecum length is about 16% that of the large and small intestines combined (Beddard 1898). There is no information on caecum length for Agelastes sp. In a Acryllium vulturinum, the length of this organ is more than 23% that of the intestines (Beddard 1898). Therefore, among guineafowl a relatively long caecum is taken to be derived.

(b) Phyletic analysis

The most parsimonious guineafowl phylogeny based on primitive-derived character sequences is given in Figure 46. In this figure, the four shared derived character-states comprising character suite 1 delineate the subfamily Numidinae from francolin-like phasianids. These derived character-states, common to all guineafowl taxa (Ghigi 1936), and their primitive counterparts (in parentheses) are:

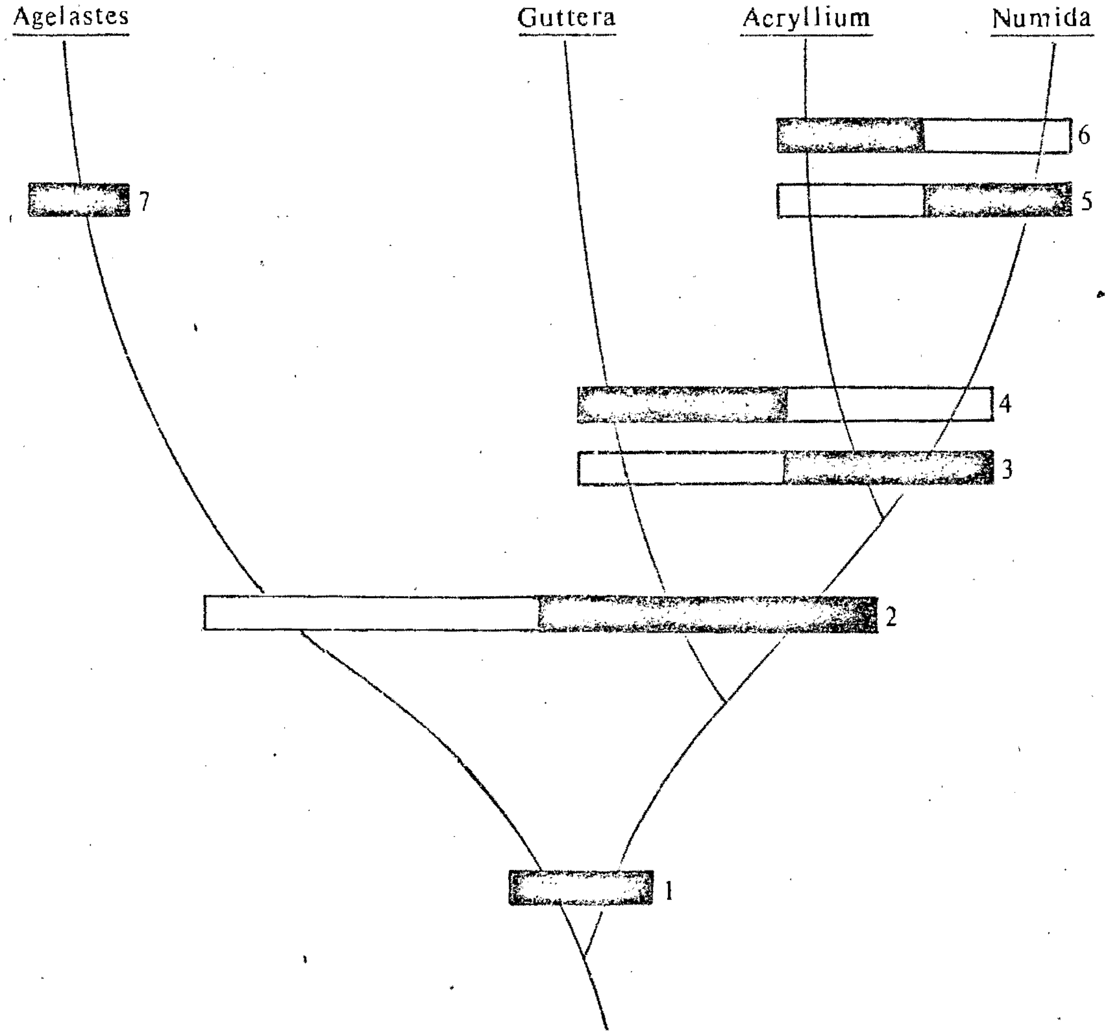

Fig. 46. A hypothetical phylogeny for the Numidinae. Each monophyletic lineage is characterized by a suite of derived character states (▨), the primitive counterparts of which (▭) are found in members of the co-ordinate sister-group.

1. large size (small size);
2. third and fourth sacral vertebrae with robust transverse processes (only third vertebra with such a process);
3. second metacarpal lacks a backward process (process present)
4. largely naked head with at least rudimentary wattles (feathered head, and no wattles)

Agelastes sp., with their preponderance of primitive character-states, probably more closely resemble the proto-guineafowl than does any other member of the subfamily. These two species share only one derived character-state, white abdominal plumage. Adult A. niger (Plate 1B) shows primitive character-states for all characters investigated except for its naked occiput. The white abdominal plumage linking it to A. meleagrides (Plate 1A) is present only in juvenile birds. It is also possible that the additional derived character-states attributable to Agelastes due to the naked head and neck of A. meleagrides are the result of convergent evolution, and do not suggest any closer affinity to other guineafowl genera.

Character suite 2 consists of three shared derived character-states (spotted body plumage; non-imbricated, pentagonal scalation of the posterior tarso-metatarsi; and unspurred tarso-metatarsi) which link the three remaining genera. Character suite 3 consists of three shared derived character-states (unfeathered crown; blue orbital and throat skin) which link Acryllium (Plate 1J and Numida (Plate 1K-S). Character suite 4 consists of four shared derived character states (folded occipital skin; white outer secondary margins; body plumage spotted without peripheral vermiculation; hollow furcula) which link the two Guttera species (Plate 1C-I), and distinguish them from Acryllium and Numida. Character suite 5 consists of four derived character-states (helmeted crown; naked occiput; well-developed wattles; cere with tufts or papilli) which distinguish Numida spp. (Plate 1K-S) from Acryllium (Plate 1J). Character suite 6 consists of three derived character-states (hackled collar; long caecum; red eye) which distinguish Acryllium from Numida.

Speciation

(a) Origin and derivation of the Numidinae

Several hypotheses have been offered concerning the origin and evolution of the Numidinae. Ghigi (1936) states that the proto-guineafowl originated in Africa, and probably was derived from a francolin ancestor. This hypothesis is based on the fact that guineafowl are found only in Africa (Arabian and Malagasy populations being probably the result of introductions by man), and phenotypic similarities between the most primitive guineafowl (Agelastes spp.) and Francolinus spp. Cracraft (1973), in support of his hypothesis of a Gondwanaland origin for the Galliformes, suggests a North American origin from New World quails. Olson (1974), based on anlaysis of a single Eocene fossil femur from Mongolia, suggests a possible Asiatic origin from a pheasant-like bird. This bone is intermediate in shape between femurs of extant pheasants and Agelastes niger. However, it is only about 70% the length of an Agelastes femur, i.e. well within the size range of many extant francolins (Mackworth-Praed & Grant

1952, 1962, 1970).

There is no compelling evidence favouring any of these three hypotheses. When, and if, sufficient information comes to the fore, it will probably support elements of all three. Accordingly, the working hypothesis taken herein is: The Numidinae are derived from a francolin-like Asiatic phasianid; but evolution and radiation of extant guineafowl has occurred solely in Africa.

(b) Evolution of genera

The first opportunity for colonization of Africa by Asiatic faunal elements arose with the mid-Miocene (ca 17-18 m.y.b.p.) union of the African and Asian plates (Axelrod & Raven in press). At this time, forest was much more extensive in Africa than at present, possibly even exceeding limits depicted in Figure 4. However, the colonization corridor connecting these two continents was covered by relatively arid savanna vegetation in the mid-Miocene, and has almost certainly not had more lush vegetation since then (Axelrod & Raven in press). Thus, any Asiatic ancestral guineafowl was probably a bird which lived in savanna habitat, and, upon its arrival in Africa encountered vast forest, and much less extensive savanna adaptive zones. Since Agelastes sp. possess so few derived character-states (see pp. 54-55), it is likely that radiation of proto-Agelastes into the forest took place soon after colonization.

With the joining of the two continents, the mild climate that favoured widespread forest vegetation throughout the late Cretaceous and early Tertiary began to deteriorate. Africa became progressively more arid; and savanna and desert-steppe biomes expanded, at the expense of forest, throughout the latter Miocene and Pliocene (Axelrod & Raven in press). Moreover, this period was characterized by widespread uplifting, rifting and tectonic activity adding considerable topographic diversity to the continent, and partitioning its expanding and contracting biomes (Axelrod & Raven in press). These conditions would have favoured radiation in and into expanding forest-edge, savanna and desert-steppe biotopes; and it is possible that proto-Guttera, Numida, and Acryllium were the result of such Mio-Pliocene radiations.

(c) Evolution of species and subspecies

After the uniformly arid Pliocene, the relatively rapid wet-dry climatic fluctuations and continuing rifting and mountain building during the Pleistocene provided additional opportunities for radiation in Africa (Moreau 1966; Livingstone 1975; Hamilton 1974; Axelrod & Raven in press). Expanding forest and wetlands in relatively moist phases would have divided savanna biome into more or less isolated tracts, and restricted desert to relatively small refugia in Somalia, northern and south-western Africa. If wet-phase forest and wetlands were distributed as in Figure 4, Acryllium vulturinum (Fig.9), and sub-Saharan subspecies attributed to Numida meleagris herein (Fig. 45) would have had the opportunity to diverge in isolation, since portions of their present-day ranges are encompassed by isolated tracts of savanna and desert-steppe refugia. Also, expanding forest may have favoured a second radiation into relatively widespread lowland forest, culminating in Guttera plumifera.

During arid phases, forest-living guineafowl, and Moroccan N. meleagris, would have been restricted to island-like refugia. If vegetation were distributed as in Figure 5, N.m. sabyi (Fig. 45), Agelastes meleagrides (Fig. 9), A. niger (Fig. 9), Guttera plumifera plumifera and G.p. schubotzi (Fig. 13) and, to a lesser extent, forest-edge taxa (subspecies attributed to G. pucherani) had the opportunity to diverge in allopatry, since portions of their present-day ranges would have had access to refuges of suitable biotope. Thus, we need look no further than the Pleistocene for biogeographic events which could have allowed allopatric evolution of extant guineafowl species and subspecies.

Biogeography

(a) Results

A map of hypothetical African avifaunal zones drawn from evolutionary patterns found in guineafowl is given as Figure 47. Zonal boundary lines in this map agree remarkably well with those in Chapin's faunal map (Fig. 48) based on distribution patterns of "many species and races of birds", and with species and subspecies boundaries in distribution maps of selected francolin species and subspecies (Figs. 49 & 50). In the hypothetical avifaunal map, sub-region boundaries are those of the relatively phenotypically homogeneous (i.e. no subspecies) genera, Agelastes and Acryllium (Fig. 9). Provincial boundaries coincide closely with those of species, and district boundaries with those of subspecies (Figs. 13, 30 and 45). Chapin (1932) neither lists the taxa whose ranges

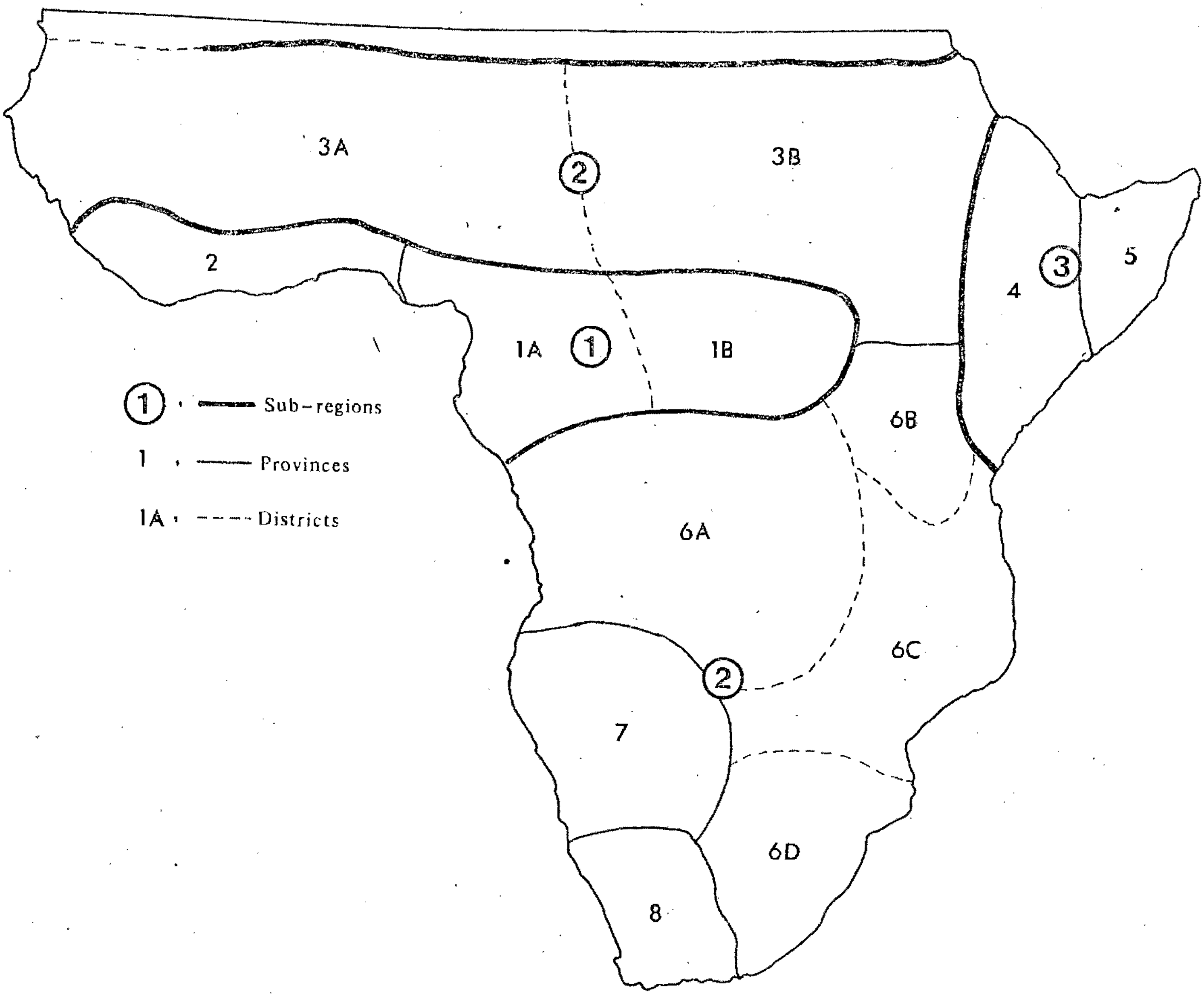

Fig. 47. Hypothetical African avifaunal zones based on evolutionary patterns found in guineafowl.

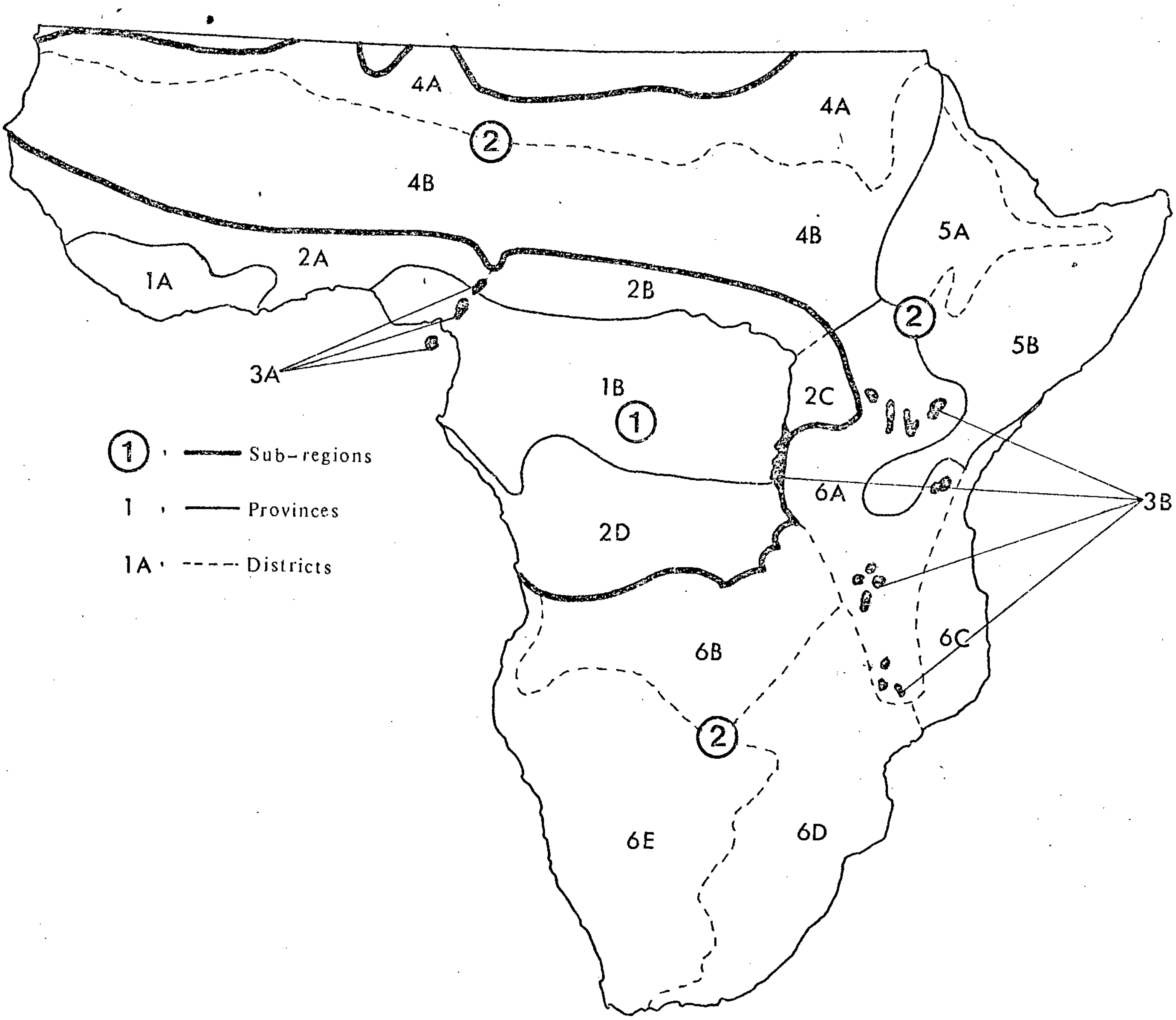

Fig. 48. African avifaunal zones based on analysis of bird species and subspecies distributions (after Chapin 1932).

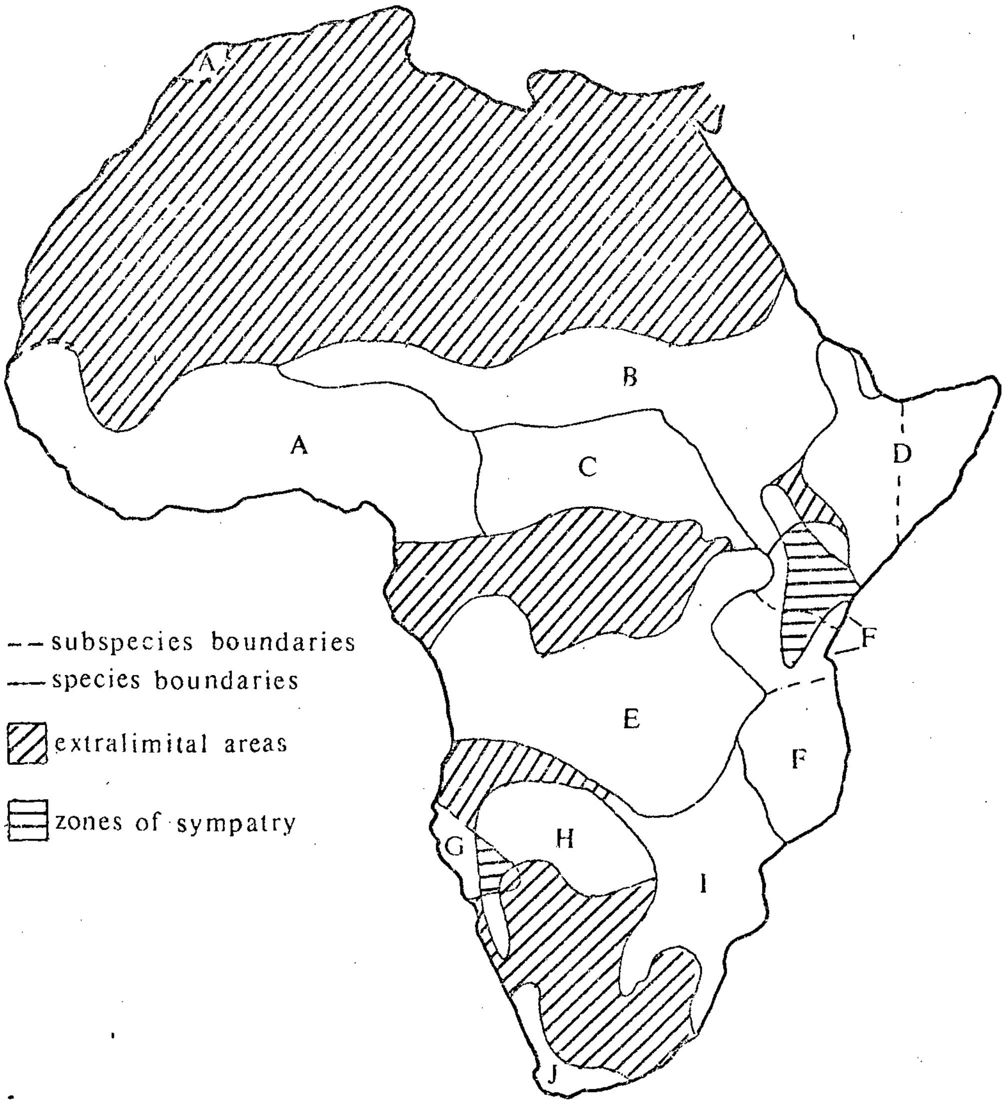

Fig. 49. Distributions of selected non-forest francolin species and subspecies (after Hall 1963 and Mackworth-Praed & Grant 1952). A = Francolinus bicalcaratus ayesha; B = F. clappertoni; C = F. icterorhynchus; D = F. leucoscepus; E = F. afer cranchii, intercedens and harterti; F = F. hildebrandti; G = F. hartlaubi; H = F. adspersus; I = F. natalensis; J = F. capensis.

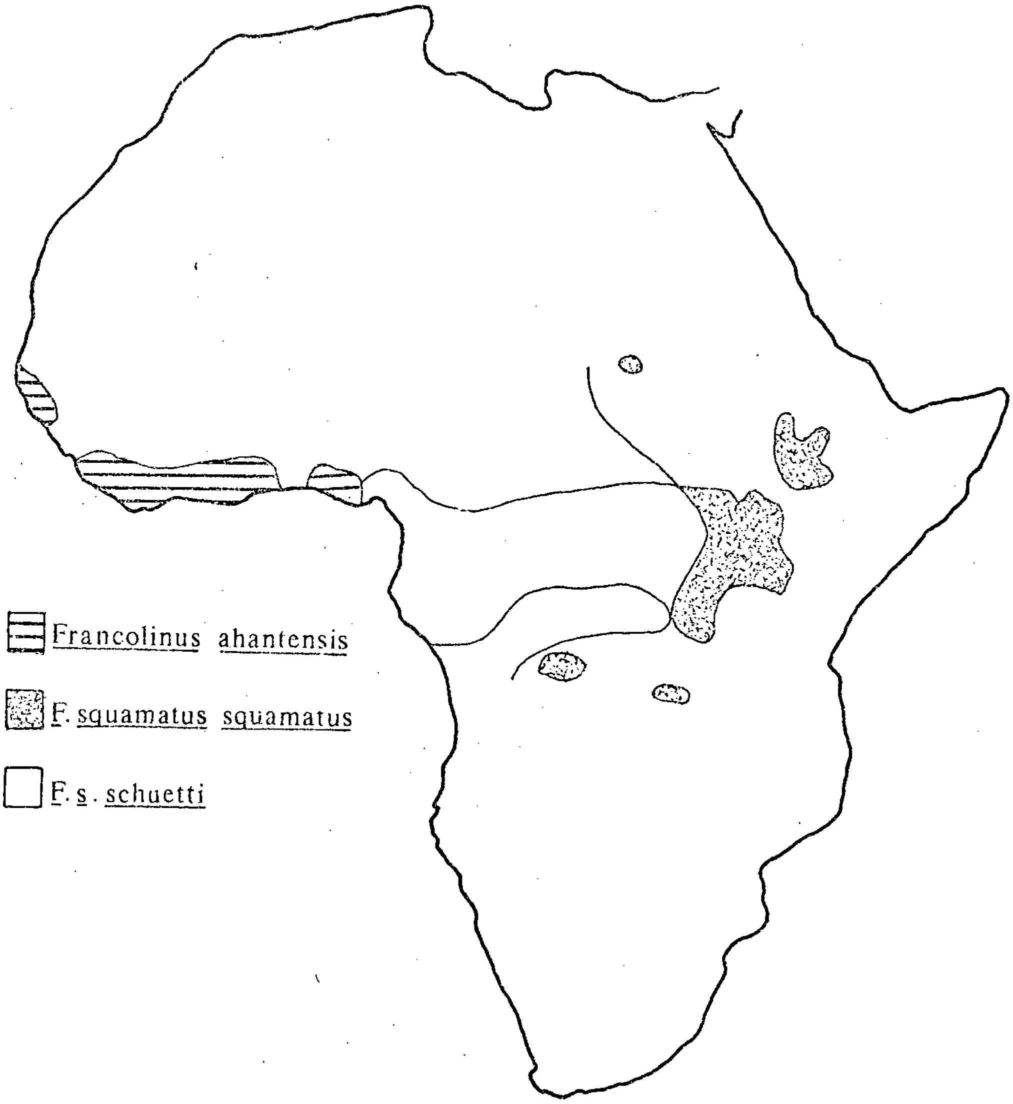

Fig. 50. Distributions of selected forest-living francolin species and subspecies (after Hall 1963).

form the basis of his map, nor specifies criteria used in distinguishing sub-regions, provinces and districts, The hypothetical map differs markedly from Chapin's in that it:

1. restricts the forest sub-region (commonly labelled ① in Figs. 47 & 48) to an area somewhat larger than Chapin's province no. 1;
2. divides his province no. 4 into eastern and western, rather than northern and southern districts;
3. divides his district 1B into two districts (1A and 1B in Fig. 47).
4. reapportions territory within the commonly labelled province no. 6;
5. divides his district no. 6E into two provinces (7 and 8 in Fig. 47);
6. does not recognize montane provinces.

The only differences between the hypothetical map and the francolin distribution maps are relatively minor shifts in boundary lines, and a still finer subdivision of districts by francolins. Also, district boundaries, which separate guinea-fowl subspecies, often delimit francolin species.

(b) Discussion

It is impossible to resolve differences between the two avifaunal maps in zonal boundaries and hierarchical assessments, since Chapin does not specify the data base and methodology underlying his map. His decision to unite the continuous block of lowland forest with the surrounding forest-savanna mosaic to form sub-region ① (Fig. 48) is probably due to the abundance, in the latter, of relict patches of lowland forest and gallery forests, which provide suitable habitats for forest birds. Indeed, when distributional data are lacking or equivocal, Chapin (1932) and other zoogeographers (e.g. Davis 1962; Moreau 1966) seem to have relied on the distribution of vegetation as a predictor of bird distributions. The division of Chapin's province no. 4 and district 1B into east-west districts in the hypothetical map is due to effects (on guineafowl evolution) of probable past forest-wetland and savanna barriers that bisected these zones during the Pleistocene (see Figs. 4 and 5). The reapportionment of territory to districts in the commonly labelled province no. 6 may reflect a lack of clear-cut avian distributional patterns within that province, a possibility already suggested by Benson and Irwin (1966). The necessity of partitioning Chapin's district no. 6E was anticipated by that author (Chapin 1932: 89), and has been done by others authors (Moreau 1952; Davis 1962). The lack of montane avifaunal zones in the hypothetical map is certainly due to the submontane altitudinal limitation of guineafowl.

(c) Conclusions

The results of comparisons of the hypothetical avifaunal map with Chapin's map and francolin distribution maps suggest three tentative conclusions, which can serve as hypotheses in future evolutionary and biogeographic studies.

1. Distribution patterns found in guineafowl can be used as models for broad patterns exhibited by African bird

species and subspecies other than those dependent on montane habitats.

2. At least some francolin species and subspecies have evolved as a result of factors that have been important in the evolution of guineafowl.
3. Physical and ecological barriers which have only allowed subspeciation in guineafowl have been sufficient to bring about speciation in francolins.

The first hypothesis is being tested by a cluster analysis (Hagemier & Stults 1964; Sneath & Sokal 1973) of 119 equally sized areas of Africa according to 1099 passerine species and well-marked subspecies in Hall & Moreau (1970)·(Crowe in prep.). The preliminary results of this study, summarized in Figure 51, are consistent with that hypothesis. The second and third hypotheses can be tested, if patterns of character variation in francolin taxa are analyzed using methodology outlined herein, and the results are compared to those for guineafowl.

SYNTHESIS

Taxonomy, phylogeny, speciation and biogeography are intimately related aspects of guineafowl evolution. Their necessary separation under different headings in the present study has been somewhat detrimental to the understanding of each. Accordingly, this section attempts to synthesize the author's conception of evolution in guineafowl (summarized in Figure 52).

Guineafowl are characteristically African birds. Although

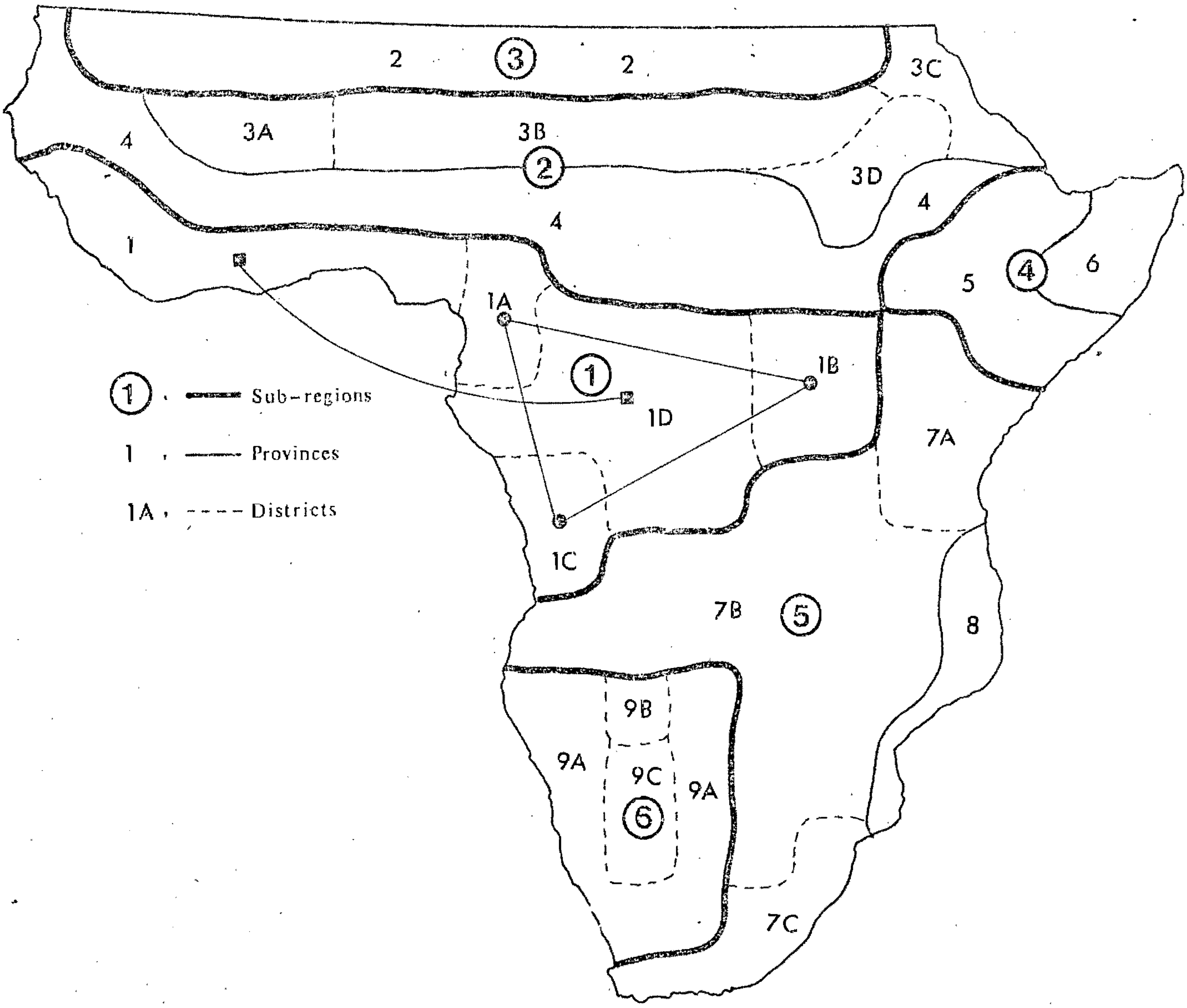

Fig. 51. Hypothetical African avifaunal zones based on a cluster analysis of 119 equally sized blocks of Africa according to 1099 species and subspecies in Hall & Moreau (1970).

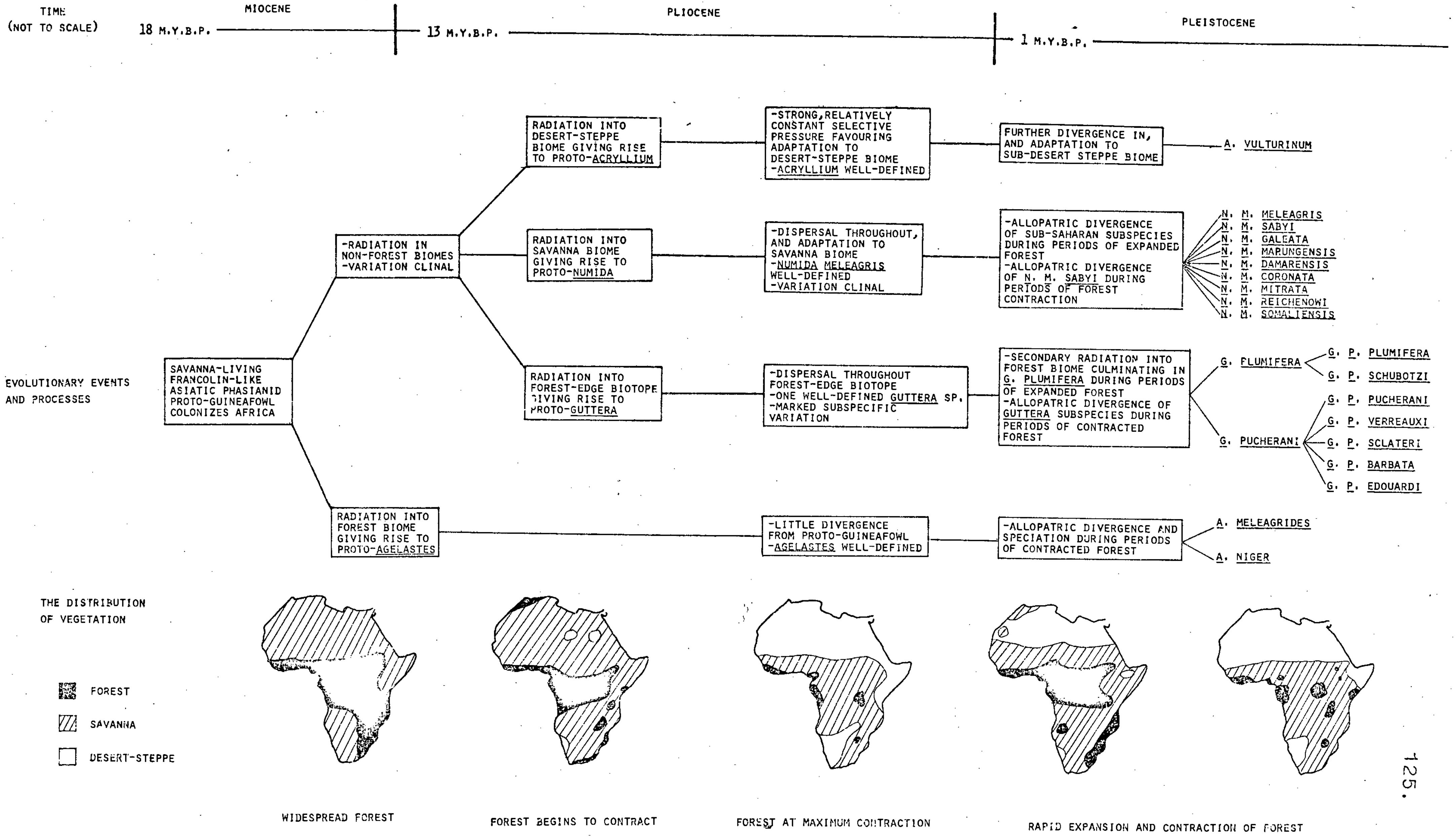

Fig. 52. A hypothetical evolutionary history of guineafowl.

the likely ancestral guineafowl was an Asiatic francolin-like phasianid which could live in arid savanna habitat, the evolution that has led to extant guineafowl taxa occurred solely in Africa. Moreover, biogeographic patterns derived from guineafowl species and subspecies boundaries closely parallel broad patterns found in African birds as a whole. The Asiatic ancestral guineafowl probably traversed the arid-savanna corridor linking Asia and Africa soon after the mid-Miocene union of the two continents. This savanna-living bird encountered an African continent dominated by forest, possibly unoccupied by potential competitors. Such conditions favoured radiation into the forest, and it is likely that Agelastes, the most primitive (i.e. most francolin-like) guineafowl genus is a result of an early radiation into forest.

Relatively soon (on a geological time scale) after this successful invasion of forest, the climate of Africa became more arid. Throughout the latter Miocene and Pliocene savanna and desert biomes expanded at the expense of forest. Such a situation favoured radiation in non-forest biomes, and into the expanding forest-edge biotope, and it is possible that proto-Numida, Acryllium and Guttera were the result of such radiations. The relatively uniformly arid conditions of the Pliocene subjected these four lineages to strongly divergent selective pressures, and it is probable that the genera recognized herein were already well-defined at the beginning of the Pleistocene.

The arid climate of the Pliocene was replaced by a fluctuating wet-dry climate in the Pleistocene. These climatic fluctuations had profound effects on the distribution of African biomes. During moist phases, the forest biome expanded considerably beyond its present extent, partitioning non-forested biomes into more or less isolated tracts. Desert biome was confined to relative small areas, and savanna biome bridged the western Sahara, allowing dispersal of *N. meleagris* into North Africa. Sub-saharan subspecies of *N. meleagris* are the result of divergence in these wet-phase isolated tracts. Also, expanded forest during mesic phases could have allowed à second radiation into lowland forest, culminating in *Guttera plumifera*. During arid phases, the forest contracted into island-like refugia, and *N.m. sabyi* was isolated, and presumably diverged from sub-Saharan populations. The species *Agelastes meleagrides* and *A. niger*, and subspecies in the genus *Guttera* are also a result of divergence in these refugia. The fact that *Guttera* subspecies are much more well-marked than are those of *N. meleagris* suggests that isolation in forest refugia has been more effective than in tracts of savanna partitioned during wet-phases.

ACKNOWLEDGEMENTS

I am grateful to P. Clancey of the Durban Museum and Art Gallery, F. Gill of the Philadelphia Academy of Natural Sciences, M. Irwin of the National Museum of Rhodesia (Bulawayo), A. Kemp of the Transvaal Museum, M. Louette of the Musee Royal de l'Afrique Centrale, R. Paynter of the Museum of Comparative Zoology, L. Short of the American Museum of Natural History, D. Snow of the British Museum (Natural History), and M. Traylor of the Field Museum of Natural History for allowing me access to the guineafowl in their institutions' collections. Mrs. J. Adams painted the guineafowl shown in the colour plate. Mr S. Piper helped with contour map analysis. Dr L. Throckmorton provided intitial encouragement to begin this analysis. Prof. W.R. Siegfried provided the necessary stimulus to finish the analysis. Mr R. Brooke commented critically on several drafts of the paper. My wife Anna helped in all phases of the study, particularly with illustrations and data processing. Generous grants from De Beers Consolidated Mines Ltd. and the University of Cape Town were essential to the project. The inclusion of the colour plate was made possible by a grant from the University of Cape Town Editorial Board. The De Beers and U.C.T. Computer Centres gave valuable advice on data processing and computer time.

REFERENCES

Archer, G.A. & Godman, E. 1937. The birds of Somaliland and the Gulf of Aden. Vol. II. London: Gurney & Jackson.

Axelrod, D.I. & Raven, P.H. (in press) Late Cretaceous and Tertiary vegetation history of Africa. Monographie Biologica.

Bannerman, D.A. 1930. Birds of tropical west Africa. Vol. I. London: Crown Agents.

Beddard, F.E. 1898. The structure and classification of birds. London: Longmans, Green & Co.

Benson, C.W. & Irwin, M.P.S. 1966. The brachystegia avifauna. Ostrich, Suppl. 6: 297-321.

Boetticher, H.V. 1954. Die Perlhühner. Wittenberg-Lutherstadt: Ziemsen.

Bourke, D. 1967. The Kazabo. Niger. Fld. 32: 17-21.

Brown, J.L. 1963. Ecogeographic variation and introgression in avian visual signal: the crest of the Steller's Jay, Cyanocitta stelleri. Evolution 17: 23-39.

Butzer, K.W. 1967. Hypothetical rainfall and vegetation zones. In: Desmond Clark, J., ed. Atlas of African Prehistory. London: University of Chicago Press.

Calcomp, 1971. GPCP: a general purpose contouring program. CALCOMP Computer Products Inc., Anaheim.

Carcasson, R.H. 1964. A preliminary survey of the zoogeography of African butterflies. East Afr. Wildl. J. 2: 122-157.

Chapin, J.P. 1932. The birds of the Belgian Congo. Part I. Bull. Amer. Mus. Nat. Hist. 65: 1-756.

Cooke, H.B.S. 1962. The Pleistocene environment in Southern Africa during the Pleistocene. Ann. Cape Prov. Mus. 2: 11-15.

Cracraft, J. 1972. The relationships of the higher taxa of birds: Problems in phylogenetic reasoning. Condor 74: 379-392.

Cracraft, J. 1973. Continental drift, Paleoclimatology and the evolution of birds. J. Zool. Lond. 169: 455-545.

Crowe, T.M. & Snow, D.W. 1978. Numidinae. In: Snow, D., ed. An atlas of speciation in African non-passerine birds. London: British Museum (Natural History).

Davis, D.H.S. 1962. Distribution patterns of Southern African Muridae, with notes on some of their fossil antecedents. Ann. Cape Prov. Mus. 2: 56-76.

Dixon, W.J. (ed.) 1975. Biomedical computer programs: University of California Publications in Automatic Computation, No. 5. Berkeley: University of California Press.

Ehrlich, P. & Raven, P. 1969. Differentiation of populations. Science 165: 1228-1232.

Elgood, J.H., Fry, C.H. & Dowsett, R.J. 1973. African migrants in Nigeria. Ibis 115: 1-45.

Ford, J. 1974. Concepts of subspecies and hybrid zones, and their application in Australian ornithology. Emu 74: 113-123.

Ghigi, A. 1936. Galline di Faraone e Tacchini. Milano: V. Hoepli.

Gould, S.J. & Johnston, R.F. 1972. Geographic variation. Ann. Rev. Ecol. Syst. 3: 457-498.

Hagemier, E.M. & Stults, C.D. 1964. A numerical analysis of the distributional patterns of North American mammals. Syst. Zool., 13: 125-55.

Hall, B.P. 1961. The relationship of the guineafowls *Agelastes meleagrides* Bonaparte and *Phasidus niger* Cassin. *Bull. Br. Orn. Club.* 81: 132.

Hall, B.P. 1963. The Francolins, A study in speciation. *Bull. Brit. Mus. Nat. Hist.* 10: 105-204.

Hall, B.P. & Moreau, R.E. 1970. *An atlas of speciation in African passerine birds.* London: British Museum (Natural History).

Hamilton, I. 1974. The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper Pleistocene palaeoenvironments: a review. *Palaeoecology* 9: 63-97.

Howell, F.C. & Bourlière, F. (eds.) 1963. *African ecology and human evolution.* Aldine. Chicago.

Jackson, F.J. 1938. *The birds of Kenya Colony and the Uganda Protectorate.* Vol. I. London: Gurney & Jackson.

Livingstone, D.A. 1975. Late Quarternary climatic change in Africa. *Ann. Rev. Ecol. Syst.* 6: 249-280.

Mackworth-Praed, C.W. & Grant, C.H.B. 1952. *Birds of eastern* and north-east Africa. London: Longmans, Green & Co.

Mackworth-Praed, C.W. & Grant, C.H.B. 1962. *Birds of the southern third of Africa.* London: Longmans.

Mackworth-Praed, C.W. & Grant, C.H.B. 1970. *Birds of central* and western Africa. London: Longmans.

Marx, H. & Rabb, G.B. 1970. Character analysis: an empirical approach applied to advanced snakes. *J. Zool. Lond.* 161: 525-548.

Mayr, E. Linsley, E.G. & Usinger, R.L. 1953. *Methods and principles of systematic zoology.* New York: McGraw-Hill Co.

Moreau, R.E. 1952. Africa since the Mesozoic: with particular reference to certain biological problems. Proc. zool. Soc. Lond. 121: 869-913.

Moreau, R.E. 1957. Variation in Western Zosteropidae (Aves). Bull. Brit. Mus. (Natur. Hist.), Zool. 7: 309-433.

Moreau, R.E. 1963. The distribution of tropical African birds as an indicator of post climatic changes. In: Africa Ecology and Human Evolution, Viking Fund Publications in Anthropology. 36: 28-42. Chicago: Aldine Publishing Co.

Moreau, R.E. 1966. The bird faunas of Africa and its islands. New York: Academic Press.

Olson, S.L. 1974. Telecrex restudied: a small Eocene guineafowl. Wilson Bull. 86: 246-250.

Peters, J.L. 1934. Check-list of the birds of the world. Vol. II. Cambridge: Harvard University Press.

Priest, C.D. 1933. The birds of Southern Rhodesia. Vol. I. London: William Clowes & Sons, Ltd.

Reynolds, J.F. 1977. Thermo-regulatory problems of birds nesting in East Africa: a review. Scopus 1: 57-68.

Roberts, T.R. 1975. Geographical distribution of African freshwater fishes. Zool. J. Linn. Soc. 57: 249-320.

Selander, R.K. 1971. Systematics and speciation in birds. In: Farner, D.S. & King J.R., eds. Avian Biology. Vol. I: 57-147.

Sibley, C.G. & Ahlquist, J.E. 1972. A comparative study of the egg white proteins of non-passerine birds. Peabody Mus. Natur. Hist. (Yale Univ.), Bull. 39.

Sneath, P.H.A. & Sokal, R.R. 1973. Numerical Taxonomy. San Francisco: W.H. Freeman & Co.

Sokal, R.R. & Rohlf, F.J. 1969. Biometry: the principles and practice of statistics in biological research. San Francisco: W.H. Freeman & Co.

Udvardy, M.D.F. 1969. Dynamic zoogeography with special reference to land animals. New York: van Nostrand Reinhold Co.

Vuilleumier, B.S. 1971. Pleistocene changes in the fauna and flora of South America. Science 173: 771-780.

Vuilleumier, F. 1975. Zoogeography. In: Farner, D.S. & King, J.R. eds. Avian Biology Vol V : 421-496. New York: Academic Press.

Wetmore, A. 1960. A classification for the birds of the world. Smiths. Misc. Coll. 139.

White, C.M.N. 1965. A revised check-list of African non-passerine birds. Lusaka: The Government Press.

Wilson, E.O., Brown, W.L., Jr. 1953. The subspecies concept and its taxonomic application. Syst. Zool. 2: 97-111.

Appendix 1

Qualitative characters and character states analyzed in this study.

No.	Character name	States
1	Crown adornment	1 = short crest of feathers 2 = long crest of feathers 3 = none, only naked skin 4 = bony helmet
2	Occipital adornment	1 = short, dense, chestnut-coloured downy feathers 2 = long filoplumes confined to a mid-dorsal line 3 = fold of blue to black skin 4 = fold of whitish skin 5 = none, only naked skin
3	Nape adornment	1 = short downy feathers 2 = long filoplumes confined to a mid-dorsal line 3 = patch of orange-yellow skin at base, similar patch anterior to ear 4 = none, only naked skin
4	Orbital skin colour	1 = pink to red 2 = light blue to black
5	Throat skin colour	1 = pink to red 2 = blue to black
6	Throat adornment	1 = no fold of skin 2 = fold of skin
7	Gape adornment	1 = rudimentary wattles 2 = well-developed and pointed wattles 3 = well-developed and rounded wattles

8	Gape wattle colour	1 = pink to red 2 = blue to blue-grey 3 = blue with red tips
9	Cere adornment	1 = none 2 = cartilaginous tufts or papilli
10	Collar plumage	1 = black with faint vermiculations 2 = black with no vermiculations 3 = black, finely barred with white 4 = grey to blue-grey 5 = spotted 6 = well-developed hackle 7 = white
11	Body plumage	1 = black with vermiculations 2 = spotted with vermiculations 3 = spotted without vermiculations 4 = as 3, with chestnut blotching between spots
12	Tarso-metatarsal scales	1 = imbricated and in a row 2 = pentagonal, not in rows
13	Tarso-metatarsal adornment	1 = spurs or bumps 2 = none
14	Iris colour	1 = brown 2 = red
15	Outer margins of secondaries	1 = brown to black with faint vermiculation 2 = white 3 = lavender 4 = alternating bands of black and white with varying degrees of black and white vermiculations
16	Furcula	1 = blade-shaped 2 = hollow, cup-shaped; Found in all guineafowl with long crests (Chapin 1932)
17	Caecum length	1 = up to 150 mm 2 = greater than 200 mm; in all specimens conforming to the description of <u>Acryllium vulturinum</u> (Beddard 1898)
18	Abdomen plumage	1 = white 2 = blue 3 = white spots with faint vermiculations 4 = bluish-white spots without vermiculations

Appendix 2

Quantitative characters analyzed in this study. See Figures 1 - 3 for a pictorial representation of many of the characters.

No.	Name	Units	Description
1	Bill length	mm	the chord measured from the base of the cere to the tip of the maxilla
2	Wing length	mm	the chord of the unflattened folded wing from the farthest anterior tip of the wrist joint to the tip of the longest primary
3	Tarsus length	mm	the diagonal chord from the posterior point of articulation of the tarsometatarsus with the tibia to the most distal undivided tarsal scute on the dorsal surface of the middle toe
4	Wattle basal width	mm	the chord from the most anterior to posterior points of juncture of the wattle with the cheek
5	Wattle length	mm	the chord from the juncture line of the wattle to the most distal point along the wattle margin
6	Wattle percent blue	%	a subjective estimate of the surface area of the wattle covered by blue pigment. It is possible to assess the amount of this colour in preserved material since, although natural colour is lost soon after death, the demarcation between red and blue can be determined because red areas revert to a yellow or translucent amber state, and blue areas to an opaque blue-grey.
7	Helmet frontal length	mm	the curvilinear distance, as measured with a flexible tape, along the anterior margin of the bony helmet from the point of juncture with the skull to the apex
8	Helmet rear length	mm	the curvilinear distance along the posterior margin of the helmet from the point of juncture with the skull to the apex
9	Helmet central height	mm	the chord perpendicular to the line of juncture with the skull to the highest point along the margin of the helmet

10	Helmet basal length	mm	the chord from the anterior to posterior juncture points of the helmet with the skull
11	Helmet thickness	mm	the maximum lateral width of the helmet at its base
12	Cere structure length	mm	the chord from the base of the cere to the distal tip of the longest tuft or papilla
13	Cere structure thickness	mm	the maximum thickness of the thickest tuft or papilla
14	Collar plumage	0-6	0 = grey; 1 = blue/violet; 2 = black, barred white with a blue wash; 3 = black, barred white; 4 = black, barred white with faint longitudinal streaking; 5 = black, barred white with some spotting; 6 = spotted
15	Nape filoplume length	mm	the chord from the base to the tip of the longest straightened nape filoplume
16	Nape filoplume antero-posterior coverage	%	the percentage of the nape, at the mid-dorsal line, from the occiput to the upper-most collar feathers, covered by filoplumes
17	Nape filoplume lateral coverage	%	the percentage of the nape covered laterally by nape filoplumes at the mid-point of the antero-posterior coverage
18	Nape filoplume density	0-4	a subjective estimate, based on a comparison with reference specimens encompassing the range of variation, of density of the nape filoplumes on a scale of increasing density. 0 = filoplumes not present, 4 = covered by a mat of filoplumes
19	Secondary remex outer web vermiculation	0-6	0 = absent; 1 = extends 1/5 way along the white bands; 2 = extends 2/5 way along the white bands; 3 = extends 3/5 way along the white bands; 4 = extends 4/5 way along the white bands; 5 = extends to full length of white bands; 6 = outer edge of white bands obliterated by vermiculation
20	Wing cover barring	0-2	0 = not present; 1 = present but faint; 2 = present
21	Dorsal vermiculation	0-4	a subjective estimate, as with character no. 18, 0 = faint, graded subjectively to 4 = dense
22	Dorsal spot size	units 6 = 1mm	the maximum width, as measured with a dissecting microscope fitted with an ocular grid, of a particular spot on a randomly selected feather from the mid-dorsal region

23	Crest frontal length	mm	the chord from the base to the tip of the longest straightened crest feather within 5 mm of the cere
24	Crest rear length	mm	the chord from the base to the tip of the longest straightened crest feather within 5 mm of the most posterior extent of the crest
25	Crest central height	mm	the chord perpendicular to the line of crest juncture with the skull from the base of the crest feathers to the highest point along the margin of the unstraightened crest
26	Crest basal length	mm	the chord from the anterior to posterior juncture points of the crest with the skull
27	Anterior crest curliness	1-3	a subjective estimate as with character no. 18. 1 = straight; 2 = moderately curly; 3 = very curly
28	Posterior crest curliness	1-3	as with character no. 27
29	Dorsal black collar	%	the percentage of black plumage extending from the most anterior dorsal aspect of the collar to the base of the tail
30	Ventral black collar	%	as with character no. 29 but the ventral surface
31	Occipital fold	%	a subjective estimate of the lateral extent of the occiput covered by a fleshy fold
32	Ear patch	mm	the maximum width of any patch of non-blue/black skin anterior to the ear
33	Throat red	%	a subjective estimate of the antero-posterior extent of red pigmented skin between the throat and the ventral base of the neck. As with character no. 6, this character may be assessed since the red colour reverts to a yellow state after preservation.
34	Orbital red	%	a subjective assessment of the amount of red pigmented skin around the eye
35	Dorsal spot number	count	the maximum number of spots falling within a circle of 1 cm radius superimposed over the dorsal feather discussed in character no. 22
36	Total spot barbs	count	the number of non-black barbs associated with the spot measured in character no. 22

37	Total within spot barbs	count	the number of barbs encompassed by the spot measured in character no. 22
38	Spot barb blueness	0-3	a subjective assessment of the amount of blue in the spot. 0 = white; 1 = faint blue; 2 = medium blue; 3 = darkest blue
39	Chestnut blotch size	units 6 = 1m	the maximum width of any chestnut blotch, as measured with a dissecting microscope fitted with an ocular grid, found on the feather examined for character no. 22
40	Chestnut blotch extent	%	the extent of the spotted area of the feather examined for character no. 22 covered by chestnut blotching
41	Tarsal structure number	count	the number of spurs or bumps on the tarsus
42	Tarsal structure length	mm	the chord measured from the juncture line of the longest tarsal bump or spur with the tarso-metatarsus to the apex of the structure
43	White collar	%	the percentage of white plumage in the collar
44	Facial filoplumes	0-10	a subjective estimate of the extent of the head, other than the occiput, nape and crown, covered by filoplumes

The evolution of guineafowl (Galliformes, Phasianidae, Numidinae). II. Adaptive differentiation

by T.M. Crowe

Received February 1978

INTRODUCTION

Patterns of geographic phenetic variation in guineafowl (Numidinae) may serve as examples of avian adaptive differentiation in Africa, since:

(1) guineafowl are endemic to, and probably evolved in Africa (Crowe 1978);

(2) at least one guineafowl taxon is confined, and is presumably adapted to virtually every African terrestrial biome and biotope (Crowe & Snow 1978);

(3) guineafowl are sedentary birds (Elgood *et al*. 1973), and thus should be more susceptible to local selection pressures than would be more mobile species (Ehrlich & Raven 1969);

(4) two widespread species, one (*Guttera pucherani*) a forest-living bird, the other (*Numida meleagris*) a bird of relatively open savanna biotopes, exhibit considerable geographic phenetic variation which appears to be correlated with patterns of physical and ecological variation (Crowe & Snow 1978).

The aims of the present study are to relate geographic phenetic variation in *N. meleagris* and *G. pucherani* to environmental variation, using a quantitative, statistical approach; and to formulate/.....

formulate testable hypotheses as to the adaptiveness of the phenetic variation. The only comparable investigation of an African avian taxon is Moreau's (1957) study of variation in white-eyes (Zosteropidae). Moreau found that, among populations of white-eyes, wing length (a presumed indicator of overall body size), and characters significantly correlated with wing length, were statistically inversely related to the mean minimum temperature for the three coldest months of the year. He also found that wing length, independent of its correlation with minimum temperature, was statistically postively related to altitude. Since increased evaporation at high altitudes tends to lower wet-bulb temperatures (James 1970), both of these results are in accordance with James' (1970) restatement of Bergmann's ecogeographic rule, i.e., within a species, individuals from populations inhabiting cooler or drier regions tend to be larger than those belonging to populations which inhabit warmer, wetter regions.

METHODS

The data-base analyzed herein consists of 339 museum specimens of N. meleagris from 24 localities (Fig. 1), 153 specimens of G. pucherani from 15 localities (Fig. 2), and 100 freshly dead N. meleagris from Rooipoort (28° 45'S, 24° 05'E), Kimberley district, South Africa. Owing to the paucity of specimens from most collection sites, a locality sample is usually an agglomeration of specimens of both sexes collected from several sites, often over many years.

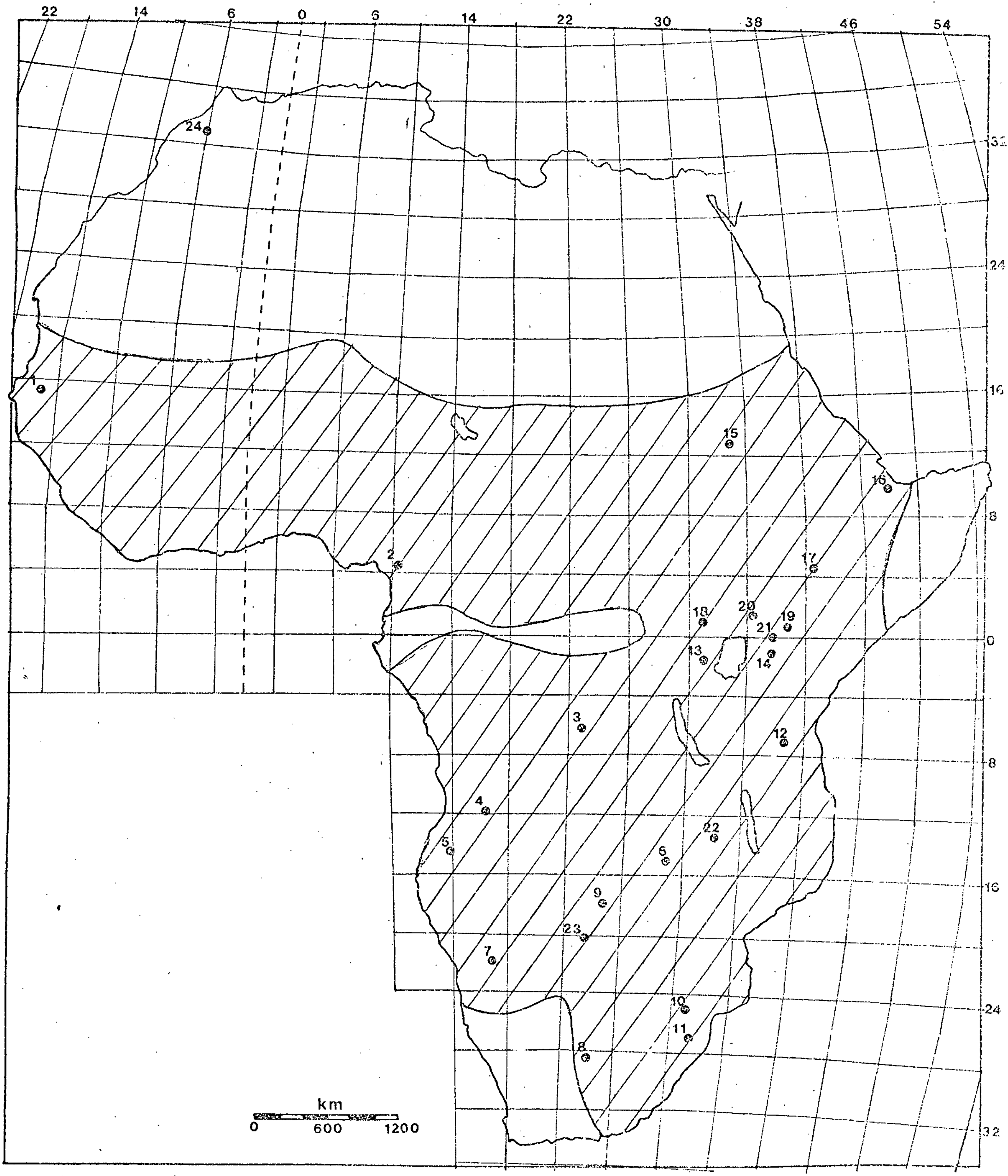

Fig. 1. A map showing *N. meleagris* sampling localities and the approximate distribution (hatched) of this species.

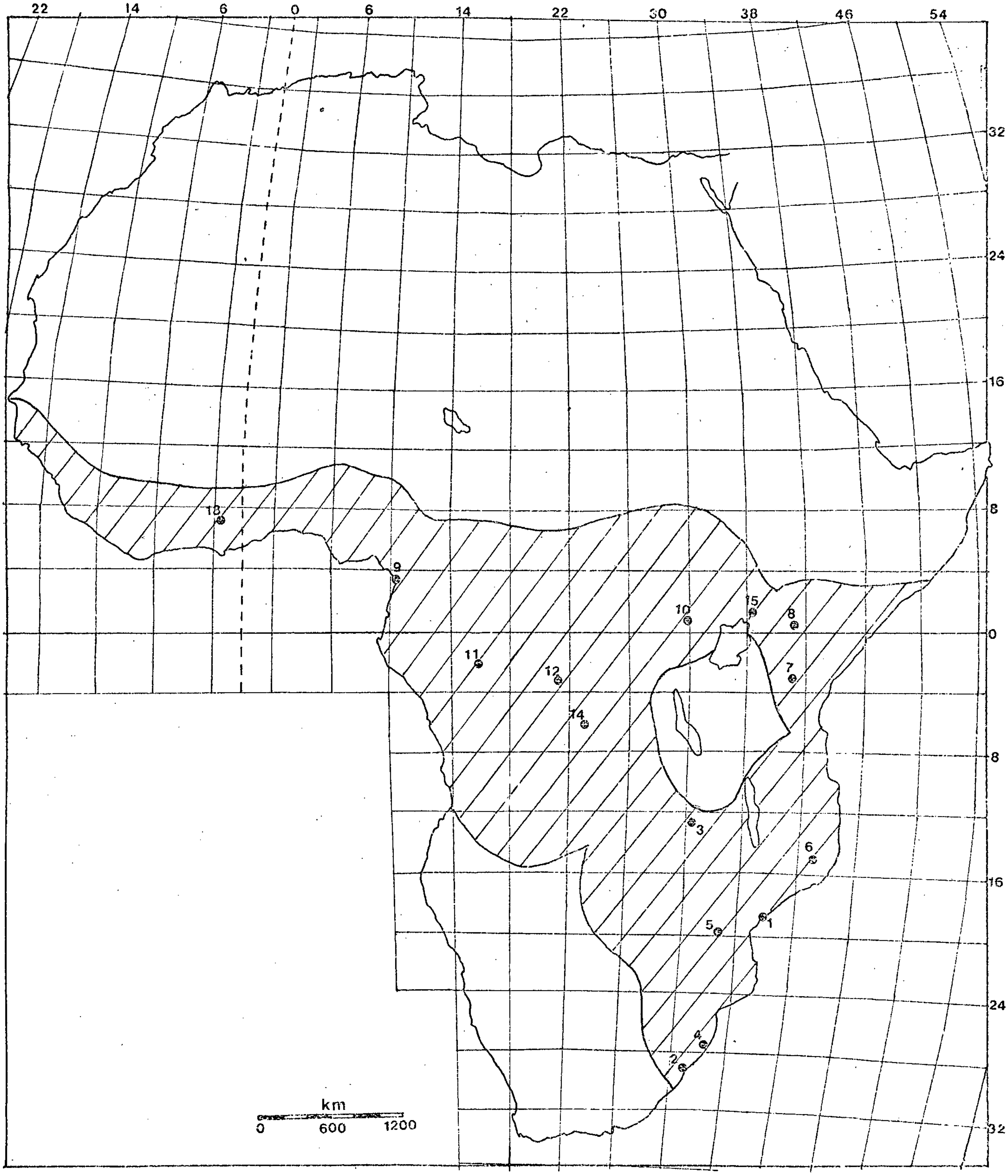

Fig. 2. A map showing *G. pucherani* sampling localities and the approximate distribution (hatched) of this species.

The grouped collection sites for each locality are within an area encompassed by a circle with a radius of, at most, 50km. When sites were grouped, the locality co-ordinates (Tables I & II) are the mean values for the individual specimens.

Each museum specimen of N. meleagris was measured or assessed according to 19 characters, each specimen of G. pucherani according to 14 characters (Table III). Specimens of N. meleagris from Rooipoort were also weighed to the nearest 10g. All characters examined in museum specimens, except helmet area and crest area, are described in detail in Crowe (1978), and appear to vary clinally (Crowe 1978). Helmet and crest area were determined by comparing the weight of a cut-out paper tracing of these structures to the weight of a piece of the same type of paper of known area.

For each species, the correlation coefficient (r, Sokal & Rohlf 1969) between all characters and wing length was computed to determine those characters which may be a function of overall size. For Rooipoort N. meleagris, the r between weight and wing length was computed to determine if wing length is an indicator of body weight. For each specimen, values for characters significantly ($P \leq 0.05$) correlated with wing length were divided by the value for that character to minimize the effect of allometry. Means were then computed for each character for each locality, and correlation and stepwise multiple linear regression analyses were used to

determine/.....

TABLE I

Map co-ordinates and environmental variable values for N. *meleagris* sampling localities

Locality no.	Latitude	Longitude	Elevation (m)	AE* (mm)	Annual rainfall (mm)	Mean max. temp. (°C)	Mean min. temp. (°C)	Visibility (m)
1	15° 00'N	15° 30'W	15	528	528	40.5	14.0	12.5
2	4° 20'N	11° 20'E	1075	1028	1543	31.0	18.5	20.0
3	5° 56'S	22° 26'E	800	1155	1384	30.0	17.5	5.0
4	12° 00'S	16° 00'E	1700	760	1479	28.3	8.3	5.0
5	14° 30'S	14° 00'E	1786	737	953	33.0	8.3	5.0
6	15° 15'S	29° 00'E	400	606	606	29.0	9.5	5.0
7	22° 00'S	17° 00'E	1665	119	119	30.0	6.0	12.5
8	28° 45'S	24° 05'E	1040	356	356	33.0	2.5	12.5
9	18° 15'S	24° 30'E	929	660	660	34.8	8.8	5.0
10	25° 00'S	31° 00'E	1479	729	1702	26.2	2.5	12.5
11	27° 20'S	32° 05'E	37	617	617	28.3	9.0	5.0
12	7° 00'S	37° 20'E	579	901	901	33.8	15.0	5.0
13	1° 50'S	30° 50'E	1870	754	997	27.0	11.8	5.0
14	1° 25's	36° 00'E	1890	675	675	27.8	7.0	12.5
15	13° 00'N	32° 30'E	382	417	417	40.0	17.0	12.5
16	10° 00'N	44° 00'E	10	59	59	42.0	11.5	12.5
17	4° 05'N	38° 06'E	439	483	483	36.0	5.5	12.5
18	1° 00'N	30° 40'E	1250	1023	1233	31.0	11.5	5.0
19	0° 50'N	36° 30'E	1900	588	588	26.6	7.8	12.5
20	1° 15'N	34° 20'E	1220	1040	1177	28.8	11.0	12.5
21	0° 30'S	36° 45'E	1280	886	1172	29.5	7.0	12.5
22	12° 30'S	32° 00'E	1140	733	891	29.6	9.0	5.0
23	20° 05'S	23° 25'E	942	401	401	34.0	5.5	12.5
24	33° 00'N	6° 00'W	831	557	557	40.2	3.0	100.0

AE* is annual evaporation

TABLE II

Map co-ordinates and environmental variable values for *G. pucherani* sampling localities

Locality no.	Latitude	Longitude	Elevation (m)	AE* (mm)	Annual rainfall (mm)	Mean max. temp. (°C)	Mean min. temp. (°C)	Visibility (m)
1	19° 10'S	35° 25'E	8	1228	1415	31.0	13.5	13
2	29° 17'S	30° 18'E	684	857	916	27.0	6.0	13
3	13° 55'S	30° 05'E	1428	701	1150	30.0	11.5	5
4	27° 58'S	32° 15'E	1000	766	918	28.0	10.2	13
5	20° 25'S	32° 43'E	1126	583	583	29.0	9.5	5
6	14° 55'S	39° 00'E	235	964	995	34.3	15.5	5
7	3° 15'S	37° 30'E	1372	800	1159	33.0	15.5	13
8	0° 15'S	37° 32'E	1143	698	698	33.5	8.5	5
9	4° 15'N	10° 03'E	280	1249	1249	31.0	22.5	20
10	0° 35'N	30° 00'E	1176	1107	1687	26.0	12.5	5
11	2° 12'S	16° 16'E	325	1465	1549	31.0	19.0	20
12	3° 27'S	21° 24'E	400	1269	1501	34.0	18.5	20
13	6° 40'N	1° 20'W	59	725	725	33.5	21.5	5
14	5° 56'S	22° 26'E	850	1155	1384	30.0	17.5	5
15	1° 00'N	34° 34'E	1896	812	1140	27.0	11.0	5

AE* is annual evapo-transpiration

TABLE III

Characters measured (mm) or assessed for specimens of *N. meleagris* and *G. pucherani*

See Crowe (1978) for detailed character descriptions

N. meleagris		*G. pucherani*
	Bill length	
	Wing length	
	Tarsus length	
	Wattle length	
	Wattle basal width	
Wattle percentage blue		Crest area
Cere structure length		Crest central height
Cere structure thickness		Anterior crest curliness
Nape filoplume length		Posterior crest curliness
Nape filoplume anteroposterior coverage		Spot number
Nape filoplume lateral coverage		Spot blueness
Nape filoplume density		Total spot barbs
Helmet area		Chestnut blotch size
Helmet central height		Dorsal black collar
Helmet thickness		
Secondary remex outer web vermiculation		
Wing covert barring		
Dorsal spot size		
Collar plumage		

determine statistically significant relations between these means and values for six environmental variables determined for each locality (Tables I & II). Correlation analysis reveals statistical relations between the dependent variables (phenetic characters) and independent variables (environmental variables), but does not consider the effects of possible intercorrelations between independent variables (Sokal & Rohlf 1969). Stepwise multiple regression analysis determines dependent-independent variable relations, irrespective of independent variable intercorrelations, since it adds independent variables into the regression equation in a stepwise manner according to which has the highest partial correlation with the dependent variable at that step (Allen 1973). The obvious advantages of regression over correlation analysis, in part, are offset by the fact that biologically more relevant, although statistically less significant correlations between a dependent and an independent variable(s), may be eliminated from the analysis.

Environmental data

As mentioned above, locality latitude and longitude were the mean values for all specimens comprising each locality. Data for altitude, actual evapotranspiration (AE) and annual rainfall (Tables I & II) were taken from Thornthwaite Associates (1962). When there was no meteorological recording station within 50km of the locality co-ordinates, data were computed by interpolation. AE was analyzed since it is an

index/.....

index of both primary productivity and water availability (Rosenzweig 1968), and since Niles (1973) has shown that size variation in horned larks (Eremophila alpestris) may be attributed to variation in primary productivity. Mean maximum and minimum temperatures (Tables I & II) were taken from Jackson (1961), and are the means for the two hottest and coldest months of the year respectively. Visibility values (Tables I & II) are the medians of subjective assessments of four botanists experienced in vegetation analysis, of the distance that one might be able to see at a height of 0,3m in the given vegetation type that appears to be dominant at each locality. If more than one dominant vegetation type occurred within a 50km radius of the co-ordinates of any locality, the visibility value for that locality was the mean for the vegetation types concerned.

RESULTS

Wing length is a statistically significant ($r = 0.32$, $P \leq 0.01$) indicator of weight in N. meleagris at Rooipoort. Mean character values for each locality sample for each species are given in Tables IV and V. In these tables, characters marked with an asterisk are significantly correlated with wing length. Statistically significant relations between phenetic characters and environmental variables are summarized in Tables VI and VII. Significant correlations between environmental variables for both species localities are given in Table VIII.

/.....

TABLE IV

Mean character values for samples from _N. meleagris_ localities

Locality no.	n	Bill length *(+)a	Wing length	Tarsus length *(+)	Wattle length	Wattle width	Wattle % blue	Cere length	Cere thickness	Filoplume length	Filoplume density	Filoplume lateral coverage *(-)	Filoplume ant.-post.	Helmet area *(+)	Helmet height *(+)	Helmet thickness	Secondary vermiculation *(-)	Covert barring *(-)	Spot size *(+)	Collar plumage	Dorsal vermiculation
1	15	0.086	230.1	0.314	18.4	13.9	8.3	0.00	0.00	23.10	2.53	0.2529	100.00	0.25	0.023	4.4	0.022	0.0014	0.0772	0.3	3.5
2	13	0.091	254.9	0.334	14.1	14.0	9.4	0.00	0.00	18.08	2.85	0.2595	93.08	0.12	0.014	3.9	0.018	0.0030	0.0481	0.2	3.8
3	24	0.091	265.5	0.333	15.3	14.1	60.0	0.00	0.00	21.21	2.96	0.1946	91.71	0.49	0.033	7.1	0.013	0.0017	0.0670	2.0	3.1
4	16	0.091	303.4	0.314	17.8	12.5	76.5	0.00	0.00	27.90	2.90	0.0622	85.60	1.90	0.070	14.1	0.001	0.0007	0.0820	2.1	1.3
5	17	0.090	287.8	0.312	17.9	11.5	72.1	1.94	2.10	23.24	2.35	0.0903	57.53	1.54	0.072	9.9	0.007	0.0000	0.0763	3.4	2.2
6	30	0.095	274.4	0.319	17.1	11.5	66.8	0.00	0.00	25.19	2.78	0.0863	61.28	1.22	0.064	9.4	0.004	0.0000	0.0719	2.9	2.1
7	9	0.089	273.7	0.309	19.4	11.6	65.8	4.33	3.00	10.89	0.11	0.2273	27.22	1.21	0.099	9.7	0.014	0.0000	0.0757	5.4	2.6
8	18	0.091	266.8	0.325	21.8	11.6	65.2	2.50	2.30	18.39	0.89	0.0556	33.39	2.47	0.099	9.4	0.008	0.0000	0.0870	4.9	2.1
9	33	0.090	279.1	0.305	18.6	10.7	65.0	1.67	1.80	20.85	1.97	0.0621	44.18	1.56	0.075	8.9	0.012	0.0000	0.0841	3.3	2.7
10	6	0.095	270.0	0.320	18.9	10.4	69.1	0.63	1.00	18.75	1.63	0.0602	34.13	1.83	0.097	8.8	0.011	0.0000	0.0764	3.6	2.6
11	8	0.097	267.8	0.327	17.9	11.0	61.4	0.00	0.00	20.00	2.00	0.0691	48.25	2.37	0.100	8.3	0.009	0.0000	0.0707	4.0	2.5
12	7	0.092	273.3	0.310	16.6	10.1	55.1	0.00	0.00	20.29	1.86	0.0690	67.57	0.94	0.071	8.1	0.000	0.0000	0.0681	3.1	1.5
13	9	0.089	283.1	0.323	13.7	12.4	63.4	0.00	0.00	21.44	3.00	0.1001	71.00	1.15	0.063	8.8	0.008	0.0009	0.0766	2.9	2.1
14	10	0.088	274.1	0.345	14.5	12.0	3.6	0.00	0.00	21.10	2.50	0.0835	47.10	2.58	0.133	8.7	0.006	0.0000	0.0811	3.0	2.2
15	12	0.094	274.9	0.328	14.9	13.9	100.0	6.92	1.00	16.67	3.00	0.4085	70.92	0.32	0.034	7.2	0.025	0.0089	0.0955	2.8	3.8
16	10	0.096	255.3	0.326	16.8	14.2	84.9	19.00	0.40	14.00	3.00	0.1810	26.30	0.22	0.022	5.9	0.024	0.0024	0.0801	3.0	2.8
17	15	0.091	267.6	0.322	14.1	15.1	99.7	10.93	1.20	16.40	3.00	0.3259	49.27	0.93	0.076	7.6	0.022	0.0035	0.0686	3.1	2.6
18	11	0.098	269.4	0.317	12.1	13.5	99.9	4.09	1.20	15.82	3.00	0.3705	61.82	0.42	0.031	5.2	0.022	0.0034	0.0749	2.7	2.5
19	11	0.099	266.6	0.327	13.3	14.5	98.8	8.55	1.40	14.73	2.91	0.3581	66.46	1.68	0.097	8.3	0.020	0.0031	0.0667	2.7	2.6
20	10	0.098	263.7	0.322	12.0	14.9	100.0	7.60	1.00	13.30	3.00	0.3470	41.80	0.64	0.050	6.1	0.027	0.0046	0.0775	2.9	2.9
21	24	0.089	283.8	0.317	13.1	11.7	2.5	0.50	0.40	19.13	2.17	0.0775	59.42	1.75	0.101	8.2	0.006	0.0000	0.0685	3.0	2.2
22	16	0.094	277.9	0.311	17.1	10.8	69.7	0.00	0.00	24.75	2.81	0.0839	62.75	0.80	0.060	6.8	0.004	0.0000	0.0640	2.9	2.1
23	9	0.087	272.2	0.303	18.2	10.7	63.9	4.33	3.00	9.11	0.44	0.0282	13.89	1.30	0.071	9.0	0.016	0.0000	0.0944	5.0	2.4
24	4	0.090	267.3	0.330	17.8	15.5	0.0	0.00	0.00	34.00	3.00	0.2619	100.00	0.64	0.051	5.3	0.014	0.0000	0.0599	2.3	2.5

* significantly correlated with wing length [a] sign of the correlation with wing length

TABLE V

Mean character values for samples from *G. pucherani* localities

ocality no.	n	Bill$^{*(+)a}$ length	Wing length	Tarsus$^{*(+)}$ length	Wattle length	Wattle width	Crest area	Crest anterior curliness	Crest posterior curliness	Crest height	Spot no.	Spot blueness	Total$^{*(+)}$ spot barbs	Chestnut blotch size	Dorsal collar
1	8	0.102	254.6	0.357	2.3	10.1	1101.3	1.3	2.0	25.0	24.4	1.1	0.022	10.3	28.4
2	13	0.096	259.7	0.354	2.4	9.2	1167.8	2.4	2.7	28.8	21.3	0.1	0.023	9.8	26.2
3	9	0.098	256.0	0.342	2.7	9.8	1091.8	1.6	2.0	25.7	26.6	0.0	0.018	10.8	28.2
4	10	0.100	253.2	0.347	2.7	9.5	1268.6	1.9	2.0	28.2	18.9	0.0	0.020	14.1	28.5
5	8	0.097	254.8	0.334	2.3	9.6	1104.4	1.0	2.0	26.5	25.0	0.0	0.019	11.0	26.9
6	10	0.095	270.1	0.340	3.0	8.5	1161.9	1.2	2.0	29.2	28.2	0.1	0.022	0.0	21.1
7	14	0.098	267.6	0.346	2.6	10.0	1180.4	1.0	2.0	28.0	23.0	0.0	0.024	0.0	6.4
8	13	0.098	274.6	0.348	3.0	9.1	1134.1	1.0	2.0	27.0	22.4	0.0	0.024	0.0	0.0
9	8	0.105	246.5	0.370	2.4	10.5	551.6	1.1	2.1	18.3	21.0	0.1	0.024	0.0	17.1
10	12	0.091	250.4	0.355	2.6	10.0	1000.8	1.2	2.0	24.6	22.0	0.0	0.025	0.0	24.3
11	13	0.099	246.5	0.363	2.6	9.4	921.5	1.3	2.0	26.5	26.8	0.0	0.022	0.0	17.5
12	8	0.098	244.3	0.363	2.6	9.5	765.1	1.3	2.0	22.9	28.8	0.0	0.023	0.0	14.8
13	7	0.094	249.0	0.352	2.9	9.7	1364.4	1.0	2.0	31.7	20.0	0.0	0.024	0.0	15.6
14	10	0.098	248.0	0.359	2.7	8.7	1144.0	1.1	2.1	28.3	24.0	0.0	0.024	0.0	23.3
15	10	0.091	253.5	0.342	2.9	9.7	111144	1.1	2.1	26.6	24.0	0.0	0.026	0.0	23.7

*significantly correlated with wing length [a]sign of the correlation with wing length

TABLE VI

Significant relations between phenetic characters and environmental variables for *N. meleagris*

Character	Correlation analysis	Regression analysis
Bill length	-	-
Wing length	elevation(+)**, max.temp.(-)**, min.temp.(-)*	elevation(+)**
Tarsus length	-	-
Wattle length	AE[1](-)**, min.temp.(-)*	AE(-)**
Wattle width	visibility(+)*	visibility(+)*
Wattle % blue	-	-
Cere length	-	-
Cere thickness	AE(-)**, ann.rainfall(-)*, min.temp.(-)*	AE(-)**
Filoplume length	visibility(+)*	visibility(+)*
Filoplume density	min.temp.(+)*, AE(+)*	min.temp.(+)*
Filoplume ant.-post. coverage	min.temp.(+)*, AE(+)*	min.temp.(+)*, visibility(+)**, ann. rainfall(+)*
Filoplume lateral coverage	-	-
Helmet area	min.temp.(-)**, max.temp.(-)**, AE(+)*	min.temp(-)**, max.temp.(-)**
Helmet height	max.temp.(-)**, min.temp.(-)*, elevation(+)*	min.temp.(-)**, max.temp.(-)**, ann. rainfall(-)*
Helmet thickness	elevation(+)*, max.temp.(-)*, min.temp.(-)*	elevation(+)*
Secondary vermiculation	max.temp.(+)*	max.temp.(+)*
Covert barring	max.temp.(+)*	min.temp.(+)*
Spot size	-	-
Collar plumage	min.temp.(-)**, AE(-)*, ann.rainfall(-)*	min.temp.(-)**, visibility(±)*, ann. rainfall(-)*
Dorsal vermiculation	min.temp.(+)**, max.temp.(+)*	min.temp.(+)**

* $\underline{P} \leq 0.05$ ** $\underline{P} \leq 0.01$ [1] actual evapotranspiration

TABLE VII

Significant relations between phenetic characters and environmental variables for *G. pucherani*

Character	Correlation analysis	Regression analysis
Bill length	visibility(+)*	visibility(+)*
Wing length	AE(-)*	AE(-)*
Tarsus length	AE(+)**, visibility(+)**, ann. rainfall(+)* elevation(-)*	AE(+)**
Wattle length	-	-
Wattle width	-	-
Crest height	visibility(-)*	visibility(-)*
Crest area	AE(-)**, visibility(-)**, ann. rainfall(-)*	AE(-)**
Crest ant. curliness	min.temp.(+)**	min.temp.(+)**
Crest post. curliness	min.temp.(+)**	min.temp.(+)**, elevation(+)*
Spot number	-	-
Spot blueness	-	-
Total spot barbs	-	-
Chestnut blotch size	-	-
Dorsal collar	max.temp.(-)**	max.temp.(-)**

* $P \leq 0.05$ ** $P \leq 0.01$ [1] actual evapotranspiration

TABLE VIII

Correlations between environmental variables. Upper half-matrix is for *N. meleagris* localities, lower for *G. pucherani* localities.

	elevation	AE	ann. rainfall	max. temp.	min. temp.	visibility
elevation	-	0.254	0.384	-0.653^{**}	-0.309	-0.070
AE	-0.542^{*}	-	0.858^{**}	-0.474^{*}	0.410^{*}	-0.136
ann. rainfall	-0.129	0.835^{**}	-	-0.546^{**}	0.230	-0.148
max. temp.	-0.489	0.101	-0.143	-	0.160	0.400
min. temp.	-0.242	0.040	-0.117	-0.262	-	-0.306
visibility	-0.447	0.656^{**}	0.422	0.166	-0.206	-

$^{*}P < 0.05$; $^{**}P < 0.01$

DISCUSSION AND CONCLUSIONS

As with African white-eyes (Moreau 1957) and certain North American birds (reviewed by Johnston 1972), much of the phenetic variation in N. meleagris and G. pucherani (22 of 34 characters) is statistically related to variation in the environment. Moreover, the nature of many of these statistical relations can be explained by a few hypotheses, some of which closely accord with classical ecogeographic rules.

Numida meleagris

Six general phenetic trends in N. meleagris emerge from examination of Table VI.

(1) Variation in size (wing length) follows predictions of Bergmann's rule , i.e., body size is inversely related to measures of temperature, and positively related to elevation. The fact that elevation, and not a measure of temperature, is the only predictor of body size in regression analysis is probably due to that variable's likely close inverse correlation with wet-bulb temperature (for which there are insufficient African data), which appears to be a better predictor of body size in birds than is dry-bulb temperature (James 1970). Elevation is also inversely correlated with maximum dry-bulb temperature (Table VII).

(2) Phenetic characters which measure the size of exposed structures of the head, i.e., helmet height, helmet area, helmet thickness, wattle length and cere structure thickness, tend to have lower values in hotter and/or drier localities. This reduction in exposed surface area may be a possible adaptation to limit uptake of heat via radiation, and/or

limit/.....

limit the loss of body water through cutaneous evaporation (Calder & King 1974).

(3) Characters which assess the amount of white in the plumage, i.e., covert barring, dorsal and secondary remex vermiculation, tend to have higher values in hotter localities. Such an increase in white may help birds living in hotter environments to reflect some of the heat of radiation (Lucas & Stettenheim 1972).

(4) Collar plumage, an estimate of the amount of white spotting, tends to have higher (= more spots) values in drier-cooler localities. In other words, birds living in relatively warm, moist localities tend to have darker collars. This result is consistent with predictions of Gloger's rules, i.e., races living in hot, humid climates tend to have more black pigment (Moreau 1957).

(5) Characters which assess the amount of nape covered by filoplumes, and the length of these structures, i.e., filoplume density, filoplume antero-posterior coverage and filoplume length, tend to have high values in hotter, moister localities with greater visibility. Since filoplumes are thought to be sensory structures which allow monitoring of environmental disturbers such as wind (Lucas & Stettenheim 1972), a possible function of these structures is to act as a heat shield. In other words, through optimal body orientation relative to the wind and the sun, heat of radiation may be absorbed and dissipated before it reaches the skin.

/.....

(6) Wattle basal width, the last phenetic character which is significantly related to an environmental variable, has higher values at localities with greater visibility. Since N. meleagris with wider wattles have the greatest amount of red pigment, and since the amount of red in the wattles is among the most useful taxonomic characters (Crowe 1978), it is possible that wattles may be structures important in individual and species recognition.

Guttera pucherani

As with N. meleagris, temperature, moisture and visibility seem to play important roles in shaping the G. pucherani phenotype (Table VIII).

(1) Variation in size (wing length) and tarsus length appear to be related to the amount of available water (AE), the former inversely, the latter directly. Since an increase in tarsus length and a decrease in overall size results in an increase in the surface to volume ratio, it is possible that this variation may improve the effectiveness of non-evaporative cooling in relatively moist areas (Niles 1973).

(2) Measures of crest curliness, i.e., anterior and posterior curliness, are strongly positively related to measures of temperature. As with nape filoplume featheration in N. meleagris, this may serve as a thermal shield.

(3) Dorsal collar black, a measure of the amount of black pigment in the collar, tends to be more extensive at cooler localities. In other words, there is more white in the collar where it is

hotter./.....

hotter. As with white vermiculation and barring in *N. meleagris*, this may be an adaptation to lessen the amount of heat absorbed via radiation.

(4) Measures of crest size, crest height and crest area, tend to be lower at localities at which there is greater visibility. This result suggests that a large crest may be useful as a 'close-in' signalling device in areas where the vegetation is dense. Bill length tends to be longer at localities with greater visibility values. This suggests that the bill may be a 'far-away' signalling device. However, visibility is positively related to *AE* (Table VIII), and therefore alternative, physiologically-based hypotheses may prove to explain this phenetic variation.

To summarize, much of the phenetic variation in *N. meleagris* and *G. pucherani* can be attributed to adaptation to the environment, particularly to the temperature-humidity environment. However, it is premature to conclude that the statistical relations derived herein establish cause and effect relationships. It is also unrealistic to minimize the function of these characters as social and incipient-species recognition signals. Behavioural, physiological and anatomical experiments are needed to test the hypotheses erected herein.

/.....

Acknowledgements:

I am grateful to P. Clancey of the Durban Museum and Art Gallery, F. Gill of the Philadelphia Academy of Natural Sciences, M. Irwin of the National Museum of Rhodesia (Bulawayo), A. Kemp of the Transvaal Museum, M. Louette of the Musee Royal de l'Afrique Centrale, R. Paynter of the Museum of Comparative Zoology, L. Short of the American Museum of Natural History, D. Snow of the British Museum (Natural History) and M. Traylor of the Field Museum of Natural History for allowing me access to the guineafowl in their institutions' collections. B. Marsh helped with data collection. My wife, Anna, helped with data collection, data analysis and drew the figures. Computations were carried out at the University of Cape Town Computer Centre.

/.....

References:

Allen, J. 1973. STEPREG 1. Stepwise multiple regression analysis. Madison: University of Wisconsin.

Calder, W.A. & King, J.R. 1974. Thermal and caloric relations of birds. In Farner, D.S. & King, J.R. eds. Avian biology Vol. IV. New York: Academic Press.

Crowe, T.M. 1978. The evolution of guineafowl (Galliformes, Phasianidae, Numidinae). I. Taxonomy, phylogeny, speciation and biogeography. Ann. S. Afr. Mus. 75 Part 4. 1-75.

Crowe, T.M. & Snow, D.W. 1978. Numidinae. In Snow, D.W. ed. An atlas of speciation in African non-passerine birds. London: British Museum (Natural History).

Ehrlich, P. & Raven, P. 1969. Differentiation of populations. Science 165: 1228-1232.

Elgood, J.H., Fry, C.H. & Dowsett, R.J. 1973. African migrants in Nigeria. Ibis 115: 1-45.

Jackson, S.P. 1961. Climatological Atlas of Africa. Pretoria: Printer.

James, F.C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51: 365-390.

Johnston, R.F. 1972. Ecologic differentiation in North American birds. Univ. Ark. Mus. Occ. Pap. 4: 101-132.

Lucas, A.M. & Stettenheim, P.R. 1972. Avian Anatomy Integument. Part II. Washington, D.C.: U.S. Government Printing Office.

Moreau, R.E. 1957. Variation in the western Zosteropidae (Aves). Bull. Brit. Mus. (Nat. Hist.) 4: 311-433.

/.....

Niles, D.M. 1973. Adaptive variation in body size and skeletal proportions of horned larks of southwestern United States. *Evolution* 27: 405-426.

Rosenzweig, M.L. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. *Amer. Natur.* 102: 67-74.

Sokal, R.R. & Rohlf, F.J. 1969. *Biometry: the principles and practice of statistics in biological research.*

Thornthwaite Associates 1962. Average climatic water balance data of the continents. *Lab. of Climatol., Publ. in Climatology* 15: 114-287.

Anatomy of the vascular system of the head and neck of the helmeted guineafowl *Numida meleagris*

T.M. CROWE

FitzPatrick Institute, University of Cape Town,
Rondebosch 7700, South Africa

(Received April, 1978)

(With 4 figures in the text)

The vascular anatomy of the head and neck of eight adult helmeted guineafowl (Numida meleagris) was investigated by latex injections and dissection, resin casting, and lipidol injections and X-ray photography. The vascular anatomy of these regions is similar to that of the domestic fowl Gallus domesticus, the main differences being in the helmet, wattle and cere vascularization, and the presence of a nape-cheek rete in N. meleagris. It is postulated that five vascular arrangements in the head and neck are important in brain temperature regulation. These arrangements are: the nape-cheek rete, the temporal rete, fine arterio-venous networks in the wattles and cere, and the cavernous sinus-intercarotid association. All but the last of these arrangements require pathways of blood flow to the brain other than the most direct route. Such pathways are discussed.

Contents Page

Introduction

The helmeted guineafowl Numida meleagris is a characteristic member of the African savanna avifauna (Chapin, 1932; Crowe & Snow, 1978). It is a widespread and polytypic species (Crowe, 1978a), and the various subspecies encounter a considerable range of environmental temperatures (Crowe, 1978b). High variation in environmental temperature presents an endotherm with acute thermoregulatory problems (Bartholomew, 1968). Therefore one would expect N. meleagris to have evolved anatomical, morphological, physiological and/or behavioural adaptations to deal with a fluctuating environmental temperature. Crowe (1978b) has shown that variation in certain phenetic characters in N. meleagris is statistically significantly related to variation in environmental temperature. Crowe & Withers (in press) have investigated possible physiological mechanisms of temperature regulation in N. meleagris. The aims of the present study are to describe the major arteries and veins of the naked head and neck regions of N. meleagris, and to hypothesize as to how cervico-cephalic vascular arrangements may help this species in the regulation of brain temperature.

Materials and methods

Three techniques were used to locate and determine the exact positions of blood vessels in the head and upper neck regions of N. meleagris. The left common carotid artery and the right jugular vein of two adult male specimens were injected with differently coloured crystic resin monomers with an added catalyst and an accelerator (Thompsett, 1970). The head and neck of one of these birds was then macerated in a pancreatin solution (Thompsett, 1970), producing a resin cast of the vascular system in relation to the skull and the cervical vertebrae. The second specimen was macerated in hydrochloric acid, resulting in a cast minus the skull and cervical vertebrae. Three specimens, two adult males and one adult female, were similarly injected with lipidol, a radio-opaque dye, and examined by X-ray photography. Three specimens, two adult males and an adult female, were similarly injected with differently coloured latex, and the vessels dissected *in situ*. Nomenclature in both the text and figures follows Richards (1967, 1968) wherever possible. The abbreviations used in the figures are as follows:

Arterial system

AVC, anterior ventral cerebellar artery; B, basilar artery; CA, inter-carotid anastomosis; CC, common carotid artery; CCa, cerebral carotid artery; CO, cerebral opthalmic artery; CW, circle of Willis; E, ethmoid artery; EC, external carotid artery; EF, external facial artery; EO, external opthalmic artery; H, hyoid artery; IC, internal carotid artery; IO, internal opthalmic artery; IOR, infra-orbital ramus; L, lingual artery; LIM, lower internal maxillary artery; MC, middle cerebral artery; MIM, middle internal maxillary artery; NC, nasal-cere artery; NCR, nape-cheek rete; O, Occipital artery; Oe, oesophageal artery; OR, opthalmic ramus; OVA occipital artery-vertebral artery anastomosis; P, palatine artery; Ph, pharyngeal artery; PVC, posterior ventral cerebellar artery; S, sphenomaxillary artery; SL, supra-laryngeal artery; SOR, supra-orbital ramus; TR, temporal ramus; UIM, upper internal maxillary artery; V, vertebral artery; Va, vagus artery; VOL, ventral optic lobe artery; VS, ventral spinal artery; W, wattle artery.

<u>Venous system</u>

AC, anterior cephalic vein; ACb, anterior cerebral vein; C, carotid vein; CFv, cutaneous facial vein; Cv, cervical sinus; DCO, dorsal cerebral opthalmic vein; EF, external facial vein; Eoc, external occipital vein; Ev, ethmoid vein; IF, internal facial vein; IM, internal mandibular vein; IOC, internal occipital vein; J, jugular vein; Lv, lingual vein; MC, middle cerebral vein; MD, mid-dorsal sinus; Moc, median occipital vein; NCv, nasal-cere vein; Oc, occipital sinus; Op, opthalmic vein; P, palpebral vein; PC, posterior cephalic vein; Rop, recurrent opthalmic vein; S, supra-palatine vein; SC, sinus cavernosus; Sp, superior pharyngeal vein; T, temporal vein; TA, transverse anastomosis; Top, temporal opthalmic vein; Tr, temporal rete; Vv, vertebral vein; Wv, wattle vein.

Results

A certain amount of individual variation in the origin and/or position of the blood vessels was found. Therefore, the results related here are a generalized picture, and only major variations are discussed.

The Arterial System

(Figs. 1 & 2)

The largest blood vessels which supply the head and neck regions in *N. meleagris* are the carotid arteries. Shortly after diverging from the innominate artery, the two common carotid arteries enter the hypophysial canal of the cervical vertebrae, and continue, side by side, up the neck without fusing. At the base of the fifth cervical vertebra, the carotids emerge from the hypophysial canal and continue relatively superficially to the base of the skull. At this level, each common carotid divides into two equal branches, the internal carotid, which is essentially a continuation of the main branch, and the external carotid.

External carotid artery (Fig. 1)

At about 5 mm from its point of origin the external carotid divides into five major, unequal arteries. The thickest of these gives rise to the internal maxillary and external facial arteries. In one male specimen, this artery gave rise to a laryngeal artery before bifurcating. In the others, the origin of the laryngeal artery is from the lower internal maxillary. The other four major arteries are the occipital artery, the lingual artery, the hyoid artery and the auricular artery.

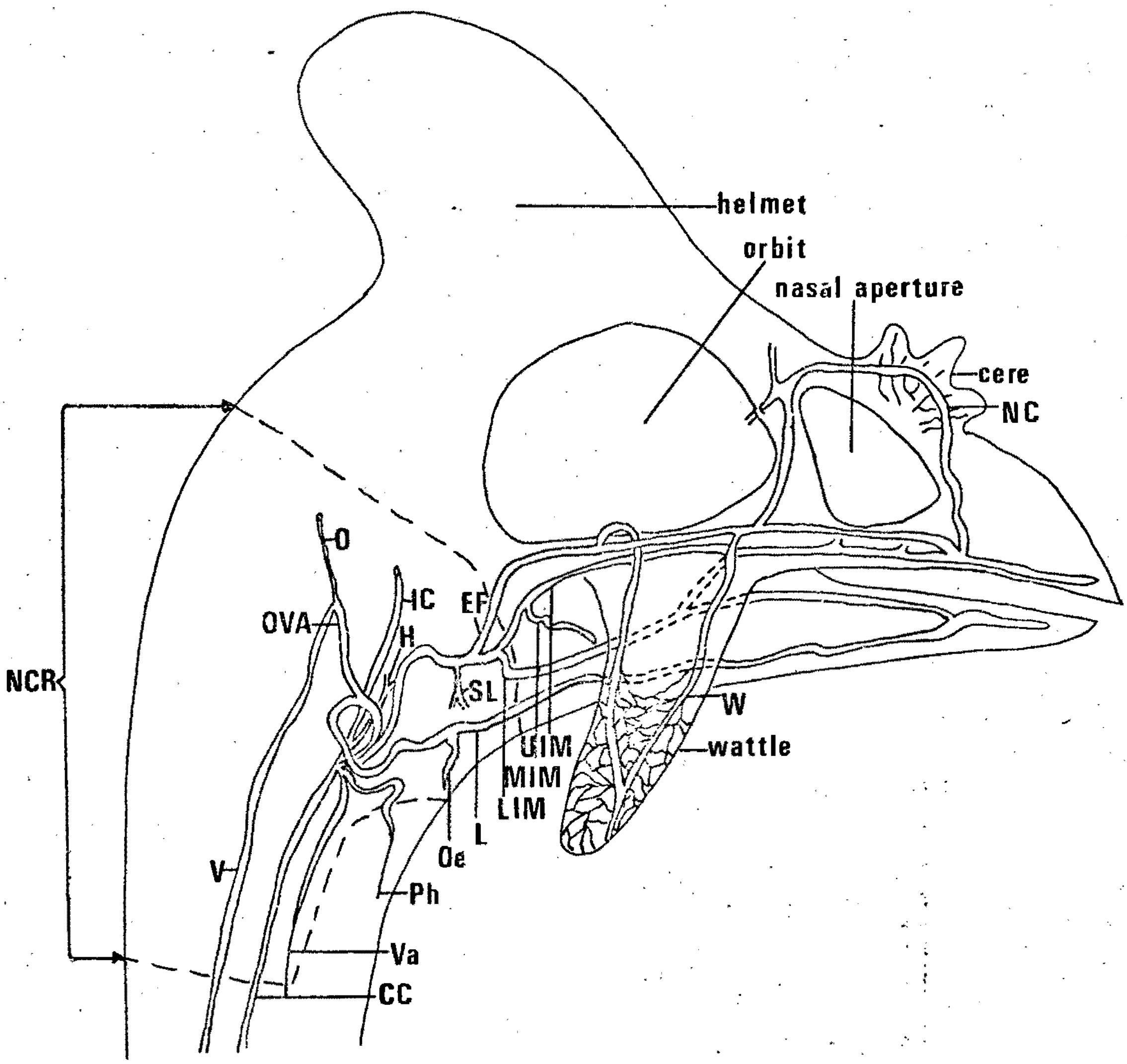

FIG. 1. A semi-diagrammatic lateral representation of the right external carotid artery and its branches. The nape-cheek rete is indicated by broken lines. For key to abbreviations, see p. 4 and p. 5.

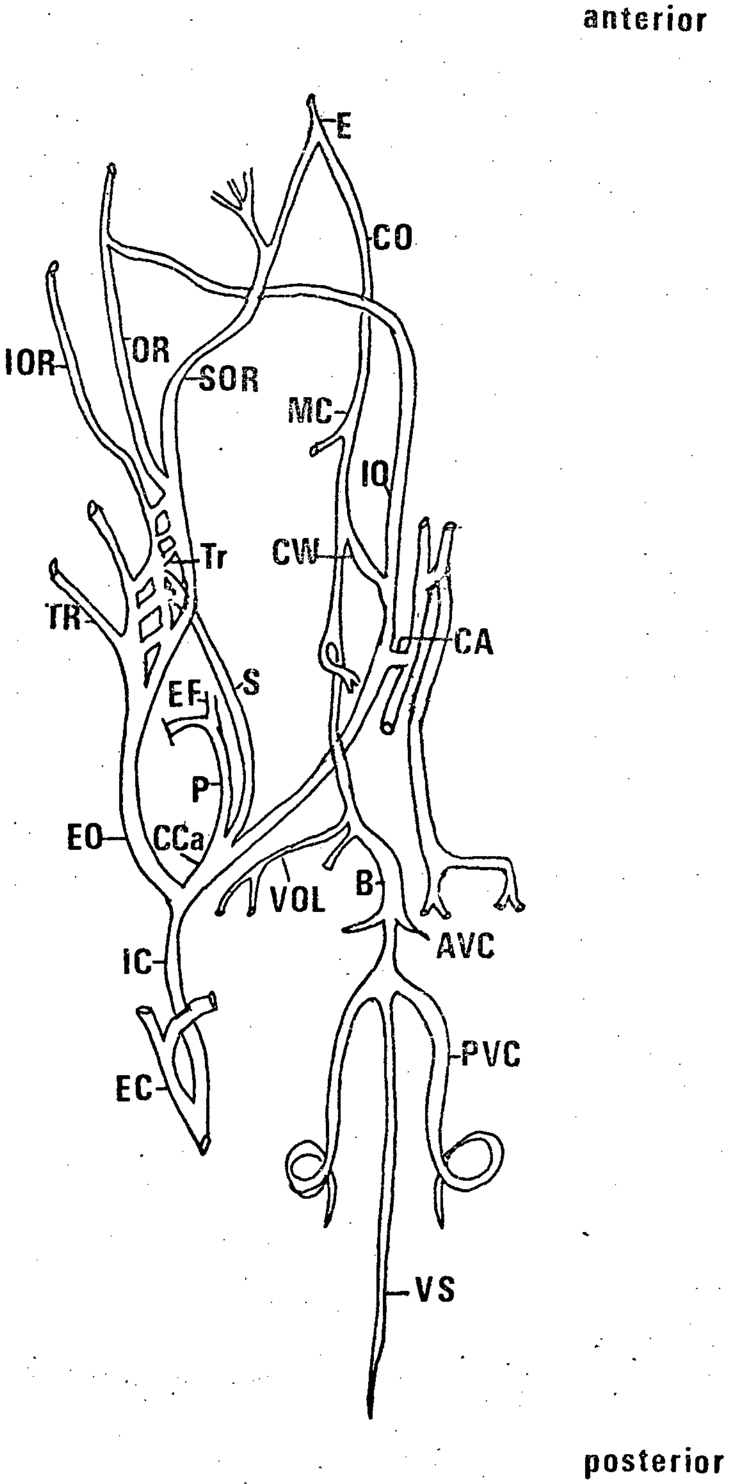

FIG. 2. A diagrammatic representation of the left internal carotid artery and its branches from the dorsal aspect. For key to abbreviations, see p. 4 and p. 5.

Internal maxillary artery (Fig. 1)

The internal maxillary artery feeds the upper and lower jaws, the nasal and buccal areas and the cere.

(i) The upper internal maxillary artery has branches to the pharynx, and anastomoses with the palatine artery and the ethmoid artery of the internal carotid. Anterior to the nasal cavity, the upper internal maxillary bifurcates, sending one large branch the nasal-cere artery, upwards to the cere, and another smaller branch to the end of the premaxilla, where it anastomoses with the same branch from the upper internal maxillary of the opposite side. The nasal-cere artery gives off a network of fine vessels in and around the cere. In two specimens fine branches of the upper internal maxillary were given off to the wattles.

(ii) The middle internal maxillary artery is approximately the same thickness as the upper internal maxillary. It supplies the salivary glands of the lower jaw and ultimately connects to the sphero-maxillary of the internal carotid.

(iii) The lower internal maxillary artery is the smallest branch of the internal maxillary, and supplies the salivary glands and the superficial areas of the mouth.

External facial artery (Fig. 1)

The external facial artery gives rise to a variable number of branches to the lower jaw and to the superficial areas of the face, including the nasal areas. This artery runs along the quadratojugal and the jugal bones, and, at the level of the wattle, gives rise to the wattle artery.

The wattle artery passes behind its parent branch into the inner side of the wattle, and has connections with branches of the upper internal maxillary artery. Examination of the resin casts revealed that the wattle artery divides extensively, while within the wattle, to form a network of fine vessels. Farther along, another small branch of the external facial artery passes dorsally upwards anterior to the orbit. This branch feeds the superficial skin of the eye and the area surrounding the nasal aperture and divides into branches serving the cere area. In two male specimens, another branch, the nasal-cere artery, was observed to enter the cere and pass ventro-laterally anastomosing with a branch of the upper internal maxillary artery.

Occipital artery (Fig. 1)

The occipital artery is the second of the five major branches of the external carotid. This artery passes posteriorly upwards, giving off branches to the neck muscles and to the base of the skull. It also bifurcates to form a fine artery, which feeds the base of the skull, and a much larger artery, the vertebral artery, which curves caudally. At the level of the atlas, the vertebral artery enters the transverse canal of the cervical vertebrae. Therein it passes caudally, giving rise at regular intervals to numerous smaller branches which feed the cervical muscles and vertebrae. This vessel continues caudally, and gives off one or two additional branches to the common carotid before joining that vessel 15-20 mm above the carotid-innominate bifurcation.

Additional branches of the vertebral artery are associated in a fine network (from approximately the fourth cervical vertebra upwards) with similar branches from the occipital, common carotid, lingual, and the internal maxillary arteries to form the arterial portion of what we call the nape-cheek rete. In two specimens, a fine branch of the posterior ventral cerebellar artery connected to the arterial vessels of this rete. It is possible that this vessel was destroyed in other dissections. Within the nape-cheek rete, near its origin, the occipital artery gives rise to the vagus artery and a small artery which feeds the pharynx.

Lingual artery (Fig. 1)

The lingual artery is the third branch of the external carotid artery. This artery supplies the tongue musculature, oesophagus and pharynx. The main branch of this artery continues to the distal end of the lower jaw, where it connects to branches of the lower internal maxillary artery. A smaller branch, the oesophageal artery feeds the oesophagus.

Hyoid artery (Fig. 1)

The hyoid artery is the fourth and smallest branch of the external carotid. This artery gives rise to several smaller arteries which terminate in the hyoid muscles and in the muscles surrounding the jaw hinge. This artery also has fine branches which contribute to the nape-cheek rete.

Auricular artery (Fig. 1)

The auricular artery varies in size from specimen to specimen. It feeds the muscles surrounding the ear. Small branches feed the inner ear, and a large branch of this artery feeds the temporal muscles.

Internal carotid artery (Fig. 2)

At the base of the basisphenoid, the internal carotid divides into two unequal vessels. The larger is the external opthlamic artery, and the smaller is the cerebral carotid artery.

External opthalmic artery (Fig. 2)

The external opthalmic artery passes through the tympanic cavity. In places, it runs in a shallow groove in the mastoid bone. After emerging from the tympanic cavity, this artery divides into two branches, a branch which gives rise to the temporal and inferior alveolar arteries, and a branch which gives rise to the orbital and opthalmic rami. In the area anterior to the tympanic cavity these arteries and their branches give rise to a network of small vessels. This network is termed the temporal rete (Richards, 1967), and is connected to the external carotid circulation via anastomoses with the sphenomaxillary.

(i) The temporal artery passes out dorsally and laterally giving off relatively large branches to the temporal muscles, and smaller ones to the masseter muscles. This artery then continues to the helmet where it divides into smaller vessels which feed the keratinaceous sheath and the bone of the helmet. Fine branches also feed the eyelid.

(ii) The alveolar artery, a very much smaller vessel, arises from the temporal artery near its origin. This artery has connections with the temporal rete.

The second of the larger external opthalmic branches gives rise to the supra-orbital ramus, the infra-orbital ramus and the opthalmic ramus. The supra-orbital ramus and the opthalmic ramus originate from the same branch. Between all three branches there are connections contributing to the temporal rete.

(iii) The supra-orbital ramus is the largest of the branches. It curves laterally and dorsally around the posterior surface of the eye, where it gives off branches to the eye musculature and a branch which anastomoses with the cerebral opthalmic artery to form the ethmoid artery.

(iv) The ethmoid artery supplies the internal nasal cavities and the frontal regions and has connections with external facial artery in the cere area.

(v) The infra-orbital ramus arises from much the same position as the supra-orbital ramus. This artery curves below the optic nerve and divides into a number of small branches which feed the eye muscles. The infra-orbital ramus also has connections with the alveolar artery and the supra-orbital ramus.

(vi) The opthalmic ramus is essentially a large branch of the supra-orbital ramus. This artery also feeds the eye musculature, and is connected to the internal opthalmic artery of the cerebral carotid artery.

Cerebral carotid artery (Fig. 2)

The cerebral carotid artery passes through a canal in the basisphenoid. After passing unbranched for about 10 mm, this artery gives rise to the palatine and sphenomaxillary arteries.

(i) The palatine artery passes ventro-laterally before dividing into two branches. One branch anastomoses with a branch of the external facial artery, and the other ramifies to form small branches which feed the palate area. The palatine artery leaves the bony portion of the skull through a foramen.

(ii) The sphenomaxillary artery is larger than the palatine artery, and separates from the internal carotid anterior to the origin of the palatine. It passes through bone via the same foramen as the palatine artery. The sphenomaxillary has branches which anastomose with branches of the external opthalmic artery.

Having given off these two branches, the internal cerebral carotid continues through the carotid canals until it forms an H-shaped anastomosis with the internal carotid of the opposite side. This anastomosis is formed caudal to the sella tunica or hypophaseal fossa. The connection between the two internal carotids is fine and short.

(iii) The internal opthalmic artery is given off before the main trunk of the cerebral carotid, the circle of Willis passes dorso-laterally. This artery passes anteriorly in association with the optic nerve, and gives rise to branches which link up with the cerebral opthalmic artery and the external opthalmic artery. It also has connections with the ethmoid artery.

Having given off the internal opthalmic artery, the circle of Willis divides into an anterior branch, the cranial ramus, and an incomplete posterior branch, the caudal ramus.

(iv) The <u>cranial</u> <u>ramus</u> supplies the cerebrum and optic lobes. It gives off the ventral optic lobe artery which ramifies, supplying the ventral surface of the optic lobe, and has connections with the anterior ventral cerebellar artery. The cranial ramus then passes antero-laterally around the cerebrum to give rise to four branches:

(a) The <u>posterior</u> <u>cerebral</u> <u>artery</u> was most developed on the right hand side of the head in the three specimens in which the brain was dissected. It gives rise to branches which feed the cerebellum and the dorsal surface of the optic lobe.

(b) The <u>middle</u> <u>cerebral</u> <u>artery</u> comes off the cranial ramus anterior to the origin of the posterior cerebral artery. This artery passes laterally around the cerebral hemispheres toward the olfactory lobes. It gives off numerous small vessels along the way.

(c) The <u>cerebral</u> <u>opthalmic</u> <u>artery</u> arises from the same point as the middle cerebral artery. This vessel passes antero-medially through the dura mater. It receives branches of the external opthalmic artery after entering the orbit via the foramen ethmoidale (Hoffman, 1900; Richards, 1967). Together, the external opthalmic artery and the cerebral opthalmic artery form the ethmoid artery, which has connections with the upper internal maxillary, and external facial arteries of the external carotid.

(d) The anterior cerebral artery is the finest of the four branches of the cranial ramus. It passes in a medial direction, and appears to enter the dura mater.

(v) In two specimens, the caudal ramus of the circle of Willis, or basilar artery, was well developed on the left hand side and rudimentary on the right hand side. The reverse was found in a third specimen. In one of the specimens with a "left-hand" basilar artery, a fine connection occurs between the rami of the two sides before the anterior ventral cerebellar arteries are given off. The caudal ramus passes posteriorly along the medial ventral surface of the medulla, gradually decreasing in size. It gives off two large, and many smaller lateral vessels along the way.

(a) The anterior ventral cerebellar arteries feed the cerebellum.

(b) The two posterior ventral cerebellar arteries arise in the vicinity of the medulla, and feed the lateral flocculus and the dorsal surface of the cerebellum. These arteries have numerous connections with the anterior ventral cerebellar artery and, in two specimens, fine connections with the nape-cheek rete.

(c) The ventral spinal artery originates from the basilar artery. This vessel passes along the ventral surface of the spinal cord as a single vessel. We were unable to trace vessels which may have passed from this artery to the dorsal surface to form the dorsal spinal artery (Richards, 1967).

The venous system

(Figs. 3 and 4)

The largest vessels which drain the superficial head and neck regions are the jugular veins. The right hand jugular is considerably larger in diameter than the left. The jugulars pass down the neck in a ventral superficial position. Near the base of the skull, they connect via the transverse anastomosis, which slopes caudally towards the right-hand side. In two specimens, branches from anterior regions of the head fed into the transverse anastomosis. We recognize five major veins, or categories of veins, which drain into the jugulars.

Lingual vein (Fig. 3)

The lingual vein runs alongside the lingual artery. It arises at the level of the second cervical vertebra, and collects blood from the branches which drain the oesophagus and the pharynx. The lingual vein enters the jugular vein midway between the entry of the posterior cephalic vein and the transverse anastomosis. Smaller branches which drain the neck muscles enter the lingual at intervals.

Anterior cephalic vein (Fig. 3)

The anterior cephalic vein is the portion of the jugular

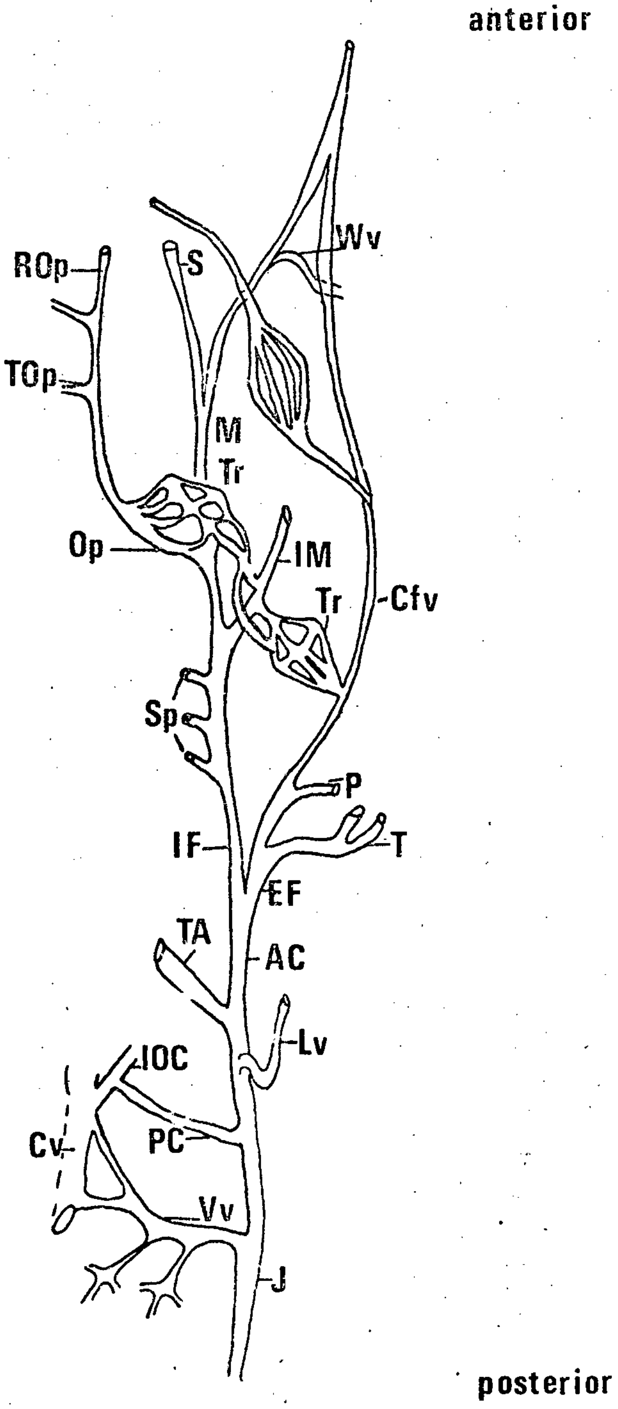

FIG. 3. A diagram of the right jugular vein and its branches from the dorsal aspect. For key to abbreviations, see p. 5.

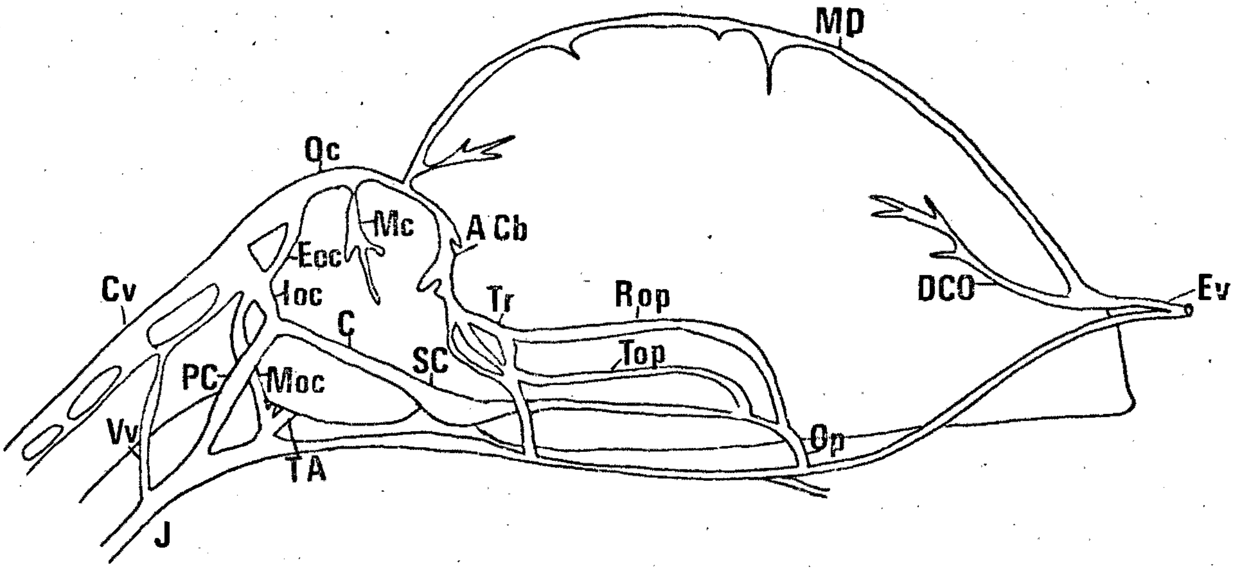

FIG. 4. A diagram of the lateral aspect of the brain showing the principle brain sinuses and their associated veins. For key to abbreviations, see p. 5.

anterior to the transverse anastomosis. It receives vessels which drain the extra-cranial regions of the head. The two main branches feeding this vein are the external facial vein and the internal facial vein.

(i) The external facial vein drains the skin and muscles of the face and jaw articulation. Three branches (two large, one small) converge to form this vein:

(a) The cutaneous facial vein, one of the large branches, drains blood from the skin, face and eye muscles, and the area of jaw articulation. Complex fine vessels from the nasal-cere vein, which drain the cere, pass down anterior to the orbit and the main branch of the cutaneous facial vein. The cutaneous facial vein has connections with branches of the internal facial vein and the maxillary vein. A vein originating from the ethmoid vein ramifies in the preorbital area before feeding into the cutaneous facial vein.

(b) The palpebral vein is the second of the two larger branches. This vein converges on the external facial vein together with the cutaneous facial vein and the temporal vein. It collects blood from the lower temporal areas, the eye and eyelids.

(c) The temporal vein is a considerably smaller vessel. The main branch of this vein is fed by numerous smaller vessels which drain the muscles of the temporal area.

Smaller branches between the cutaneous facial and the palpebral vein, as well as connections with the internal facial vein branches, form a part of the venous component of the temporal rete.

(ii) The internal facial vein is the larger of the two veins which unite to form the anterior cephalic vein. It is made up of vessels which drain the pharyngeal and palate areas, the tongue musculature, the eyeball and the superficial orbit. There are connections between this vein, the temporal rete and the cutaneous facial vein.

(a) The superior pharyngeal veins are the most posterior vessels which drain into the internal facial vein. These small vessels drain the ventral palate and dorsal pharyngeal areas. They also form a link between the left internal facial vein and the right internal facial vein. In both specimens in which they were observed, three of these veins were found to be present.

(b) The next veins which bring blood to the internal facial vein are small branches which link it to the temporal rete and the cutaneous facial vein.

(c) The internal mandibular vein is a large vein which collects blood from the lower jaw. It has connections with the cutaneous facial vein, the temporal rete and the opthalmic veins.

Progressing anteriorly, the next vessels feeding the internal facial vein are the maxillary vein and the opthalmic vein.

(d) The maxillary vein has branches which collect blood from the anterior buccal muscles, the tongue and the palate area. It also has small branches which drain sections of the nasal area and eventually contribute to the temporal rete. The supra-palatine vein is the largest of these branches. This vessel drains a network of small vessels which ramify between the palate mucosa. There is a direct connection between the maxillary vein and the cutaneous facial vein. A vein consisting of numerous smaller branches, the wattle vein, drains the wattle. It feeds into the maxillary vein after passing ventral to the cutaneous facial vein.

(e) The _opthalmic vein_ joins the maxillary median to the eyeball. This vessel gives off many small branches which spread over the eyeball. Together with the middorsal sinus, it is fed by the ethmoid vein, which drains the frontal areas. Two large branches, the temporal opthalmic vein and the recurrent opthalmic vein drain the orbit and the cerebral areas. The temporal opthalmic vein has two anastomoses with the temporal rete. The recurrent opthalmic vein has connections with the temporal vein. The complexity of such anastomoses could not be fully determined in our dissections. The temporal opthalmic vein, however, was observed to communicate with the cerebral circulation via the anterior cerebral vein. Small vessels draining the helmet pass through foramina in the frontal bone before draining into branches of this vein.

Posterior cephalic vein (Fig. 3)

The posterior cephalic vein is the major posterior division of the jugular vein. It joins the jugular prior to the transverse anastomosis. This vein receives blood from both the dorsal and ventral brain sinuses.

(i) The auricular vein is a small vessel which receives blood from the ear musculature. It feeds into the posterior cephalic vein at a point in common with the occipital vein. Very fine branches of the posterior cephalic vein, the occipital vein, and the vertebral veins form the extensive venous component of the nape-cheek rete. The fine branches of these veins drain into three to four larger branches, on either side of the neck. These branches then feed into a large vertebral vein which feeds into the jugular vein.

(ii) The carotid vein completely surrounds the internal cerebral artery. This vein extends from the sinus cavernosus, which encloses the intercarotid anastomosis, and drains into the posterior cephalic vein.

The brain sinuses and occipital venous system (Fig. 4)

The dorsal cerebral opthalmic vein and the ethmoid vein together feed into the mid-dorsal sinus. This fine vessel receives blood from the dorsal parts of the cerebrum. Near the junction of the cerebrum and the cerebellum, the anterior cerebral vein and the middle cerebral vein merge with the mid-dorsal sinus to form the occipital sinus. The anterior cerebral vein drains the area between the cerebrum and the cerebellum, as well as that between the cerebellar hemispheres. This vein has large connections with the temporal rete. The middle cerebral vein drains the cerebellum and the optic lobes, and has connections with the auricular vein.

The posterior cephalic vein and the carotid vein merge to form the internal occipital vein. This vessel connects dorsal and ventral components of the cerebellar brain sinuses. Near the origin of the middle cerebral vein from the occipital sinus, the external occipital vein branches off and connects to the internal occipital vein. The lateral occipital veins connect the internal occipital vein and the vertebral vein. At the point of fusion between the external occipital vein and the internal occipital vein, the middle occipital vein is given off. This vein passes ventrally around the cerebellum, and fuses with the same vein from the opposite side, before entering the transverse anastomosis. The opthalmic vein fuses with the dorsal sinus to form the ethmoid vein. The vertebral vein connects to the internal occipital vein. This vein passes down the cervical canal, anastomosing with the cervical sinus, and the vertebral vein from the opposite side. It drains into the jugular vein level with the third or fourth cervical vertebra.

The cervical sinus is essentially an extension of the occipital sinus. It is connected to the jugular veins by two pairs of large veins, which we also call vertebral veins. Branches of these vertebral veins and those previously mentioned are fed by a network of small veins which form the venous component of the nape-cheek rete.

Discussion

The cervico-cephalic vascular system of *N. meleagris* is, in general, similar to that of Gallus domesticus (Richards 1967, 1968). Therefore, we will discuss only major differences between the two species.

In N. meleagris the upper internal maxillary artery gives rise to a nasal-cere artery, which feeds the cere and connects to the external facial artery. There is no comparable artery in G. domesticus. This could be due to the fact that the cere of this species lacks well-developed papillae which are often found on N. meleagris (Crowe 1978a). The nasal-cere vein also has no counterpart in G. domesticus.

No vein and artery comparable to the wattle vein and artery in N. meleagris are described for G. domesticus. As with the nasal-cere artery and vein this is to be expected, since G. domesticus lacks a homologue for the cartilaginous wattle which hangs from the upper jaw of N. meleagris (Ghigi, 1936). In G. domesticus, wattles are fleshy structures which hang from the lower jaw (Lucas & Stuttenheim, 1972).

The external facial artery in G. domesticus has a branch which feeds the comb. This branch is absent in N. meleagris. The helmet in N. meleagris is fed by a large branch of the temporal artery. The temporal artery in G. domesticus is much more reduced, and feeds mainly the temporal muscles. A number of vessels which drain the comb of G. domesticus empty into the cutaneous facial vein. In N. meleagris, vessels from the helmet feed into branches of the opthalmic vein.

Tenous connections between the occipito-vertebral and internal carotid systems occur in both species. In _N. meleagris_ these connections are with the posterior ventral cerebellar artery, in _G. domesticus_ with the ventral spinal artery. The ventral spinal artery in _N. meleagris_ arises from the basilar artery, rather than from one of the posterior cerebellar arteries as it does in _G. domesticus_. Also, to the level of the fourth cervical vertebra, the ventral spinal artery of _N. meleagris_ is a single vessel, whereas in _G. domesticus_ it is, in some places, a double structure.

The most striking difference between the cervico-cephalic vascular systems of _G. domesticus_ and _N. meleagris_ is the presence of the nape-cheek rete in the latter. No rete in this area has been described for any other bird. It must be stressed that the complexity of the nape-cheek rete was apparent only in resin casts. Therefore, we cannot exclude the possible existence of similar retia in other species. However, Frost _et al_. (1975), in the only other similar study of a bird, did not report a nape or cheek rete in their resin casts of the vascular system of the Jackass penguin (_Spheniscus demersus_).

There are five vascular arrangements in the head and neck of _N. meleagris_ which we feel may be important in the regulation of brain temperature. These are the temporal and nape-cheek retia, the fine arterio-venous associations in the wattles and cere, and the intercarotid anastomosis-cavernous sinus association. The major problem in describing the possible ways in which these vascular arrangements could function in brain temperature regulation is understanding the alternative ways by which blood passing through these arrangements could reach the brain.

The most obvious direct route for blood to the brain is via the internal carotid artery and the caudal ramus of the circle of Willis. One alternative, less direct, route is via the anastomoses between branches of the external carotid and the palatine and sphenomaxillary branches of the internal carotid. Another pathway is from the vertebral artery via retrograde flow through the carotid bifurcation. Richards (1967) and Richards & Sykes (1967) have shown in *G. domesticus* that these routes of blood supply to the brain are able to maintain life indefinitely, in the absence of a direct route. Connections between the cerebral arterial circulation of the two hemispheres at the intercarotid anastomosis could allow lateral communication between the brain hemispheres.

Richards (1970) has discussed the feasibility and mechanisms by which relatively warm arterial blood on its way to the brain could be cooled in the temporal rete and in the intercarotid-cavernous sinus association. He, however, questions (Richards, 1970) the temporal rete as being the primary site of brain temperature regulation in *G. domesticus*. However, until more is known about intravascular temperatures, patterns of cervico-cephalic blood flow, and physiological responses of *N. meleagris* to varying temperature regimes we cannot demonstrate conclusively a thermoregulatory function for these vascular arrangements.

Summary

The anatomy of the cervical and cephalic arteries and veins of the helmeted guineafowl Numida meleagris was investigated by latex injections and dissection; by resin casting and maceration in pancreatin and hydrochloric acid; and by lipidol injections and X-ray photography.

The cervico-cephalic vascular anatomy of N. meleagris is similar to that of the domestic fowl Gallus domesticus. Major differences, particularly the existence of a nasal-cere and wattle arteries, and an extensive arterio-venous rete in the nape and cheek regions of N. meleagris, are discussed.

Five vascular arrangements in the head and neck are postulated to be important in brain temperature regulation. These are: the nape-cheek rete, the temporal rete, fine arterio-venous networks in the wattles and cere, and the cavernous sinus-intercarotid anastomosis association. All but the last of these require arterial blood to flow to the brain via relatively indirect pathways. These pathways are discussed in the light of occlusion experiments carried out by other workers.

We thank Mrs B. Marsh and Miss L. LeRoux for help with resin casting, Dr J. Jarvis for advice in latex preparations, and Dr A. Goldin for taking the X-rays. Specimens were provided by the Cape Province Department of Nature and Environmental Conservation, and the University of Cape Town provided essential equipment and housing facilities for the guineafowl.

REFERENCES

Bartholomew, G.A. (1968). Body temperature and energy metabolism. In _Animal function: Principles and adaptations_: 290-354. Gordon, M.S. (ed.). London: Collier-MacMillan Limited.

Chapin, J.P. (1932). The birds of the Belgian Congo. Part 1. _Bull. Am. Mus. nat. Hist._ 65: 1-756.

Crowe, T.M. (1978_a_). The evolution of guineafowl (Galliformes, Phasianidae, Numidinae). Taxonomy, phylogeny, speciation and biogeography. _Ann. S. Afr. Mus._ 75: in press.

Crowe, T.M. (1978_b_). The evolution of guineafowl (Galliformes, Phasianidae, Numidinae). Adaptive differentiation. _Bull. Br. Orn. Club._ in press.

Crowe, T.M. & Snow, D.W. (1978). Numidinae. In _An atlas of speciation in African non-passerine birds_: in press. Snow, D.W. (ed.). London: British Museum (Natural History).

Crowe, T.M. & Withers, P.C. (in press). Guineafowl: A naked head as a thermal window. _Science_

Frost, P.G.H., Siegfried, W.R. & Greenwood, P.J. (1975). Arterio-venous heat exchange systems in the Jackass penguin _Spheniscus demersus_. _J. Zool., Lond._ 175: 231-241.

Ghigi, A. (1936). _Galline di faraone e tacchini_. Milano: V. Hoepli.

Hoffman, M. (1900). Zur verleichenden Anatomie der Gehirni und Ruckenmarksarterien der Vertebraten. _Z. Morph. Anthrop._ 2: 247-322.

Lucas, A.M. & Stuttenheim, P.R. (1972). Avian anatomy. Integument Part I. Washington, D.C.: U.S. Government.

Richards, S.A. (1967). Anatomy of the arteries of the head in the domestic fowl. J. Zool., Lond. 152: 221-234.

Richards, S.A. (1968). Anatomy of the veins of the head in the domestic fowl. J. Zool., Lond. 154: 223-234.

Richards, S.A. (1970). Brain temperature and the cerebral circulation in the chicken. Brain Res. 23: 265-268.

Richards, S.A. & Sykes, A.H. (1967). Responses of the domestic fowl (Gallus domesticus) to occlusion of the cervical arteries and veins. Comp. Biochem. Physiol. 21: 39-50.

Thompsett, D.H. (1970). Anatomical techniques. London: Livingstone Press.

Guineafowl: A Naked Head as a Thermal Window.

Abstract. Helmeted guineafowl, unlike other endotherms, regulate brain temperature less precisely than body temperature. By breathing through the nares, guineafowl can cool their brain, probably by countercurrent heat exchange in the temporal rete. The mechanism for brain temperature regulation becomes ineffective when heat-stressed guineafowl pant and gular flutter through the mouth. Convective heat loss through thermal windows of the head and neck becomes critical to brain temperature regulation under these conditions.

Some birds may use unfeathered areas of the head and neck to facilitate uptake and/or dissipation of heat (1). This hypothesis has not been tested experimentally, despite the possible role of such a thermal window in the regulation of brain temperature. Brain temperature (T_{br}) is precisely regulated in many species of birds and mammals (2). The likely mechanism for regulation of T_{br} involves evaporative cooling of venous blood in the nasal mucosa, and countercurrent heat exchange between this cool blood and relatively warm arterial blood in a temporal or carotid rete (3).

We have examined the hypothesis that naked areas of the head and neck of helmeted guineafowl (Numida meleagris) act as a thermal window to facilitate convective heat loss, thereby assisting in the regulation of T_{br}. The largely unfeathered head and neck of this species, combined with patterns of cutaneous pigmentation (4), behavior, and cervico-cephalic vascular anatomy (5), suggest that the head and neck could be used as a thermal window.

At low ambient temperature (T_a), guineafowl have relatively dark facial skin, and usually assume a "head-retracted"

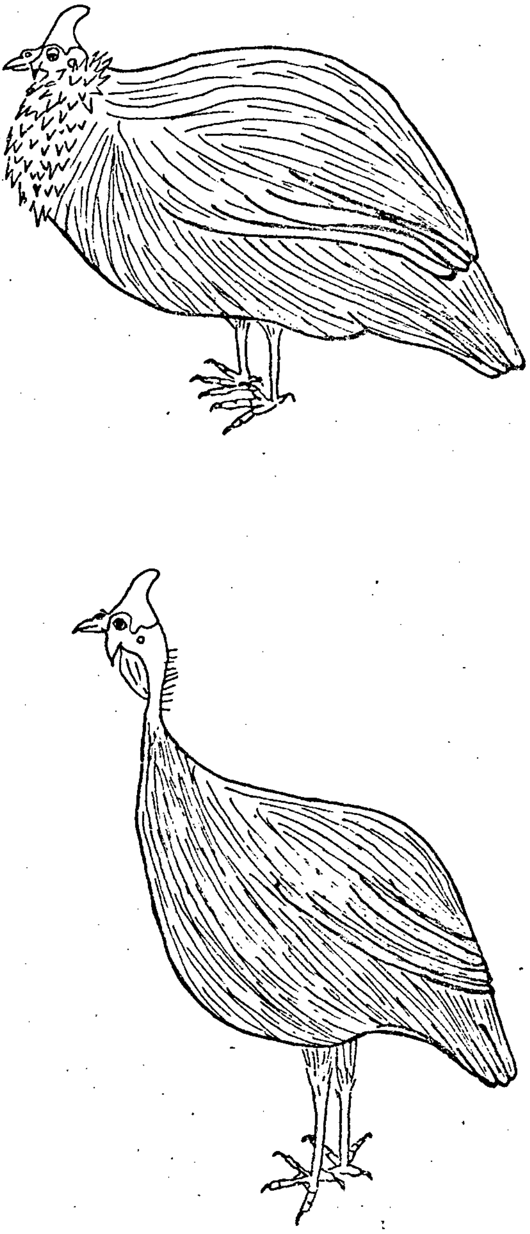

Figure 1. "Head-retracted" posture of guineafowl at low ambient temperature (above), and upright posture at high ambient temperature (below).

posture (Fig. 1). In this posture, the head and neck are nestled among erected collar feathers, thus reducing the area of exposed naked skin. This reduction of exposed area should retard heat loss via conduction and convection, and the darkened facial skin may promote heat uptake via radiation. Guineafowl at high T_a have a more lightly colored face and assume an upright posture with the head and neck extended (Fig. 1). This posture increases the area of exposed naked skin and should promote heat loss via conduction and convection, while reducing the radiative heating of the pale facial skin. Immediately underlying those areas of facial skin which show color changes, is an extensive arterio-venous rete which could provide the vascular component of a thermal window (5).

Nine adult guineafowl (mean weight and standard deviation, 1130 ± 50 g) were maintained in an outdoor aviary, and given free access to water and mixed grain. Oxygen consumption (V_{O_2}), respiratory quotient (RQ), and total evaporative water loss (TEWL) were measured by open flow respirometry (6), in birds which had fasted overnight. Unrestrained guineafowl were placed in a 40 l metabolic chamber at a T_a of 10 °C and were left at that T_a until V_{O_2} was stable for 30 minutes. The T_a was then increased in 5 or 10 °C steps up to 40 °C. The birds were kept at each T_a until V_{O_2} was stable for 30 minutes.

All temperatures were measured with copper-constantan thermocouples (7). Deep body temperature (T_{cl}) was measured with a thermocouple inserted 5 cm into the cloaca. The T_{br} was measured with a 0.13 mm diam thermocouple implanted in the forebrain through a 2 mm diam hole, which was drilled through the skull about 8 mm above the external ear opening. This thermocouple was cemented to the helmet with epoxy resin. Position of the thermocouples in the brain was verified by X-ray.

The effect of radiation and wind on $\underline{T}_{br}$ was tested for guineafowl held at $\underline{T}_a$ of 26-28 °C. The birds were immobilized in a plastic-mesh bag, and their legs were taped to a heavy splint. A 200 W incandescent light bulb and an electric fan (air flow 3-5 m sec^{-1}) inside the chamber were used to simulate the effects of natural radiation and convection. The beaks of three guineafowl were taped shut during these radiation/convection experiments, forcing them to breathe through the nares, and preventing panting and gular fluttering with an open gape.

As expected, the $\underline{V}_{O_2}$ of guineafowl increased at low $\underline{T}_a$, whereas TEWL/V_{O_2} increased at high $\underline{T}_a$ (Fig. 2). The $\underline{T}_{cl}$ remained virtually constant at all $\underline{T}_a$ investigated, while $\underline{T}_{br}$ varied by over 4.5 °C, and exceeded $\underline{T}_{cl}$ at $\underline{T}_a \geq 41$ °C (Fig. 2). Heat-stressed guineafowl ($\underline{T}_a > 35$ °C and/or $\underline{T}_{br} > 42.5$ °C) showed synchronous panting and gular flutter. The rate of this flutter-panting increased rapidly from typical breathing rates (20-40 min^{-1}) to rates of 240-400 min^{-1}. Synchronous flutter-panting appears to be common among gallinaceous birds (8).

The $\underline{T}_{br}$ of immobilized guineafowl was not different from that of unrestrained birds held at the same $\underline{T}_a$. The $\underline{T}_{br}$ was, however, markedly altered by both radiation and convection (Table 1). The rate of increase in $\underline{T}_{br}$ with both the light and fan in operation was about 2.8 times slower than with only the light. Similarly, the rate of cooling of $\underline{T}_{br}$ with only the fan on, was about 1.8 times greater. The $\underline{T}_{br}$ of dead birds increased more rapidly, and decreased more slowly, than did that of living

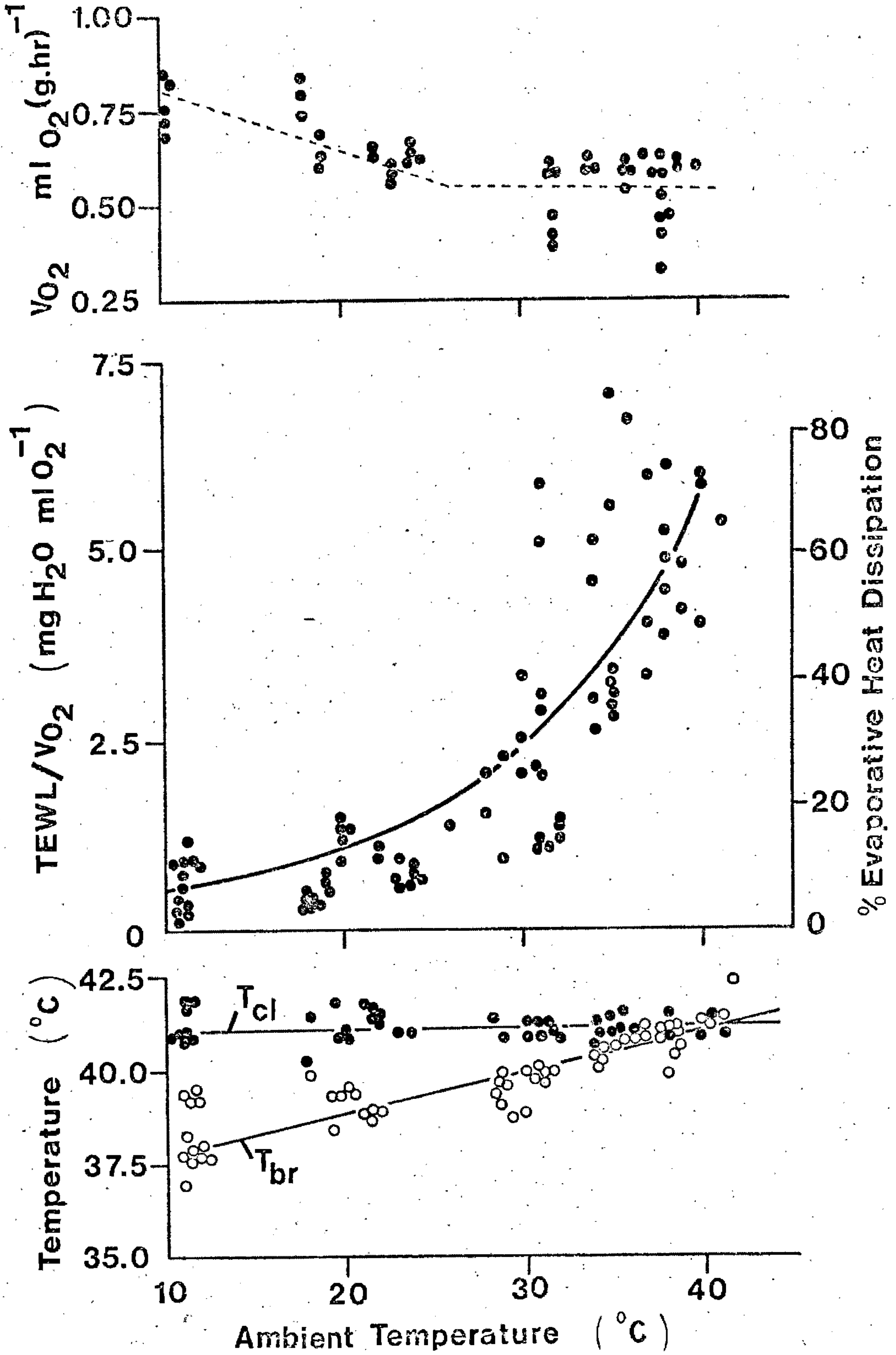

Figure 2. Oxygen consumption (V_{O_2}), total evaporative water loss per ml O_2 consumed (TEWL/V_{O_2}) and per cent of metabolic heat production which is dissipated through evaporative cooling, and brain and body temperature (T_{br}, T_{cl}) of guineafowl at differing ambient temperatures. Regression equations are: $V_{O_2} = 0.92 - 0.01T_a$, $r^2=0.65$, N=32 (calculated for T_a 33 °C); TEWL/$V_{O_2} = 0.22\ e^{0.08T_a}$, $r^2=0.77$, N=56; $T_{br} = 37.01 + 0.10T_a$, $r^2=0.76$, N=58; $T_{br} = 41.1 + 0.002T_a$, $r^2=0.0005$, N=58.

Table 1. Rates of heating and cooling ($^{o}C\ min^{-1}$) of the forebrain of living and dead guineafowl. * indicates that values are different at P 0.05, ** is P 0.001, NS is nonsignificant difference, using paired t-test. Values are mean ± standard error.

		Living				Dead		
Heating	no fan	0.0124	0.002	(10)	**	0.0266	0.004	(3)
			**				*	
	fan	0.0055	0.001	(10)	**	0.0215	0.004	(3)
Cooling	no fan	0.0123	0.002	(11)	*	0.0069	0.0003	(3)
			*				NS	
	fan	0.0229	0.004	(10)	*	0.0093	0.001	(3)

birds held under similar conditions (Table 1). These differences demonstrate a physiological capacity of live birds to regulate T_{br}.

Sudden increases and decreases in T_{br} (up to 0.4 °C) were often noted during the radiation/convection experiments. These changes in T_{br} were correlated with the onset or termination of flutter-panting (Fig. 3). Somewhat unexpectedly, the T_{br} increased after the onset of flutter-panting in birds with an open gape. However, the T_{br} decreased after the onset of flutter-panting in birds which were forced to breathe through their nares (Fig. 3).

The basic mechanisms for temperature regulation in helmeted guineafowl are similar to those found in other birds and mammals (9). At low T_a, the increased rate of heat loss is offset by elevated metabolic heat production (Fig. 2). The bulk of excess metabolic heat at high T_a is dissipated by enhanced evaporative cooling due to flutter-panting. During flutter-panting, there was no evidence of respiratory alkalosis since RQ remained essentially constant (0.78 ± 0.02, $N=51$). This suggests that most of the enhanced evaporative water loss occurs from non-respiratory exchange surfaces.

The poor T_{br} regulation by guineafowl is unlike the relatively precise regulation reported for other birds and mammals (2). The contrasting effect of T_a on T_{br} and T_{cl} in guineafowl must reflect, to some extent, the physical dimensions of the head and body. The small, unfeathered head has a much higher thermal conductivity ($0.020\ ^{o}C\ min^{-1}$) than does the larger body ($0.0036\ ^{o}C\ min^{-1}$). Therefore, it would be impossible for guineafowl to

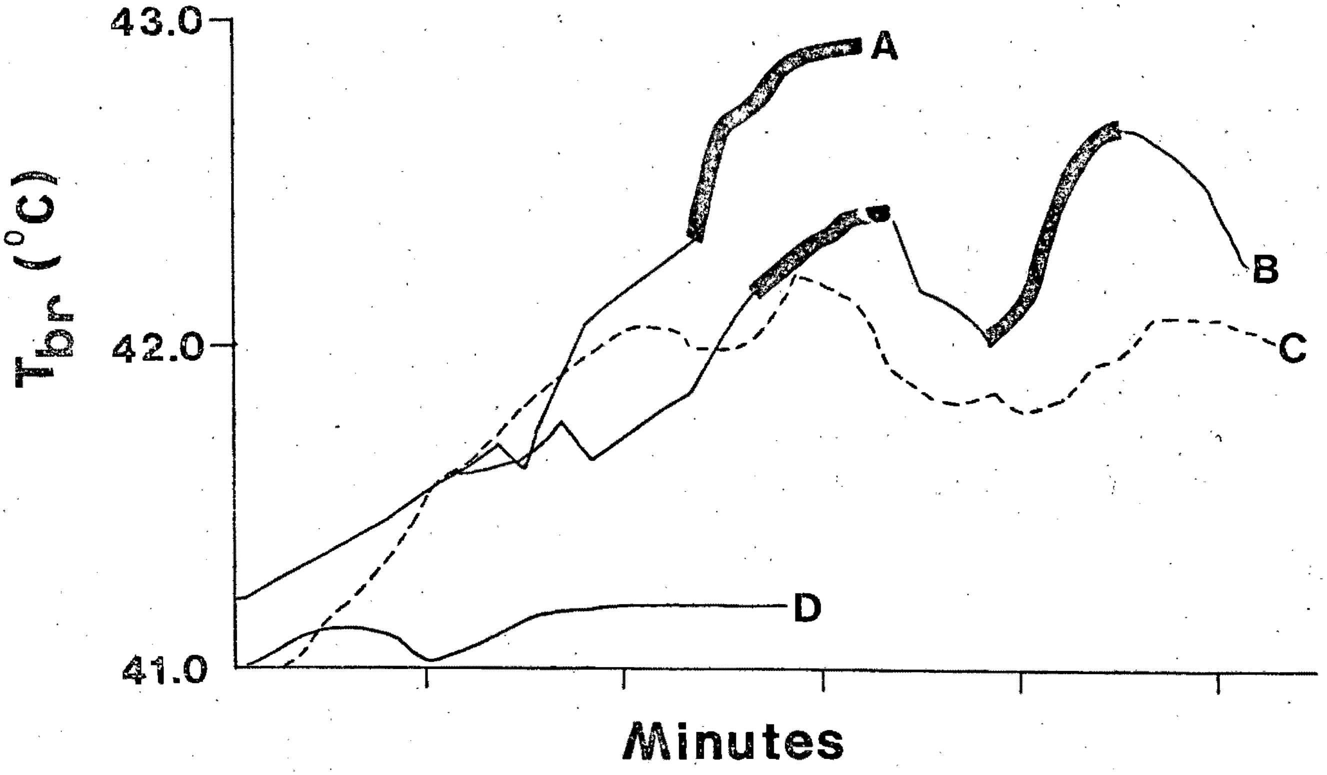

Figure 3. Brain temperature (T_{br}) of guineafowl with head subjected to simulated solar radiation and wind. A: typical result, beak not taped shut, no convection; B: atypical result noted once with one bird, beak not taped, no convection; C: typical result with beak taped shut, no convection; D: typical result, beak not taped, with convection. Thickened portions of lines indicate occurrence of gular flutter and panting.

regulate T_{br} as effectively as T_{cl} without having either a higher capacity for heat production and dissipation in the head, or a rate of blood flow to the head which was far in excess of that required for O_2 transport.

However, the poor T_{br} regulation of guineafowl must not be taken to mean there is a total lack of control, since T_{br} alters by only 0.1 °C per 1 °C change in T_a, despite the high thermal conductivity of the head. At low and high T_a, postural changes alter the exposed surface area of the head and neck, thereby facilitating the maintenance of tolerable T_{br}. Moreover, we have demonstrated that heat-stressed guineafowl can lower T_{br} by breathing through the nares. This finding is consistent with the hypothesis that heat exchange in the temporal rete between cool venous blood from the nasal mucosa and relatively warm arterial blood can cool the brain. Similar retia have been hypothesized to allow T_{br} regulation in heat-stressed birds and mammals (2), but have been demonstrated to do so only in a few cases (3).

Guineafowl appear to abandon nasal cooling of T_{br} when they flutter-pant through an open gape. Gape breathing is probably favored over nares breathing because 1) gape breathing bypasses the nasal countercurrent heat exchanger, hence avoiding recondensation of water in the respiratory passage (10), and 2) the airway's resistance during periods of hyperventilation may be lower when breathing through the mouth rather than the nares. During flutter-panting with an open gape, the evaporative surfaces are shifted to the gular area, where patterns of venous drainage cannot selectively cool blood flowing to the brain (5).

With the loss of nasal evaporative cooling, the naked areas of the head and neck become the most likely sites for heat exchange which could be important for T_{br} regulation. The radiation/convection experiments demonstrated that these areas can act as thermal windows, and that the bulk of excess heat can be dissipated by convection. Convection at $T_a \geq T_{br}$ did not result in a decrease in T_{br}. Heat loss was therefore non-evaporative. Convective heat loss under our experimental conditions was more effective in dissipating a radiative than an endogenous heat load. Convection resulted in a 2.8 fold decrease in heat gain via radiation, but only a 1.7 fold increase in heat loss without radiation. The highest head temperature during radiative heating would be at the surface, where convective heat dissipation occurs, whereas the surface temperature during loss of an endogenous heat load is the lowest head temperature. Therefore, convective cooling might be more effective for T_{br} regulation than nasal evaporative cooling, if guineafowl in their natural habitat (relatively open savannah) were more likely to become heat-stressed through a solar heat load than through endogenous heat production.

A large arterio-venous rete underlying the naked areas of the nape and cheeks provides additional evidence in favor of the thermal window hypothesis. We found that localized cooling of the nape (11) lowered T_{br} of live birds by up to 0.6 °C within 10 seconds, whereas the T_{br} of similarly treated dead birds decreased more slowly, and by less than 0.2 °C. However, we cannot state unequivocally that this rete assists in the control of T_{br} because there are only tenuous direct arterial connections between the nape-cheek rete and the brain (5). There would probably have to be an alternative pathway(s) and/or retrograde blood flow to allow an adequate supply of cool arterial blood from the nape-cheek rete to reach the brain. Richards and Sykes (12) have demonstrated such alternative pathways in the domestic fowl (Gallus domesticus), a close relative of the guineafowl.

T. M. CROWE

Fitzpatrick Institute, University of Cape Town, Rondebosch
7700, South Africa.

REFERENCES AND NOTES

1. J. F. Reynolds, Scopus 1, 57 (1977).

2. D. L. Kilgore, M. H. Bernstein, K. Schmidt-Nielsen, Am. J. Physiol. 225, 739 (1973); D. L. Kilgore, M. H. Bernstein, D. M. Hudson, J. Comp. Physiol. 110, 209 (1976); C. R. Taylor, Sci. Am. 220, 88 (1969); C. R. Taylor and C. P. Lyman, Am. J. Physiol. 222, 114 (1972).

3. M. A. Baker and J. N. Hayward, Nature 216, 139 (1967). M. A. Baker and J. N. Hayward, J. Physiol. Lond. 198, 561 (1968); J. N. Hayward and M. A. Baker, Brain Res. 16, 417 (1969).

4. T. M. Crowe, Ann. S. Afr. Mus., in press.

5. T. M. Crowe and A. A. Crowe, in preparation.

6. P. C. Withers, J. Appl. Physiol. Respirat. Environ. Exercise Physiol. 42, 120 (1977); we used an Applied Electrochemistry oxygen analyser.

7. A Bailey Instruments Laboratory Thermometer, Model Bat-4 with automatic temperature compensation was used.

8. W. A. Calder and K. Schmidt-Nielsen, Am. J. Physiol. 215, 477 (1968).

9. G. C. Whittow, Comparative Physiology of Thermoregulation (Academic Press, New York and London, 1973).

10. K. Schmidt-Nielsen, F. R. Hainsworth, D. E. Murrish, Respir. Physiol. 9, 263 (1970); K. Schmidt-Nielsen, How 11Animals Work (Cambridge University Press, Cambridge, 1972).

11. The nape was sprayed with an aerosol bacteriocide, and localised evaporative cooling was enhanced by blowing with air at 8-10 m sec^{-1}.

12. S. A.RRichards and A. H. Sykes, Comp. Biochem. Physiol. 21,

39 (1967).

12. We thank W. R. Siegfried and G. N. Louw for encouragement, criticism and logistical support. Guineafowl were kindly provided by the Cape Province Department of Nature and Environmental Conservation.

The use of Rainfall in Predicting Guineafowl Population

T.M. Crowe

FitzPatrick Institute, University of Cape Town,
Rondebosch 7700, South Africa

Identification of those factors which can predict the population of a species in its natural habitat is a first step towards understanding how the population is limited, and is a valuable tool in its effective management. Such information is of greater practical value if the species is economically important. In southern Africa, the helmeted guineafowl <u>Numida</u> <u>meleagris</u> is a popular upland gamebird[1] and, in some farming areas, it has been classed (probably unjustly[2]) as an agricultural pest. This paper reports a method which uses rainfall to forecast the population of guineafowl at Rooipoort (28°45'S, 24°05'E), an estate near Kimberley, in the northern Cape province, South Africa.

Methods

<u>Data source</u>

Based on records accumulated at Rooipoort during 1917-1976, for each year for which there were adequate data we computed: a guineafowl shooting index; total rainfall (mm) and frequency (number of days) of rainfall during the 12 months prior to each hunting season (June-July); total rainfall and frequency of rainfall during the guineafowl breeding season (November–February) prior to each hunting season; and, total rainfall and frequency of rainfall for the months of November, December, January and February prior to each hunting season. The shooting index was the total number of guineafowl shot during each hunting season divided by the number of days on which guineafowl were hunted during that season. This shooting index was taken to be a relative measure of guineafowl population. The reasoning behind this assumption was that the number of birds shot per hunting day will be relatively higher when there are more birds to shoot. Variation in the shooting index due to differences in shooting ability and size of hunting party is, in part, offset by the fact that the same hunters tend to visit Rooipoort year after year.

Statistical methods

Correlation and forward-selection stepwise multiple linear regression analyses[3] were used to determine the predictive value of the various rainfall measures (independent variables) for the shooting index (dependent variable). The coefficient of determination ($\underline{R}^2$) was used as the measure of predictive value. This statistic is an estimate of the proportion of the total variance in a dependent variable due to variation in an independent variable[4]. The statistical limitations of correlation and regression analyses of ecological data have been discussed by Sepkoski and Rex[5]. Log-log and semi-log (rainfall measures log-transformed) as well as a linear model were used to detect possible non-linear relationships between rainfall and the shooting index.

Results

In all regression models, the frequency of rainfall during the 12 months prior to the hunting season (*YFRF*) is the best predictor of the shooting index (Table 1). The shooting index - *YFRF* relation is a positive one (Table 2, Fig. 1). In a log-log model, January total rainfall (*JRF*) and December frequency of rainfall (*DFRF*) are significant but poorer predictors of the shooting index (Table 1). The relation between the shooting index and these two variables is also a positive one (Table 2). For all measures of rainfall, the correlation between the shooting index and frequency of rainfall is higher than that for total rainfall (Table 2). A linear model gives the highest total R^2. In this model, *YFRF* accounts for nearly 72% of the variance in the shooting index, and the formula for estimating the shooting index is: $S.I. = -11.13 + 0.68\ YFRF$, in which *S.I.* is the shooting index.

Discussion

Our results suggest that frequency of rainfall,

Table 1 Summary of the results of multiple regression analyses of the guineafowl shooting index and rainfall measures for Rooipoort

Model	Significant predictor variables	R^2	Significance level
Linear	YFRF[1]	0.7152	0.001
Semi-log	YFRF	0.6440	0.001
Log-log	YFRF	0.5624	0.001
	JRF[2]	0.0612	0.014
	DFRF[3]	0.0435	0.026
		0.6671	

[1] frequency (days) of rainfall during the 12 months prior to the hunting season.

[2] rainfall (mm) during January

[3] frequency of rainfall during December

Table 2 Correlation coefficients between the guineafowl shooting index and rainfall measures for Rooipoort: the upper half-matrix is for raw data, the lower half-matrix for log-transformed data

		S.I.	YRF	N-FRF	NRF	DRF	JRF	FRF	YFRF	N-FFRF	NFRF	DFRF	JFRF	FFRF
	Shooting Index (S.I.)	-	0.475*	0.326	0.292	0.372	0.160	0.266	0.846	0.719	0.585	0.641	0.411	0.357
Total rainfall (mm)	year (YRF)	0.533	-	0.818	0.285	0.531	0.499	0.635	0.643	0.648	0.202	0.476	0.564	0.417
	Nov.-Feb. (N-FRF)	0.261	0.711	-	0.352	0.436	0.626	0.778	0.406	0.685	0.221	0.404	0.611	0.501
	Nov. (NRF)	0.006	0.249	0.329	-	-0.052	-0.131	0.095	0.303	0.422	0.772	0.152	0.160	0.183
	Dec. (DRF)	0.413	0.534	0.400	0.077	-	0.215	0.181	0.474	0.483	0.046	0.788	0.310	0.226
	Jan. (JRF)	0.297	0.495	0.570	-0.141	0.254	-	0.445	0.178	0.493	-0.092	0.218	0.729	0.276
	Feb. (FRF)	0.230	0.627	0.802	0.039	0.150	0.413	-	0.334	0.515	0.108	0.099	0.368	0.633
Frequency of rainfall (days)	year (YFRF)	0.750	0.677	0.348	0.214	0.556	0.245	0.268	-	0.794	0.538	0.688	0.494	0.477
	Nov.-Feb. (N-FFRF)	0.631	0.656	0.556	0.340	0.603	0.489	0.425	0.811	-	0.591	0.704	0.778	0.642
	Nov. (NFRF)	0.327	0.197	0.236	0.757	0.116	-0.081	0.046	0.489	0.551	-	0.349	0.189	0.181
	Dec. (DFRF)	0.638	0.454	0.392	0.152	0.775	0.265	0.068	0.702	0.723	0.354	-	0.449	0.178
	Jan. (JFRF)	0.423	0.562	0.600	0.125	0.391	0.827	0.392	0.498	0.733	0.190	0.478	-	0.407
	Feb. (FFRF)	0.361	0.460	0.556	0.065	0.260	0.241	0.685	0.489	0.612	0.180	0.201	0.380	-

---

* The critical values of r for significance levels are: r = 0.325, P = 0.05; r = 0.418, P = 0.01

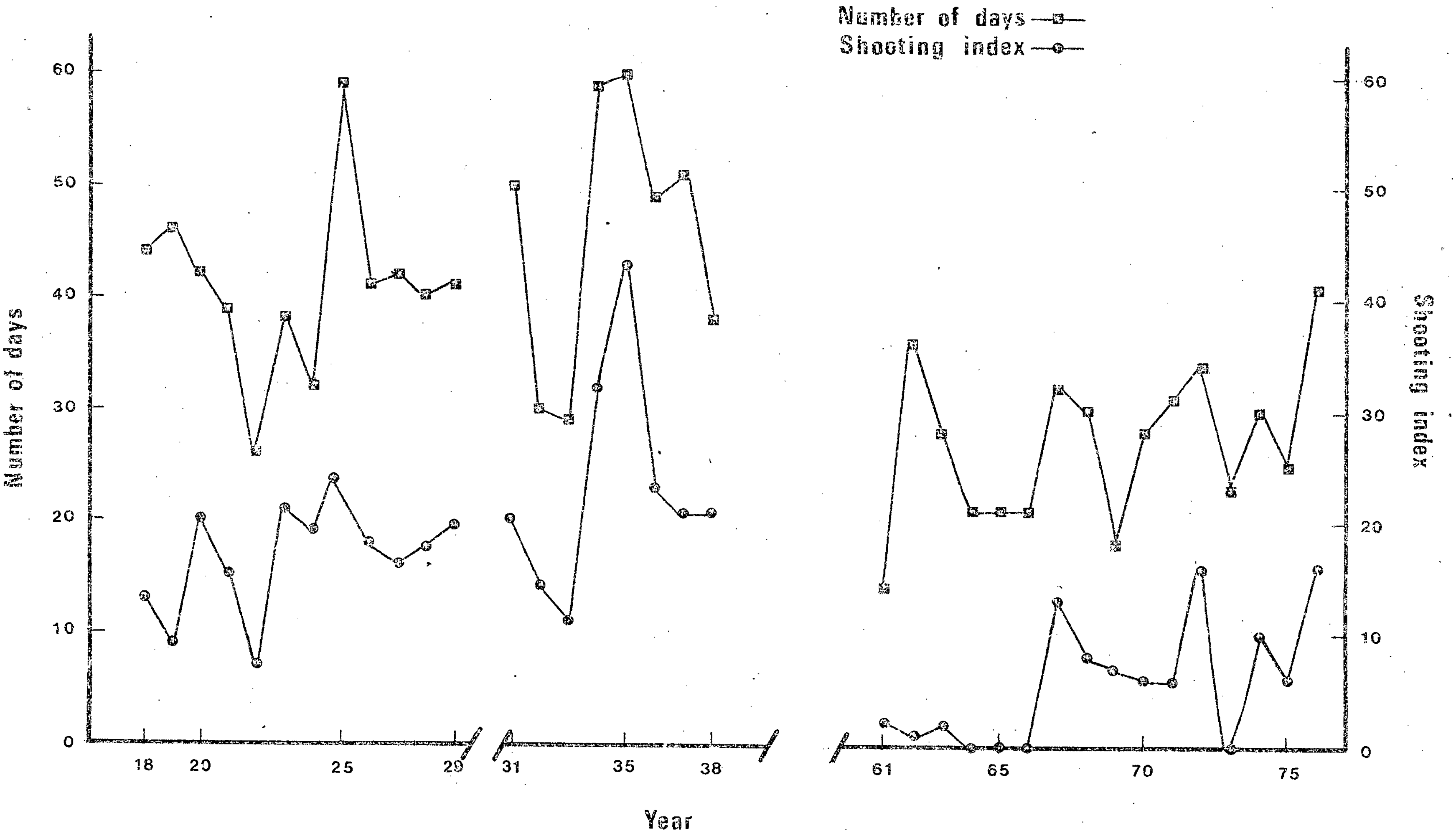

Fig. 1. A plot of the guineafowl shooting index at Rooipoort against annual frequency of rainfall (number of days) for 36 hunting seasons.

particularly frequency of rainfall during the 12 months prior to the hunting season is the best predictor of the June-July guineafowl population at Rooipoort. Odum[6] states that a population can be limited by a physical factor, such as rainfall, which fluctuates markedly and unpredictably. Onesta and Verhoeff[7] have demonstrated that rainfall in the northern Cape is highly variable and unpredictable. Liversidge[8] has hypothesized that bird populations in southern Africa are limited, in a density-independent manner, primarily by unpredictable rainfall. Skead[9] and Mentis _et al._[10] have noted evidence of low guineafowl population and poor breeding success during years of relatively low rainfall. Mentis _et al._[10] have speculated that poor breeding success may have been due to the negative effects of low rainfall on the availability of high-protein insect food, an important component in the diet of breeding guineafowl.

Conclusions

Our results, and the observations mentioned above, suggest that the frequency of rainfall affects guineafowl population directly, or indirectly through its effect on a critical food source. However, until we have reliable data to test these hypotheses, we can only say that rainfall is probably a good predictor of guineafowl population in the northern Cape. In the meantime the hypothesis that it can rain guineafowl as well as cats and dogs is as tenable as any other.

---

[1] Grafton, R.N. (1970). Winter food of the helmeted guineafowl in Natal. *Ostrich*, Suppl. 8, 475-485.

[2] Angus, A. and Wilson, K.J. (1964). Observations on the diet of some game birds and Columbidae in Northern Rhodesia. L. The helmeted guineafowl (*Numida meleagris*). *Puku*, (2), 1-9.

[3] Dyer, T.G.J. and Dyer Gillooly, J.F. (1977). Corn yields: an early warning system. *S. Afr. J. Sci.*, 73, 252-253.

[4] Sokal, R.R. and Rohlf, F.J. (1969). *Biometry*. W.H. Freeman & Co., San Francisco.

[5] Sepkoski, J.J. and Rex, M.A. (1974). Distribution of fresh water mussels: coastal rivers as biogeographic islands. *Syst. Zool.*, 23, 165-188.

[6] Odum, E.P. (1971). *Fundamentals of ecology*. W.B. Saunders Company, London.

[7] Onesta, P.A. and Verhoeff, P. (1976). Annual rainfall frequency distributions for 80 rainfall districts in South Africa. *S. Afr. J. Sci.*, 72, 120-122.

[8] Liversidge, R. (1966). Fluctuations in a breeding population in the eastern Cape. *Ostrich*, 37, Suppl. 6, 419-424.

[9] Skead, C.J. (1962). A study of the crowned guineafowl *Numida meleagris coronata* Gurney. *Ostrich*, 33, 51-65.

[10] Mentis, M.T., Poggenpoel, B. and Maguire, R.R.K. (1975). Food of the helmeted guineafowl in highland Natal. *J. sth. Afr. Wildl. Mgmt. Ass.*, 7, 23-26.

LIMITATION OF POPULATION IN THE HELMETED GUINEAFOWL

T.M. CROWE

FitzPatrick Institute, University of Cape Town

Rondebosch 7700

ABSTRACT. - The hypothesis that a population of helmeted guineafowl is limited in a density-independent manner by rainfall (the "rainfall hypothesis") is tested by analyzing the hunting bags for 36 seasons, and data from a 28-month intensive study of the population. A shooting index (season total hunting bag/number of hunting days) is used as a measure of the population. The "rainfall hypothesis" is rejected, since changes in the shooting index are statistically dependent on, and inversely related to the size of the population, and since frequency of rainfall, the best predictor of the shooting index, is also a significant positive predictor of potential available food. An alternative, more holistic, physio-etho-ecological model, based on density-dependent population limitation by food is offered.

INTRODUCTION

In an ecosystem subjected to unpredictable and large environmental fluctuations, the size of populations tends to be limited by physical factors, such as rainfall, temperature, wind, etc. (Odum 1971). By "limited", I mean prevented in some way from realizing the population growth dictated by the species' intrinsic rate of natural increase (r). A population is said to be limited in a density-dependent manner if its growth rate is negatively related to the size of the population, and limited in a density-independent manner if its growth rate shows no relation to population size (Ricklefs 1973). A population is said to be regulated if its size varies, within narrow limits, around some equilibrial value (Ricklefs 1973). Liversidge (1966, 1970) has hypothesized that bird populations in Southern Africa are limited primarily by density-independent factors, of which unpredictable rainfall is the most important. His hypothesis is based on data from studies of 30 species of graminivorous, frugivorous and insectivorous birds, which breed regularly near Cape Receife (34° S, 25° 40'E) in the eastern Cape Province, South Africa.

The helmeted guineafowl (Numida meleagris) is endemic to Africa, and is a relatively common and widespread member of savanna biome (Crowe 1978). Clutch size in N. meleagris ranges from 6 to 19 eggs (Clancey 1967; McLachlan and Liversidge 1972); hence, the species has a potentially high r value. Fergin (1964), from histological and behavioural studies of N. meleagris from equatorial Uganda, has suggested that rainfall may directly or indirectly control breeding activities in this species. Skead (1962) and Mentis et al. (1975) have noted evidence of low guineafowl population and poor breeding success in South Africa during years with relatively low rainfall. In some drought years, guineafowl virtually disappeared from Skead's study area. Mentis _et al_. (1975) have suggested that poor breeding success may have been due to the negative effects of low rainfall on the availability of high-protein insect food. Crowe and Siegfried (1978) have shown that frequency of rainfall (number of days) is a highly statistically significant predictor of the guineafowl shooting index (number of guineafowl shot per season/number of days of hunting), an assumed index of the guineafowl population, at Rooipoort (28° 45'S, 24° 05'E), an estate near Kimberley, South Africa. Rainfall in the Kimberley district is much more unpredictable than in the district in which Liversidge worked (Onesta and Verhoef 1976). Therefore, the effect of rainfall on the guineafowl population at Rooipoort should be even more marked than at Cape Receife (Liversidge 1966, pers. comm.).

My aims in this paper are to:

1. test the hypothesis that the guineafowl population at Rooipoort is limited in a density-independent manner by rainfall (hereinafter termed the "rainfall hypothesis");
2. discuss the results of the test within a physio-etho-ecological framework, based on my 28-month study of the Rooipoort guineafowl;
3. formulate a more holistic model of the guineafowl population limitation on the estate.

STUDY AREA AND METHODS

Rooipoort is approximately 175 km^2 in extent, and has more than 25 km of frontage along the Vaal River (Fig. 1). According to Bigalke and Leistner (unpublished data), the

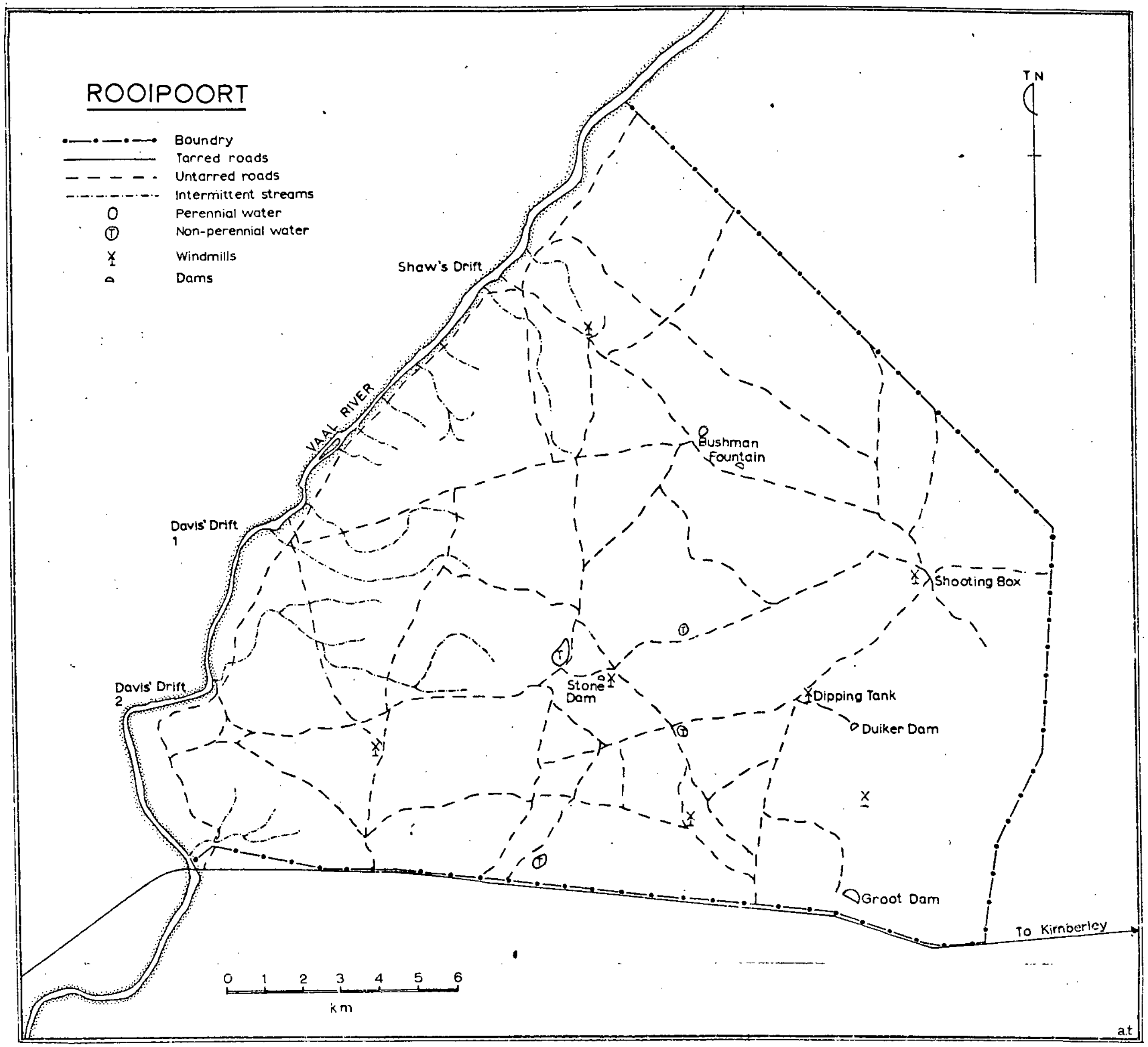

FIG. 1. Rooipoort: its major geographical features.

estate supports 11 vegetation types (Fig. 2). The only major artificial modification of the natural habitat has been the construction of seven watering points (Fig. 1).

The owners of Rooipoort have maintained a policy of culling, at most, excess guineafowl above a subjectively determined lower limit thought to be necessary to maintain the population. This policy is implemented by a resident managerial staff, who estimate, through _ad hoc_ counts, the number of birds that may be culled annually. If counts of guineafowl indicate poor breeding success and low population, hunting is suspended. Not more than 25% of the estimated total guineafowl population has been culled in any of the last 20 hunting seasons.

Author's field data

My field observations of guineafowl at Rooipoort (October 1973 - January 1976) spanned three consecutive breeding seasons. Two of these breeding seasons were relatively successful (1973-74 and 1975-76), and one was very poor (1974-75). As part of a general etho-ecological study of _N. meleagris_ at the estate, I collected data on: distribution of guineafowl, potential drinking sites, group size, emigration-immigration, hatching dates, relative production of juveniles, relative food availability and intake, fresh weights and intestinal helminth burdens of shot birds, individual and group agonistic behaviour, and male-female pairing. Data for agonistic behaviour and male-female pairing were for 103 individually identifiable birds which had been trapped

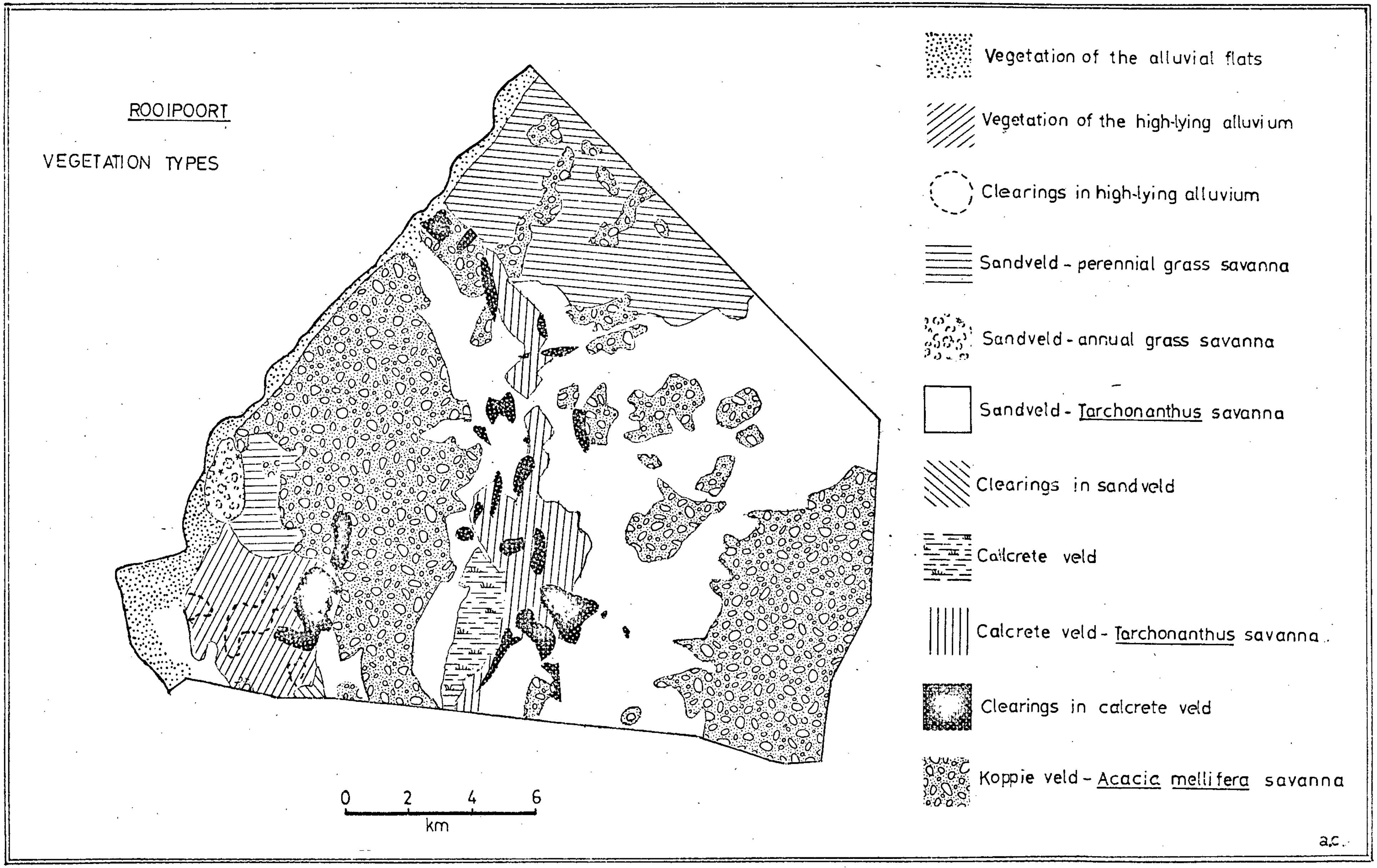

FIG. 2. Rooipoort: its major vegetation types.

and marked with neck-tags and/or colour-coded leg rings at Stone Dam, an isolated watering point (Fig. 1). Distribution of potential drinking sites was noted because guineafowl at Rooipoort are rarely seen more than two km from a potential drinking water (Crowe unpublished data). Male-female pairing was monitored since it seems to be a pre-requisite for successful reproduction (Crowe in prep.). A male and female were said to be paired if the male exhibited courtship feeding behaviour (Stokes and Williams 1971; Crowe, in prep.).

Distribution of guineafowl and temporary streams and pools of water were determined from aerial photographs, and from sightings along regularly travelled Rooipoort roads. Data for October 1973 - September 1974 were analyzed separately from that for October 1974 - September 1975 to determine possible year-to-year variation in dispersion of birds and water. Owing to a bush fire which destroyed much of the vegetation on Rooipoort in late January 1975, I was able to search for signs of the usually well-concealed nests (Skead 1962). Data for male-female pairing and emigration-immigration were collected only for birds ringed at Stone Dam. Estimates of relative emigration rates of adult and juvenile guineafowl were obtained by comparing sightings of individually identifiable birds at Stone Dam during June-July 1974 and June-July 1975. Emigration distance was estimated from recoveries of birds ringed at Stone Dam. Hatching dates were estimated through age determination (Siegfried 1966) of juveniles shot during the hunting season. Relative production of juveniles was estimated by the number and percentage of juvenile birds in the total bag for each hunting season. Food availability was estimated from the results of 800 sweeps taken monthly (200 sweeps each week) with a 30 cm sweep-net. Sweeps were taken along two fixed transects of grassland habitat (100 sweeps along each transect) in the Stone Dam area known to be used by guineafowl. Number and biomass (dry weight) of arthropods, and biomass of grass seed in the sweep catch were used as relative indices of animal and vegetable food availability. Patterns of food intake were inferred from crop contents of shot guineafowl. Statistically adequate samples of crops, fresh weights and intestinal helminths were obtainable only from birds shot during the hunting seasons. Methods used in collection and analysis of helminth data are discussed in Crowe (1977).

Mean monthly group size, monthly total number and biomass of arthropods, and total monthly biomass of grass seed in the sweep samples were compared with the frequency of rainfall during the month to determine if they too were statistically related to this significant predictor of the shooting index.

Conditions for density-independent limitation by rainfall

Conditions I set as necessary for rainfall to be a density-independent limiting factor were:

(1) Some measure of rainfall must be statistically significantly ($\underline{P} < 0,05$) related to the shooting index.

(2) The shooting index-rainfall relation must be a positive one.

(3) The annual percentage change in population, as estimated by the formula

$$\frac{S.I._{Y} - S.I._{Y-1}}{S.I._{Y-1}} \times 100$$

in which $S.I._{Y}$ is the shooting index of the year Y, and $S.I._{Y-1}$ is the shooting index of the preceding year, must not be related significantly to the shooting index of the preceding year. In other words, the annual percentage change in population must be statistically independent of the size of the population in the preceding year. Percentage change, rather than absolute change was specified in an attempt to minimize the effects of a fluctuating population equilibrium (Sinclair 1974).

(4) Variables significantly related to the shooting index must not also be significantly related to the availability of food, a possible density-dependent limiting factor (Lack 1966).

RESULTS

The "rainfall" hypothesis

Raw data used in the investigation of conditions 1-3 for density-independent limitation by rainfall are given in Table 1. Crowe and Siegfried have shown that the shooting index is strongly positively related to frequency of rainfall during the 12 months prior to the hunting season. Thus, conditions 1 and 2 specified for density-independent limitation are satisfied.

TABLE 1. Guineafowl hunting and rainfall data for Rooipoort.

Year	No. of birds shot	No. of days	Shooting index	% change	Frequency of rainfall
1918	188	14	13,4	-	44
1919	193	22	8,8	-34,3	46
1920	202	10	20,2	129,5	42
1921	197	13	15,2	-24,8	39
1922	82	11	7,5	-50,7	26
1923	233	11	21,2	182,7	39
1924	169	9	18,8	-11,3	32
1925	516	22	23,5	25,0	59
1926	339	18	18,8	-20,0	41
1927	230	14	16,4	-12,8	42
1928	421	24	17,5	6,7	40
1929	387	20	19,4	10,9	41
1931	120	6	20,0	-	50
1932	42	3	14,0	-30,0	30
1933	79	7	11,3	-19,3	29
1934	617	19	32,5	187,6	59
1935	516	12	43,0	32,3	60
1936	207	9	23,0	-46,5	51
1937	412	20	20,6	-10,4	53
1938	227	11	20,6	0,0	38
1961	30	14	2,1	-	12
1962	11	9	1,2	-42,9	36
1963	23	13	1,8	50,0	28
1964	0	0	0,0	-70,0*	21
1965	0	0	0,0	0,0	21
1966	0	0	0,0	0,0	21
1967	13	1	13,0	200,0**	32
1968	121	15	8,1	-37,7	30
1969	141	20	7,1	-12,3	18
1970	96	15	6,4	-9,9	28
1971	95	15	6,3	-1,6	31
1972	184	12	15,3	142,0	34
1973	0	0	0,0	-70,0*	23
1974	247	25	9,9	200,0**	30
1975	93	15	6,2	-37,4	25
1976	356	22	16,2	161,3	41

* arbitrary value assigned to show large loss

** arbitrary value assigned to show large gain

Condition 3 is not satisfied. There is a significant inverse relation between percentage change in the shooting index and the shooting index of the preceding year (Fig. 3; $\underline{b} = -3,12 \pm 1,40$, $\underline{P} < 0,05$).

Data used in the investigation of condition 4 are listed in Table 2. Condition 4 is not satisfied. Both arthropod biomass (Fig. 4; $0,62 \pm 0,08$, $\underline{P} < 0,001$), and number of arthropods (Fig. 5; $\underline{b} = 44,70 \pm 6,11$, $\underline{P} < 0,001$) are significantly related to frequency of rainfall during each month. Biomass of grass seed caught in the sweep net (Fig. 6; $b = 1,17 \pm 0,32$, $\underline{P} < 0,01$) and mean group size (Fig. 7; $\underline{b} = -2,03 \pm 0,55$, $\underline{P} < 0,001$) are also significantly related to the frequency of rainfall. A decreasing mean group size is an indication of group break-up and male-female pairing.

Distribution of birds, water and nests

As judged from sightings of guineafowl along regularly travelled roads (Fig. 8), birds were more widely dispersed during October 1973 - September 1974, than during October 1974 - September 1975. Temporary streams and pools of water were widespread during 1974, but were virtually non-existent during 1975. No nests or eggs were found after the bush fire of January 1975.

Emigration and Immigration

Of 33 individually identifiable adult guineafowl which were observed at Stone Dam during June - July 1974, 14 (42%)

TABLE 2. Rainfall, ecological and behavioural data collected at Rooipoort.

Month	Year	Rainfall (days)	Arthropods (wt. in g)	Arthropods (no.)	Grass seed (wt. in g)	Mean group size
Oct.	1973	1	-	-	-	10,06
Nov.	1973	8	-	-	-	5,93
Dec.	1973	9	-	-	-	1,78
Jan.	1974	13	6,04	385	0,09	1,67
Feb.	1974	9	6,06	675	10,02	1,68
Mar.	1974	17	14,77	1093	20,08	4,87
Apr.	1974	13	4,95	312	41,34	11,00
May	1974	4	6,02	110	12,43	16,53
Jun.	1974	0	0,02	3	3,60	27,26
Jul.	1974	0	0,00	0	0,30	51,12
Aug.	1974	2	0,00	0	0,32	45,50
Sep.	1974	0	0,04	21	0,19	22,35
Oct.	1974	2	3,53	45	0,00	15,57
Nov.	1974	2	0,68	51	0,00	7,06
Dec.	1974	2	1,08	111	0,23	8,00
Jan.	1975	4	3,63	90	0,00	7,95
Feb.	1975	4	0,58	62	0,00	11,11
Mar.	1975	7	0,28	12	1,11	18,83
Apr.	1975	2	0,16	23	4,46	55,33
May	1975	3	0,45	45	1,01	35,37
Jun.	1975	1	0,04	1	0,42	30,21
Jul.	1975	0	0,00	0	0,00	28,33
Aug.	1975	0	0,04	1	0,00	30,00
Sep.	1975	0	0,02	1	0,00	46,92
Oct.	1975	0	0,14	8	0,00	12,56
Nov.	1975	3	0,19	11	0,00	6,06
Dec.	1975	8	2,02	96	0,00	2,40
Jan.	1976	9	6,32	314	0,00	1,67

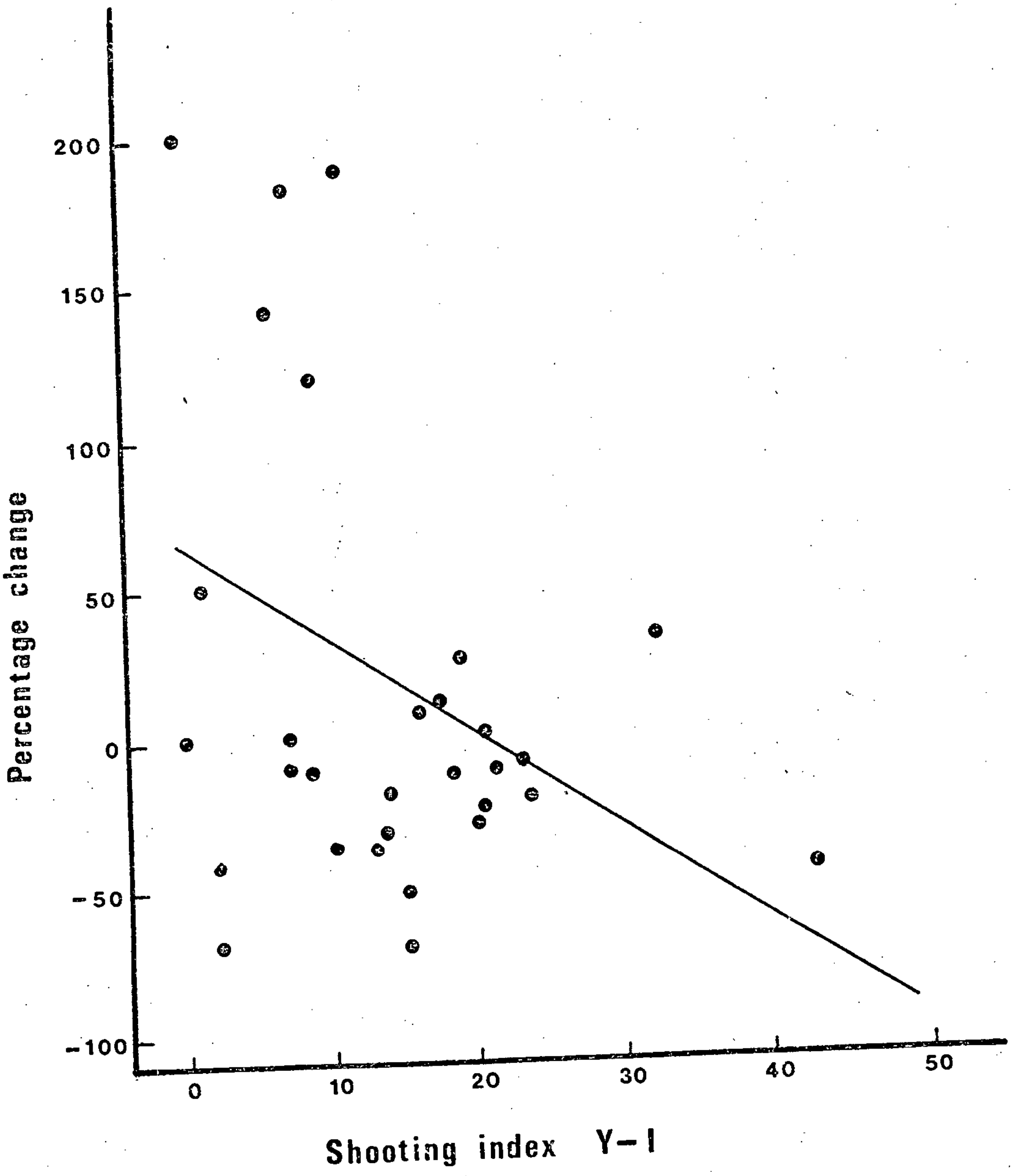

FIG. 3. A plot of percentage change in the shooting index at Rooipoort against the shooting index of the previous year.

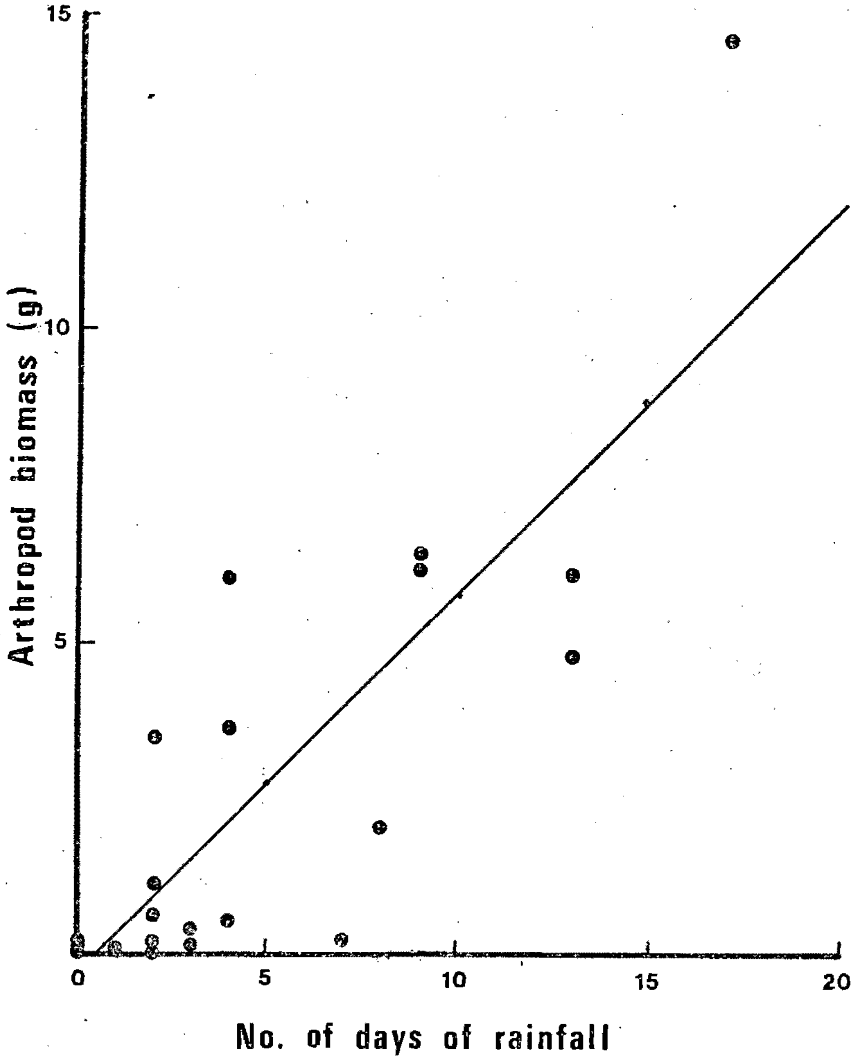

FIG. 4. A plot of arthropod biomass against monthly frequency of rainfall at Rooipoort.

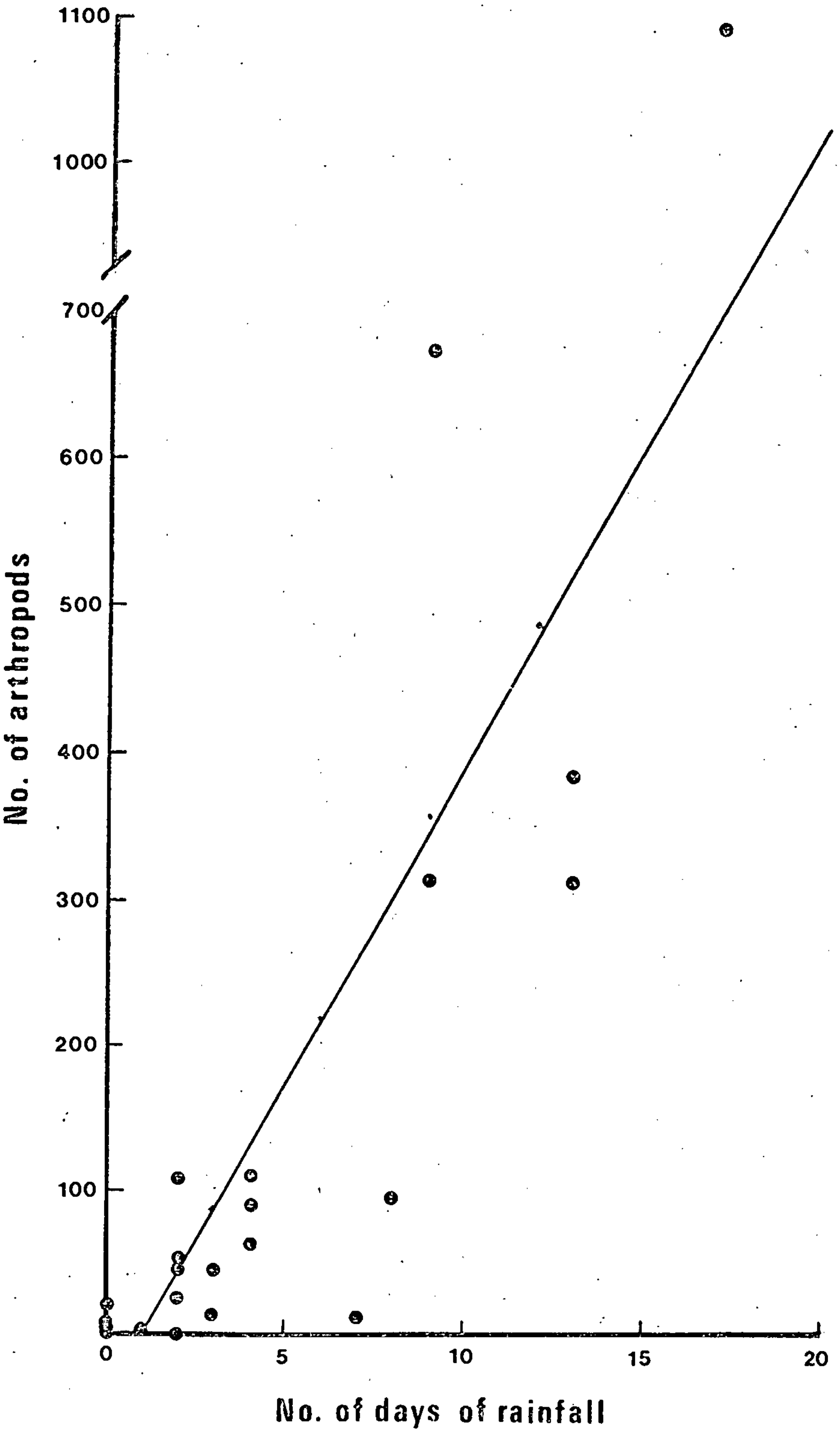

FIG. 5. A plot of the number of arthropods caught in sweep net samples against monthly frequency of rainfall at Rooipoort.

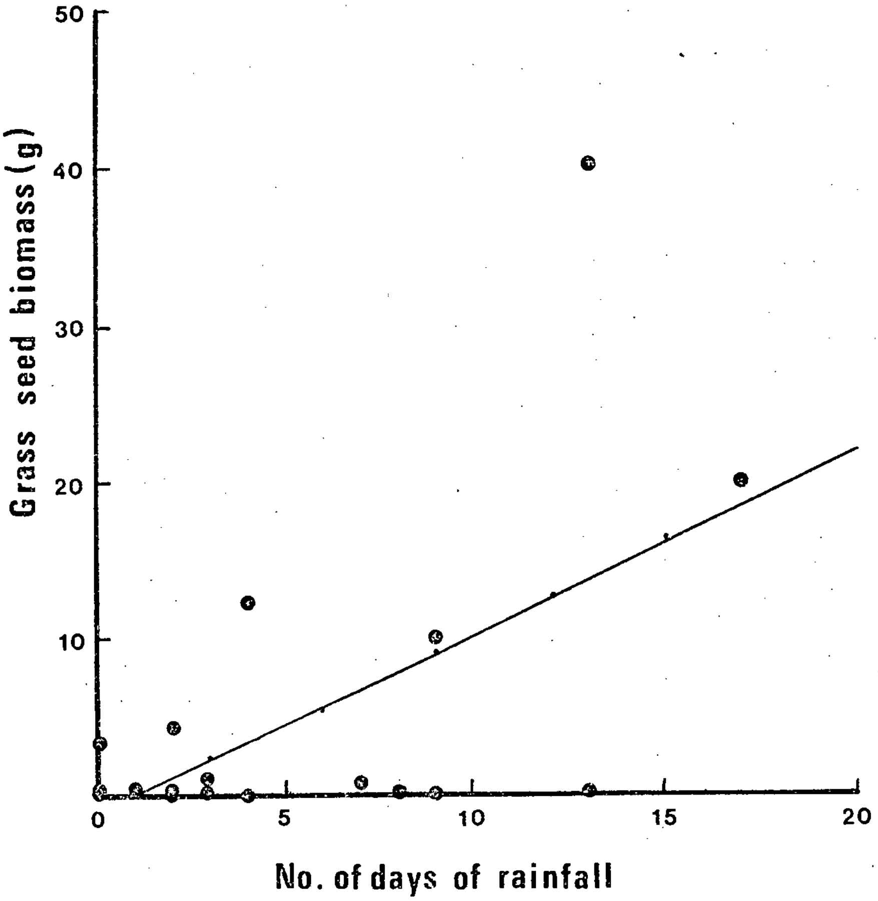

FIG. 6. A plot of biomass of grass seed caught in sweep net samples against monthly frequency of rainfall at Rooipoort.

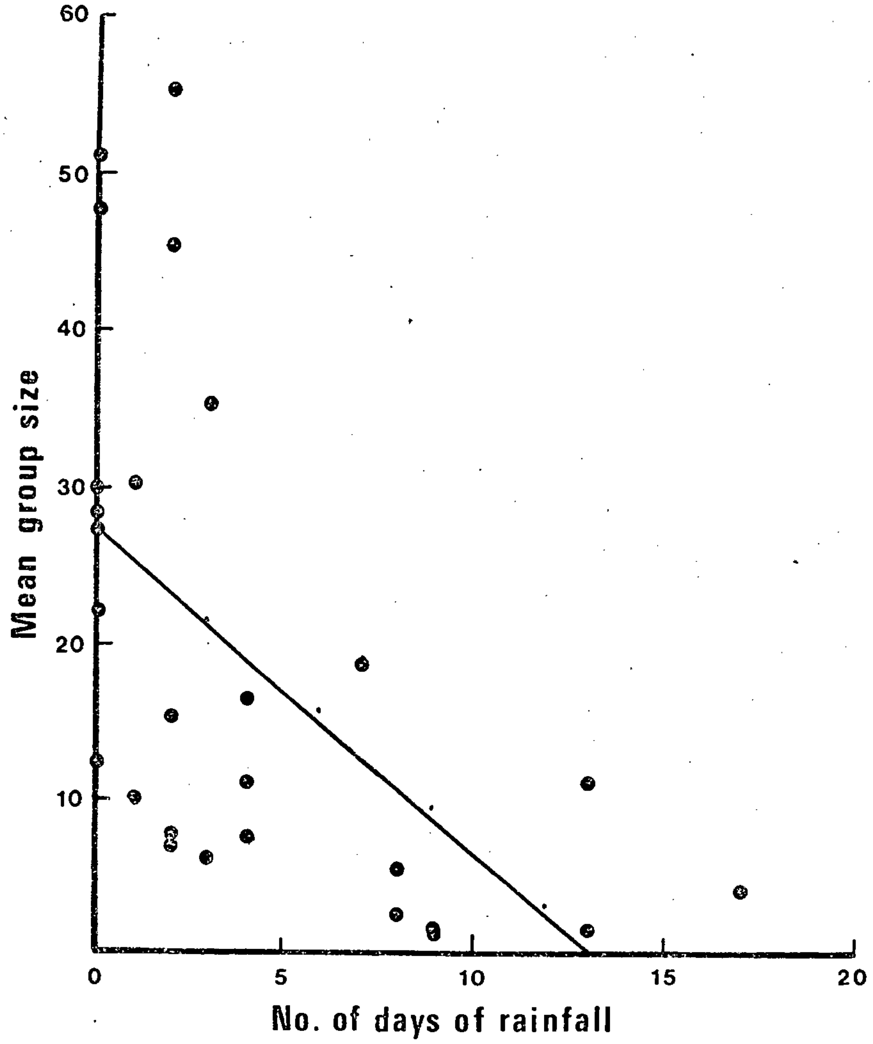

FIG. 7. A plot of mean monthly group size against monthly frequency of rainfall at Rooipoort.

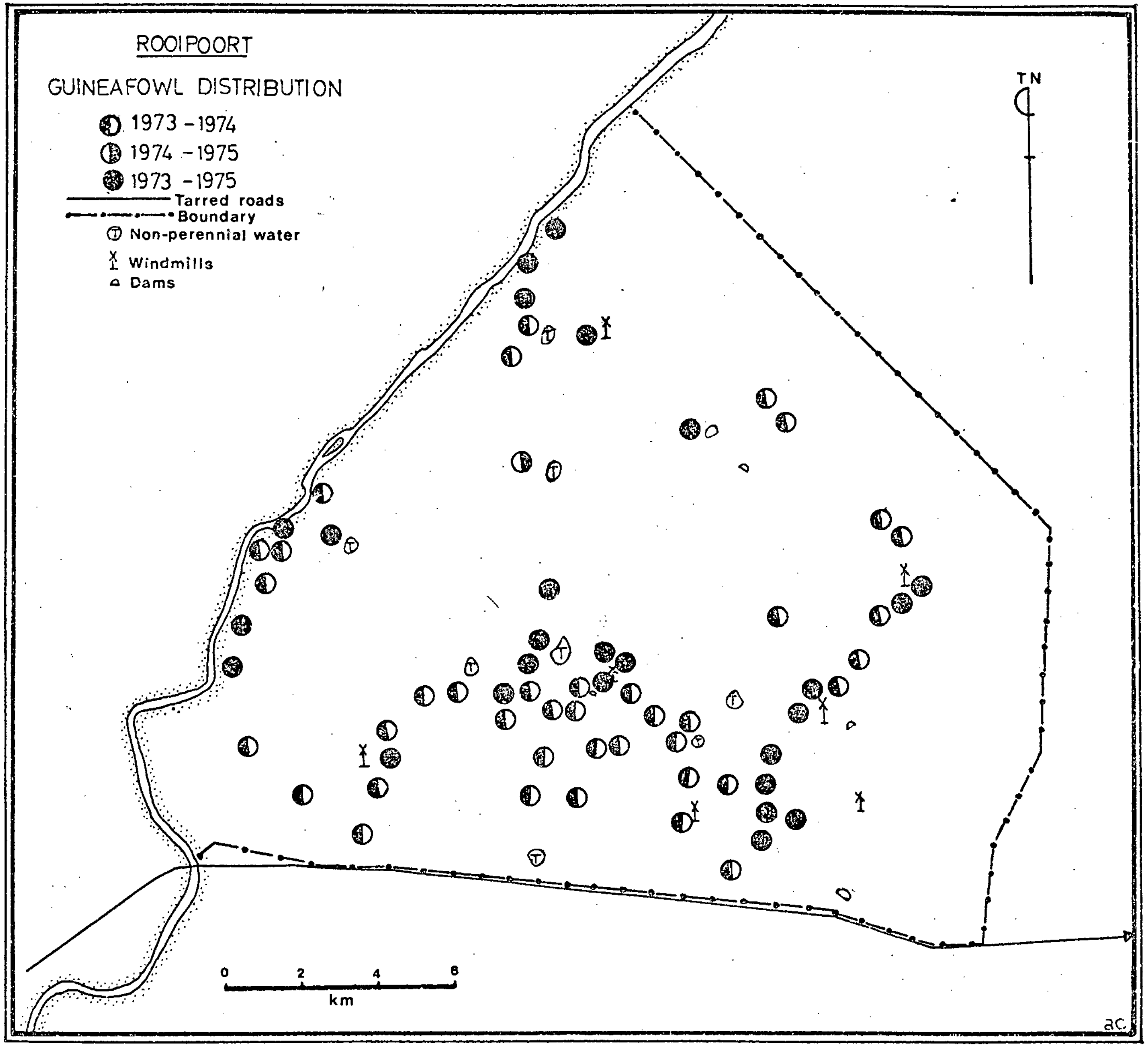

FIG. 8. A comparison of dispersion of *N. meleagris* at Rooipoort during October 1974 - September 1975.

were observed there again during June - July 1975. Of 56 individually identifiable juveniles which were observed at Stone Dam during June - July 1974, only 11 (20%) were seen there again in 1975. Thus, relatively more juveniles than adults ($\chi^2 = 7{,}04$, $\underline{P} < 0{,}01$) apparently died or left Stone Dam during August 1974 - May 1975.

Emigration of guineafowl ringed at Stone Dam appeared to be restricted to short distances. The mean distance from Stone Dam for 21 recoveries was 2,29 km. All birds recovered were found within 2 km of permanent water. Six of seven birds recovered more than 3,00 km from Stone Dam were males. Four of these six males were ringed as juveniles. Both long-distance recoveries, 4,5 and 10 km respectively, were male birds ringed as juveniles.

Immigration into the Stone Dam area during the breeding seasons (Nov. - Feb.) was virtually non-existent, and the population during this phase of the annual cycle remained fairly constant: 28 in 1973-74, 20 in 1974-75, 23 in 1975-76. Those Stone Dam adult guineafowl which died or emigrated in 1973-74 seemed to be replaced in the 1974-75 breeding season by recruitment of yearling birds which had been ringed as juveniles at Stone Dam. Adult and yearling mortality in 1974-75 seemed to be counterbalanced by immigration of one pair of mated adults drawn from a locality other than Stone Dam, and second year birds that had been ringed as juveniles at Stone Dam.

Hatching dates and production of juveniles

The annual modes of hatching for juvenile guineafowl shot during the hunting seasons occurred in January for both 1974 and 1975, and in March for 1976. The modes of hatching in 1974 and 1975 occurred when the relative availability of arthropod food was high, and the availability of food was higher in 1974 (Table 2). Relative production of juveniles, as judged by the number and percentage juveniles in the following hunting season's total bag, was high in the 1973-74 (N = 179, 72%) and 1975-76 (67%) breeding seasons, and very low in the 1974-75 (N = 2, 2%) breeding season. No juveniles were observed at Stone Dam during 1975. A total bag for juveniles was not available for the 1976 hunting season. The percentage value given is based on a sample of 98 birds shot on one weekend.

Food intake

Both arthropod and vegetable food intake, as judged from analysis of crop contents of adult guineafowl shot in the same habitat at approximately the same time of day, were higher in 1974 and 1976 than in 1975 (Table 3).

Fresh weight

In all three hunting seasons, adult male guineafowl were significantly ($\underline{P} < 0{,}05$; $\underline{t}$ test) heavier than adult females (Table 4). Adults shot during the 1974 and 1976 hunting seasons were significantly heavier than adults shot during the 1975 hunting season (Table 4).

TABLE 3. Crop contents of adult N. meleagris shot at Rooipoort during the three hunting seasons.

Hunting season	*n*	Mean dry weight (g) of vegetable material	*t* and *P* values*	Mean % weight of arthropods	*t* and *P* values*
1974	19	11,23 (11,25)**	3,23 $P < 0,01$	3,68 (6,32)	2,51 $P < 0,02$
1975	25	3,44 (3,93)	–	0,48 (0,92)	–
1976	8	13,43 (19,86)	2,45 $P < 0,02$	1,88 (2,59)	2,33 $P < 0,05$

* comparison with 1974 mean value, *t* test

** standard deviation

TABLE 4. Mean fresh weights of adult N. meleagris shot and trapped at Rooipoort during three hunting seasons.

Hunting season	Males			Females		
	n	$\bar{x}$ (g)	S.D.	n	$\bar{x}$ (g)	S.D.
1974	86	1503,49	93,82	36	1427,78	99,32
1975	43	1419,30	84,20	22	1339,32	86,10
1976	45	1482,79	53,24	40	1425,20	82,05

Intestinal helminth burdens

The helminth burden of adult birds shot during the hunting seasons, showed little seasonal variation. The mean level of infestation (Crowe 1977) was 2,71 (N = 66) in 1974, 2,87 (N = 82) in 1975, and 2,93 (N = 18) in 1976.

Agonistic behaviour

Agonistic behaviour, i.e. chases, pecks and fighting, was, with few exceptions (all during group encounters), restricted to males. My impression, consistent with that of Skead (1962), is that chases were more frequent and of longer duration immediately prior to and during the breeding season. In the Stone Dam area, chases were more frequent during group interactions than during normal movements of a single group ($\chi^2 = 4658$, $\underline{P} < 0{,}001$). In all group interactions, the resident group, i.e. individually identifiable guineafowl that regularly visited the Stone Dam area, made the initial advances. In all cases in which one group withdrew, it was the non-Stone Dam group.

Dominance hierarchies and male-female pairing

The dominance hierarchy among male guineafowl which frequented the Stone Dam area, as judged by undirectional agonistic behaviour, varied from season to season (Table 5). Rather than a linear hierarchy with ranks, there seemed to be a system with levels. Within each level, there was no decisive superiority. There seem to be two "shapes" of hierarchical system in Table 7. During the two successful

TABLE 5. The dominance hierarchy among male N. meleagris frequenting Stone Dam during three stages of the study.

Level	Nov. 1973 - May 1974	June 1974 - May 1975	June 1975 - Jan 1976
I	10^{*} 4^{*} 5^{*}	4 5^{*}	73^{+*} 5^{*} 101^{*}
II	20^{*} 14^{*} 95 8^{*}	86^{+}	14^{*} 82^{+*} 4^{*} 31^{*}
III	9^{*} 15	25 14 29	77^{*}
IV	6^{+}	47^{+} 48^{+} 73^{+} 55 13 49^{+}	

* observed in courtship feeding, i.e. paired

\+ juvenile birds in 1974

breeding seasons, 1973-74 and 1975-76, the system took the shape of an inverted triangle, i.e. there were many dominant (Level I and II) individuals. During the unsuccessful breeding season of 1974-75, the system took the shape of a normal triangle, i.e. few dominant individuals. There was no obvious dominance hierarchy among females.

Male-female pairing also varied from season to season (Table 5). In the 1974-75 breeding season, only male number 5, a dominant bird, secured a female partner. No offspring were produced from their union. In the other two seasons, males from all but the lowest level in the dominance system secured mates.

DISCUSSION AND CONCLUSIONS

The results of this study are inconsistent with the hypothesis that population is limited in a density-independent manner by rainfall. Analysis of shooting indices and weather data suggests that the guineafowl population tends to increase, in a linear manner, when there is frequent rainfall during the 12 months prior to the hunting season (Crowe and Siegfried 1978); but, increases are not independent, statistically at least, of the size of the population in the preceding year. Increases tend to be greater when the population in the preceding year's population is low. This negative relation between population growth and size of population satisfies the definition of density-dependent limitation given in the Introduction. That the breeding season population of guineafowl in the Stone Dam area remained relatively constant during my field study, suggests, but by no means proves, that the size of sub-populations of guineafowl is regulated.

A hypothetical density-dependent model of population limitation of Rooipoort guineafowl based on the results of my field study is given in Fig. 9. Guineafowl are not uniformly distributed over Rooipoort. Sub-populations apparently cluster around areas with drinking water. If there is a relatively high frequency of rainfall during the year, existing sub-populations will breed successfully, utilizing the abundant high-protein arthropod food that becomes available. Furthermore, new areas of suitable habitat will arise with the addition of temporary drinking water. Many of these new areas are colonized by emigrants, probably mainly juveniles, from areas with more persistent drinking water. If, in the subsequent year(s), the frequency of rainfall becomes relatively low, ephemeral water will dry up, and sub-populations that used this resource must seek out other areas with drinking water, or else go extinct. Immigrants are resisted, usually successfully, by guineafowl resident at areas with more persistent water. However, social disturbances by potential immigrants, plus competition for mates between resident males, lead to an increase of energy expenditure in agonistic behaviour, and may hinder male-female pairing and reduce the feeding efficiency of resident birds. Moreover, the increased population, albeit temporary, may lead to heavier infestation by intestinal helminths (Crowe 1977), and will deplete further the already low availability of high-protein arthropod food. Since breeding

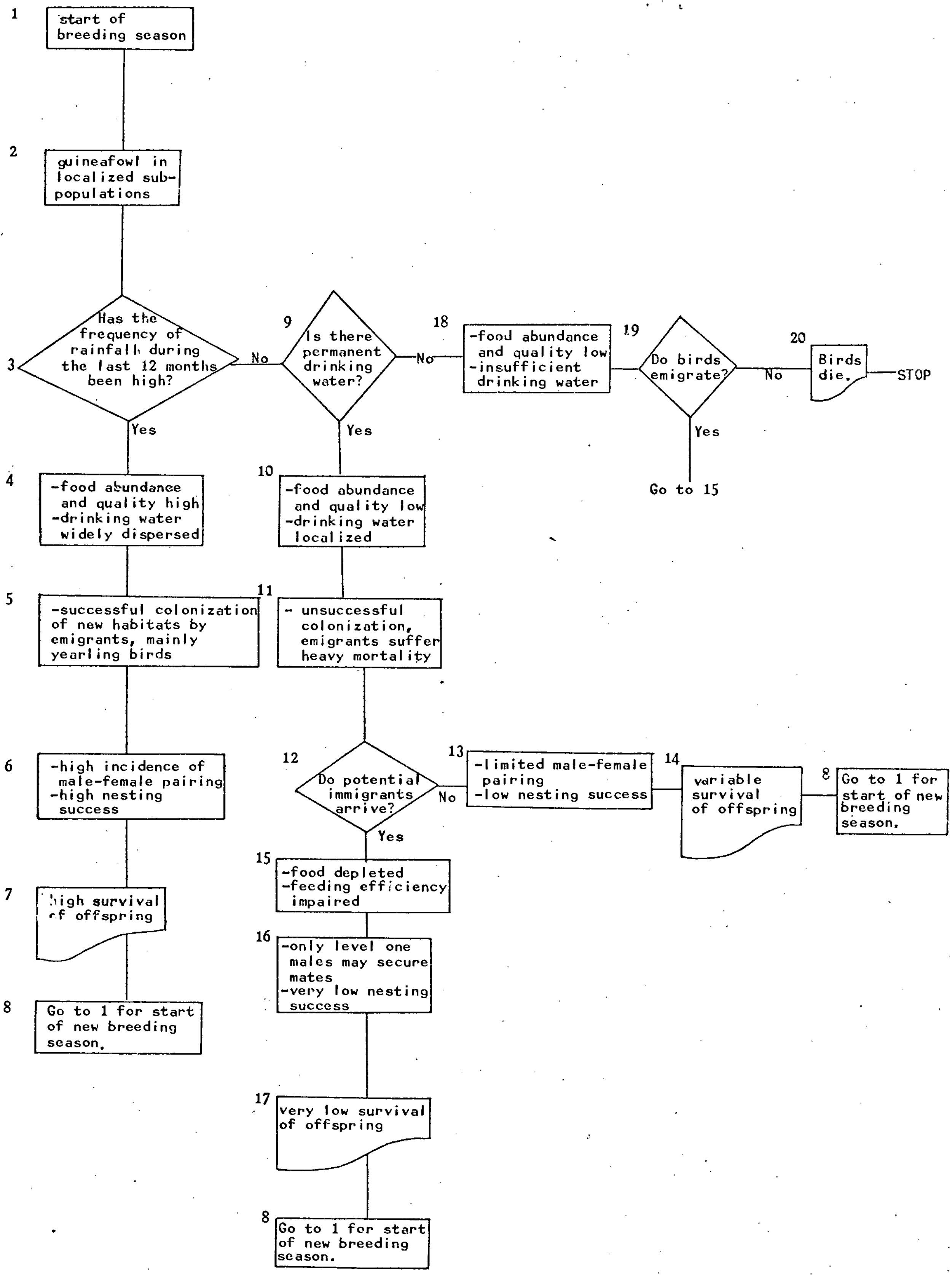

FIG. 9. A flow diagram model illustrating a possible density-dependent mechanism of population limitation for N. meleagris at Rooipoort.

in female birds in general, and rapid growth of young guineafowl in particular, seems to depend on the acquisition of high-protein food (Jones and Ward 1976; Davis 1943), any factor which decreases the effective consumption of arthropods can depress breeding success. Thus, in a socially unstable, poor food-quality situation, those few females which pair successfully may not have the necessary protein reserves to lay and incubate successfully, and those few chicks that hatch may suffer heavy mortality, ultimately due to nutritional deficiency. In summary, although rainfall is an important factor in creating new habitat for colonization by guineafowl, its primary effect on population is probably an indirect one mediated through the availability of high-protein food.

ACKNOWLEDGEMENTS

This research was financed by grants from the University of Cape Town and DeBeers Consolidated Mining Corporation Ltd. Special thanks go to DeBeers and Mr A.B. Fischer, manager of Rooipoort, for allowing me access to Rooipoort, and for unflinching logistical support during my field work. My wife Anna drew the figures. My advisors Professor W.R. Siegfried and Dr R. Liversidge provided a seemingly endless stream of ideas and criticism.

REFERENCES

CLANCEY, P.A. 1967. Gamebirds of Southern Africa. American Elsevier Publishing Company, Inc., New York.

CROWE, T.M. 1977. Variation in intestinal helminth infestation of the helmeted guineafowl. S. Afr. J. Wildl. Res. 7: 1-3.

CROWE, T.M. 1978. The evolution of guineafowl (Galliformes, Phasianidae, Numidinae). I. Taxonomy, phylogeny, speciation and biogeography. Ann. S. Afr. Mus. 75: 131-200.

CROWE, T.M. and W.R. SIEGFRIED. 1978. It's raining cats, dogs and guineafowl in the northern Cape. S. Afr. J. Sci. 74:

DAVIS, G. 1943. Studies of Reproduction and growth in the guineafowl Numida meleagris. M.Sc. thesis, Oklahoma Agricultural and Technical College.

FERGIN, T.J. 1964. Reproductive behavior of certain African birds. M.Sc. Thesis, Washington State University.

JONES, P.J. and P. WARD. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch size in the Red-billed Quelea Quelea quelea. Ibis 118:547-574.

LACK, D. 1966. Population Studies of Birds. Clarendon Press, Oxford.

LIVERSIDGE, R. 1966. Fluctuations in a breeding population in the eastern Cape. Ostrich 37 (Suppl 6):419-424.

LIVERSIDGE, R. 1970. The Ecological Life History of the Cape Bulbul. Ph.D. thesis, University of Cape Town.

MCLACHLAN, G.R. and R. LIVERSIDGE. 1972. Roberts Birds of South Africa. Trustees of the John Voelcker Bird Book Fund, Central News Agency, Cape Town.

MENTIS, M.T., B. POGGENPOEL and R.R.K. MAGUIRE. 1975. Food of the helmeted guineafowl in highland Natal. J. sth. Afr. Wildl. Mgmt. Ass. 5:23-26.

ODUM, E.P. 1971. Fundamentals of Ecology. W.B. Saunders Company, London.

ONESTA, P.A. and P. Verhoeff. 1976. Annual rainfall frequency distributions for 80 rainfall districts in South Africa. S. Afr. J. Sci. 72:120-122.

RICKLEFS, R.E. 1973. Ecology. Chiron Press, Massachusetts.

SIEGFRIED, W.R. 1966. Growth, plumage development and moult in the crowned guineafowl *Numida meleagris coronata* (Gurney). Dept. Nat. Cons. Invest. Rept. no. 8.

SINCLAIR, A.R.E. 1974. The natural regulation of buffalo populations in East Africa. III. Population trends, and mortality. E. Afr. Wildl. J. 12:185-200.

SKEAD, C.J. 1962. A study of the crowned guineafowl *Numida meleagris coronata* (Gurney). Ostrich 33:51-65.

STOKES, A. and H. WILLIAMS. 1971. Courtship feeding in gallinaceous birds. Auk 88:543-559.

S. Afr. J. wildl. Res. 7(1): 1-3 (1977)

VARIATION IN INTESTINAL HELMINTH INFESTATION OF THE HELMETED GUINEAFOWL

TIMOTHY M. CROWE
FitzPatrick Institute, University of Cape Town,
Rondebosch 7700

ABSTRACT. — Intestinal tracts from 206 helmeted guineafowl (*Numida meleagris*) shot during June and July of 1974 and 1975 from two discrete habitat types were examined for helminths. Six species (three cestodes, two nematodes and one acanthocephalan) were identified. Helminths were found in all but one of the tracts. Nematodes were found only in the caeci, cestodes and acanthocephalans in the intestinal lumen. Using a volumetric index of level of infestation, juvenile guineafowl had higher levels of infestation by cestodes and acanthocephalans than did adults. The highest levels of helminth infestation of adult guineafowl were found in specimens collected in July 1975. In savanna habitat, adults had higher levels of nematode infestation in June 1974 than in June 1975. In July 1975, adult guineafowl in riverine habitat had higher levels of helminth infestation than those in savanna habitat. In June 1975, in riverine habitat, adult males had higher levels of nematode infestation than females. High levels of infestation in juvenile guineafowl are presumed to be the result of a greater intake of intermediate hosts and a lower resistance to infection. High levels of infestation in adult guineafowl are attributed to an interaction between high population density and soil moisture content at the time of infection. None of the guineafowl showed any signs of gross pathological condition. Therefore observed infestation is presumed to be at a tolerable level.

INTRODUCTION

Although many species of intestinal helminths have been found in the helmeted guineafowl (*Numida meleagris*) (Biester and Schwarte 1959, Yamaguti 1959 and 1961, Ortlepp 1963, Oosthuizen and Markus 1967), only Saayman (1966) has attempted to quantify the level of helminth infestation of guineafowl in their natural state. He gave means and ranges by species for numbers of worms found in the intestines of 36 adult guineafowl collected throughout the year, but did not express his data in a manner that would allow discussion of patterns of variation in level of infestation.

As part of a general etho-ecological survey of *N. meleagris* complete intestinal tracts of 206 guineafowl shot during June and July of 1974 and 1975 on Rooipoort Farm (28° 45′ S, 24° 05′ E), Kimberley district, South Africa, were examined for helminths. Level of helminth infestation was related to year and month, age and sex of the guineafowl, and the habitat in which the bird was shot. Various hypotheses concerning variation in level of infestation were investigated.

METHODS

Each guineafowl was weighed and examined for signs of gross pathological condition, e.g. emaciation, excessive feather loss, heavy ectoparasite infestation, tissue inflammation or damage. All guineafowl older than ten months (Siegfried 1966) were classified as adults. The sex of all guineafowl shot in 1975 was noted. Intestinal tracts were preserved in 10% formalin solution. The tracts were examined for helminths in a shallow grey pan (for maximum contrast to the white worms) containing clear water 3 cm deep. Each tract was cut open and helminths were removed with forceps. Helminths from the intestine and caeci were analysed separately. Spatial and relative numerical distribution of helminths by gross form (rounded and smooth = nematode, rounded and pseudo-segmented = acanthocephalan, flat and segmented = cestode) were noted for a random sample of 50 intestinal tracts (25 from adult, 25 from juvenile guineafowl). A sample of individual helminths encompassing the range of phenotypic variation was set aside for specific indentification.

The helminths were washed and placed in a graduated cylinder filled to a certain level with water. Level of infestation was expressed to the nearest 0,1 ml in ml of water displaced. This measure of infestation, although an approximation to the actual numbers of helminths present, provides a volumetric index of the amount of intestinal and caecal space occupied by helminths.

Guineafowl flock-size, and rainfall were monitored in the study area during the months prior to specimen collection.

Guineafowl helminth specimens were grouped into samples according to year, month, sex, age, and habitat (riverine vs savanna). All possible (56) comparisons of samples of guineafowl were made to determine statistical significance of intergrouping differences in level of infestation. The Mann-Whitney U test was used instead of the standard *t*-test because preliminary analysis indicated that the data did not meet the assumptions for the *t*-test (Sokal and Rohlf 1969). Within samples of adult guineafowl the correlation coefficient between level of infestation and body weight was computed to determine a possible correlation between weight and infestation.

Habitat classification followed Bigalke and Leistner's (unpublished data) vegetation survey of Rooipoort Farm. Riverine habitat was characterized by relatively moist soil, often with clay deposits, and vegetation dominated by willow (*Salix capensis*) and karee (*Rhus lancea*) trees, and perennial sedges and grasses, e.g. *Cyperus longus* and *Panicum coloratum*. Savanna habitat was characterized by relatively well drained soil types and evenly spaced bushy vegetation dominated by vaalbos, (*Tarchonanthus camphoratus*), and tall perennial grasses, e.g. *Eragrostis lehmanniana* and *Schmidtia pappophoroides*. Trees were rare, occurring locally in sandy pockets (*Acacia giraffae*) or near ground water (*Ziziphus mucronata*).

RESULTS

Helminths were found in 205 of the 206 tracts. None of the guineafowl examined showed signs of gross pathological condition. There was no significant correlation between body weight and level of infestation.

Six species of helminths were indentified: the acanthocephalan *Mediorhynchus taeniatus* (Listow 1901); the cestodes Raillietina (*Raillietina*) *pintneri* (Klaptocz 1906), *Ascometra numida* (Fuhrmann 1909), and *Porogynia paronai* (Moniez 1892); and the nematodes *Subulura dentigera* (Ortlepp 1937) and *S. suctoria* (Molin 1860). Cestodes and nematodes were the predominant helminths in the specimens examined (Table 1). Nematodes were found only in the caeci, cestodes only in the intestinal lumen (Table 1).

TABLE 1. *Percentage of guineafowl infected, distribution and occurrence (presence – absence) of intestinal helminths from a sample of 25 adults and 25 juveniles.*

	Small intestine			Caecum			Rectum[1]			% infected		
Age	A[2]	C[2]	N[2]	A	C	N	A	C	N	A	C	N
Adult	4	25	0	0	0	16	0	12	0	16	100	64
Juvenile	1	25	0	0	0	18	0	4	0	4	100	72
Totals	5	50	0	0	0	34	0	16	0	10	100	68

[1] presence likely due to migration after death of host (Verster *pers. comm.*)

[2] A = acanthocephalan, C = cestode, N = nematode

A summary of sample comparisons showing significant differences in helminth infestation is given in Table 2. Juvenile guineafowl had higher levels of infestation by cestodes and acanthocephalans than did adults. The heaviest helminth infestations of adult guineafowl were found in specimens collected in July 1975. In savanna habitat, adults had higher levels of nematode infestation in June 1974 than in June 1975. In July 1975, adult guineafowl in riverine habitat had higher levels of helminth infestation than those in savanna habitat. In June 1975, in riverine habitat adult males had higher levels of nematode infestation than females.

TABLE 2. *Summary of comparisons of intestinal helminth samples from* N. meleagris

Month & Year	Habitat	Age	Sexes	n	C & A[1] L.O.I.[3]	N[2] L.O.I.	vs	Month & Year	Habitat	Age	Sexes	n	C & A L.O.I.	N L.O.I
6/74	riverine	J	M & F	6	*7,50**	*0,83*		6/74	riverine	A	M & F	5	2,15	0,65
6/74	savanna	J	M & F	47	5,03*	0,51		6/74	savanna	A	M & F	44	2,18	0,51
7/75	savanna	A	M & F	18	*2,93*	*0,42***		6/75	savanna	A	M & F	17	2,15	0,09
7/75	riverine	A	M & F	10	*4,45**	*1,68***		6/75	riverine	A	M & F	37	1,89	0,16
7/75	riverine	A	M	6	*5,04**	*2,08***		6/75	riverine	A	M	27	1,95	0,21
7/75	savanna	A	M	3	*4,00*	*1,00***		6/75	savanna	A	M	9	2,75	0,02
7/75	riverine	A	F	4	*3,56***	*1,06***		6/75	riverine	A	F	10	1,71	0,02
6/74	savanna	A	M & F	44	*2,18*	*0,51***		6/75	savanna	A	M & F	17	2,15	0,09
7/75	riverine	A	M & F	10	*4,45**	*1,68***		7/75	savanna	A	M & F	18	2,93	0,42
6/75	riverine	A	M	27	1,95	*0,21***		6/75	savanna	A	M	9	*2,75*	0,02
6/75	riverine	A	M	27	*1,95*	*0,21***		6/75	riverine	A	F	10	1,71	0,02

[1] cestodes and acanthocephalans

[2] nematodes

[3] mean level of infestion (ml); higher L.O.I. in italics.

* U significant at $P < 0,05$

** U significant at $P < 0,01$

Total rainfall in May and June was 10 mm in 1974 and 44 mm in 1975. Mean flock size was 24,0 ($n = 49$) in 1974 and 35,8 ($n = 17$) in 1975.

DISCUSSION AND CONCLUSIONS

The absence of signs of gross pathological condition due to parasitism in all guineafowl examined indicates a tolerance, during the non-breeding season at least, to helminths at the existing levels of infestation. If emaciation is a fair index of harm done to the host by the helminths, the lack of a negative correlation between body weight and level of infestation supports this conclusion. It must be stressed that a volumetric measure of level of helminth infestation can be used as a gauge of collective harm done to the host only if there is no great disparity in pathogenicity among the helminth species. This condition is met in this study since under natural conditions internal parasites are rarely pathogenic (Condy 1972). The acanthocephalan *M. taeniatus*, the only identified helminth likely to be pathogenic (Verster *pers. comm.)*, is uncommon among guineafowl examined (Table 1).

Assuming mild pathogenicity on the part of the helminths, the most likely components of harm done to the guineafowl by these parasites are competition for nutrients with the host, simple physical blockage of the gut, and interference with absorption (Soulsby 1969). The last two components of harm are accounted for by the volumetric measure. Competition for nutrients is also a function of helminth volume, since cestodes and acanthocephalans absorb nutrients over their entire body surface, and since preliminary analysis indicated that nematodes found were uniform in size.

That sexual variation in helminth infestation was found in only one of eight comparisons made between the sexes, relates to the lack of dietary, physiological (moult and reproductive), and behavioural sexual dimorphism in guineafowl during the non-breeding season (Crowe unpubl. data). Investigation of sexual variation in helminth infestation before and during the breeding season, when such a dimorphism exists (Crowe unpubl. data), could reveal sexual differences in species composition and level of infestation.

In *Gallus domesticus*, as well as *N. meleagris*, juveniles tend to have higher helminth infestation than do adults, due to the juveniles' lower resistance to infection (Biester and Schwarte 1959). Resistance to infection is higher in fowl older than three months and in those previously infected (Ackert and Reid 1937, Ackert *et al.* 1939). Soulsby (1969) suggests than the lower resistance of juvenile domestic fowl could be due to an insufficiency of antibodies necessary for preventing infection. Dogiel (1964) adds that attainment of resistance could be a consequence of normal development in which an unsuitable habitat for the parasite is created, such as a thickening of skin or an increase in mucus secretion.

The high levels of infestation of adult guineafowl, especially those in riverine habitat (Table 2), in July 1975 are possibly an indirect result of the relatively high rainfall and larger flock sizes observed during May and June, i.e. when infection by the helminths found in the gut would have occurred. High soil moisture, is a favourable medium for the development, survival and reproduction of helminths (eggs) and their intermediate hosts (Biester and Schwarte 1959). Soil moisture was higher in the heavier, often clay-bearing soil in riverine habitat. Larger flocks presumably produce droppings at higher densities, e.g. under communal roosts. A higher dropping density would increase probability of ingestion of dung (containing helminth eggs) by the invertebrate intermediate hosts.

ACKNOWLEDGEMENTS

This research was made possible by grants from the University of Cape Town and De Beers Consolidated Mining Corporation Ltd. Special thanks must go to De Beers for allowing me access to their properties and for unflinching logistical support in the field. Mr. A.B. Fischer, manager of Rooipoort Farm aided in collection and sorting of specimens. Dr A. Verster of the Department of Agricultural Technical Service Veterinary Research Institute made specific identification of the helminths. Data analysis was greatly speeded through help from staff members of the FitzPatrick Institute, and Kimberley's McGregor Museum. Helpful comments on content and presentation were given by my advisor Professor W.R. Siegfried, Dr R. Liversidge, Dr A. Verster, Dr L. Underhill, and an anonymous referee.

REFERENCES

ACKERT, J. and W. REID. 1937. Age resistance of chickens to the cestodes *Raillietina cesticillus* (Molin) on growing. *J. Parasit.* 23:558-563.

ACKERT, J., S. EDGAR and L. FRICK. 1939. Goblet cells and age resistance of animals to parasitism. *Trans. Am. Micr. Soc.* 58:81-96.

BIESTER, H.E. and L. SCHWARTE. (eds.). 1959. Diseases of poultry. Iowa State College Press, Ames.

CONDY, J.B. 1972. Observations on levels of internal parasites in free living Rhodesian wildlife, I. Kudu (*Tragelaphus strepsiceros*). *Zool. afr.* 7:413-418.

DOGIEL, V.A. 1964. General parasitology. Oliver & Boyd Edinburgh and London.

OOSTHUIZEN, J.H. and M.B. MARKUS. 1967. The haematozoa of South African birds. 1: Blood and other parasites of two species of game birds. *Ibis* 109:115-117.

ORTLEPP, R. 1963. Observations on cestode parasites of guineafowl from Southern Africa. *Onderstepoort J. Vet. Res.* 30:95-118.

SAAYMAN, J. 1966. A study of the diet and parasites of *Ardeola (Bubulcus) ibis, Numida meleagris* and *Gallus domesticus* from the Eastern Cape Province, South Africa. Ph.D. thesis, University of South Africa.

SIEGFRIED, W.R. 1966. Growth, plumage, development and moult in the Crowned Guineafowl *Numida meleagris coronata* (Gurney). *Dept. of Nature Conservation Investigational Report.* no. 8.

SOKAL, R.R. and F.J. ROHLF. 1969. Biometry. W.H. Freeman and Company, San Francisco.

SOULSBY, E.J.L. 1969. Helminths, arthropods, and protozoa of domesticated animals. Bailliere, Tindall and Cassell, London.

YAMAGUTI, S. 1959. Systema Helminthum Vol II. The cestodes of vertebrates. Interscience Publishers, New York, London.

YAMAGUTI, S. 1961. Systema Helminthum Vol. III. The nematodes of vertebrates Part II. Interscience Publishers, New York, London

Received 12 May 1976
Revised 18 August 1976

ACKNOWLEDGEMENTS

Although I have already expressed my gratitude to many persons, in the foregoing acknowledgement sections, I have neither included all who merit thanks, nor awarded proper recognition to some. Throughout the ontogeny of this dissertation, my supervisor Professor W.R. Siegfried provided guidance, stimulation, criticism and logistical support, without which this finished article would yet lay unwritten. Dr and Mrs R. Liversidge and Mr and Mrs A.B. Fischer helped greatly to make my period of field-work a pleasurable experience. Miss D. Gibbons and Miss R. Searle patiently typed most of the material herein.

The first two years of my research were funded by generous grants from the University of Cape Town (an Overseas Students' Scholarship) and DeBeers Consolidated Mines Ltd. The final period of data analysis and interpretation was carried out while I was a Research Officer at the FitzPatrick Institute of the University of Cape Town. I thank my colleagues, particularly Mr R.K. Brooke, for their constructive criticism.