Original article

The mountain bees of the Kilimanjaro region and their relation to neighbouring bee populations

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Summary — To study the nature of transition from one subspecies to another in a region without geographic barriers, 27 samples of honey bees were collected in the region of Arusha, Tanzania, at altitudes ranging from 800 to 2800 m, and morphometrically analyzed. Gradients of increasing size and hair length, with respect to increasing altitude, were found. Multivariate analysis, however, resulted in separation of two groups of samples, one below, the other above 2000 m, corresponding to two races, *Apis mellifera scutellata* and *A.m.monticola*. The *monticola* populations of Kilimanjaro and Mt. Meru differ in two characteristics. The evolution of the disjunct *monticola* populations of East Africa is discussed in the light of well documented climatic changes during the Quarternary.

***Apis mellifera monticola* — *Apis mellifica scutellata* — morphometry — Africa — evolution**

Résumé — Les abeilles des montagnes de la région du Kilimandjaro et leurs relations avec les populations d'abeilles avoisinantes. *On a trouvé chez les abeilles d'Afrique orientale (Kenya, Tanzanie) une gradation des caractères morphométriques corrélée avec l'altitude. Cette gradation commence avec l'abeille de la plaine côtière, très petite, à pilosité courte et très jaune, et se termine par les abeilles relativement grandes, à longue pilosité et principalement noires, des forêts montagnardes jusqu'à 3 000 m d'altitude. L'échelle de la gradation est divisée en 3 segments, chacun d'eux étant occupé par une race bien définie géographiquement : A.m. litorea sur la côte, A.m. scutellata dans la savane des hauts plateaux et A.m.monticola dans la forêt montagnarde (Fig. 1). Le but de cette étude est d'étudier la nature de la transition d'une race à l'autre dans une région dépourvue de barrières géographiques.*

Matériel et méthodes. Vingt sept échantillons d'abeilles ont été prélevés dans la région d'Arusha, aussi bien dans la savane des hauts plateaux que dans la forêt montagnarde des monts Meru et Kilimandjaro, à des altitudes allant de 800 m à 2 800 m (Tableau I). On a fait une étude morphométrique de 15 ouvrières par échantillon, portant sur 18 caractères de taille, pilosité, vénation alaire et pigmentation (Tableau II). Les données ont été analysées par les méthodes de corrélation et d'analyse multivariée, afin de savoir s'il existait une corrélation entre la variation des caractères individuels et/ou du groupe d'échantillons d'une part, et l'altitude d'autre part.

Resultats. La plupart des caractères se rapportant à la taille et à la longueur de la pilosité sont corrélés significativement avec l'altitude (Fig. 2). La longueur du proboscis (r = 0,114) et les angles de la vénation alaire (par ex. J16; r = 0,044) ne montrent pas de corrélation significative avec l'altitude. La question de savoir si la corrélation avec l'altitude est linéaire ou par degrés n'a pu être résolue avec les données disponibles, les fonctions ne différant pas dans les 2 cas (Tableau III).

Néanmoins, l'analyse factorielle (PCA) a montré la présence de 2 groupes sans recouvrement comprenant respectivement les échantillons pris au-dessous et au-dessus de 2 000 m (Fig. 3). Ce regroupement est confirmé par l'analyse discriminante (Fig. 4). Ces groupes correspondent exactement à l'abeille de la savanne d'Afrique orientale (A.m.scutellata Lep.) et à l'abeille des montagnes (A.m. monticola Sm.). Des différences significatives existent entre les abeilles de montagne du Mt Meru et celles du Mt Kilimandjaro, mais pour deux caractères seulement (longueur de T3 et angle de vénation J16); elles permettent de classer chaque échantillon individuel, même s'il a été prélevé il y a 20 ans, et de les différencier d'un autre point de vue (Fig. 5).

Discussion. Les différences entre les populations d'abeilles de la savanne des hauts plateaux et celles de la forêt montagnarde ne sont pas simplement des adaptations écologiques en réponse aux conditions climatiques différentes, mais des caractères de deux races géographiques différentes résultant d'un processus évolutif spécifique. Cette idée trouve sa confirmation dans la comparaison avec les populations montagnardes tropicales de l'Afrique occidentale (Cameroun) chez lesquelles, pour la plupart des caractères, on n'a trouvé aucune différence entre les populations d'abeilles de la côte et celles de la forêt montagnarde (Fig. 6). Il n'y a pas de passage graduel dans les zones de contact (altitude proche de 2 000 m) des 2 races d'Afrique orientale scutellata et monticola, mais celles-ci sont présentes l'une à côté de l'autre sans hybrides phénotypiques malgré l'absence de barrières physiques. De toute évidence les échantillons sont distribués au hasard à travers les diverses zones d'altitude pour une même race (Fig. 3). On peut estimer que des différences dans le comportement (par ex. dans la reproduction) agissent comme facteur d'isolement. Les nombreuses populations monticola des montagnes isolées de l'Afrique orientale sont probablement des reliques d'une ancienne population de forêt, distribuée uniformément et couvrant presque tout le haut plateau. De nombreux exemples de biocénoses de forêt et de savanne (Hamilton, 1982; Nagel, 1987) ont montré que la majeure partie du haut plateau d'Afrique orientale, jusqu'à la Rift Valley, était couverte d'une forêt tropicale dense jusqu'à 6 000 avant J.C. Cette date correspond bien avec le fait que les populations monticola ont développé entre elles des différences faibles mais néanmoins typiques, sans pour autant atteindre le niveau d'une sous-espèce.

Apis mellifica monticola — Apis mellifera scutellata — *morphométrie — Afrique — évolution*

Zusammenfassung — Die Gebirgsbiene der Kilimanjaro-Gegend und ihre Beziehungen zu den angrenzenden Bienenpopulationen. *Bei den Bienen Ostafrikas (Kenya, Tanzania) wurde eine mit der Höhenstufe korrelierte Merkmalsgradation gefunden, die von sehr kleinen, kurzhaarigen und sehr gelben Bienen an der Küste zu relativ großen, langhaarigen und überwiegend dunklen Bienen in den Bergwäldern bis in eine Höhe von 3 000 m reicht. Die Skala dieser Gradation wird von drei gut charakterisierbaren Rassen eingenommen, A.m.litorea an der Küste, A.m.scutellata in den Savannen des Hochlandes und A.m.monticola in den Bergwäldern (Fig. 1). Ziel der vorliegenden Arbeit war es, die Art des Überganges von einer Rasse zur anderen in einem Areal zu untersuchen, in dem geographische Barrieren fehlen.*

Material und Methoden. In der Gegend von Arusha wurden 27 Bienenproben sowohl von der Hochland-Savanne wie von den Bergwäldern des Mt. Meru und Kilimanjaro gesammelt, aus Höhenlagen von 800-2 800 m (Tabelle I). Pro⁻Probe wurden 15 Arbeitsbienen morphometrisch vermessen, wobei 18 Merkmale der Größe und der Behaarung, des Flügelgeäders und Pigmentierung berücksichtigt wurden (Tabelle II). Die gewonnen Daten, ausgewertet mit den Methoden der Korrelations- und Multivariat-Analyse, sollten Auskunft darüber geben, ob die Variation der einzelnen Merkmale und/oder die Gruppierung der Proben einen Zusammenhang mit der Höhenlage erkennen lassen.

Ergebnisse. Die meisten Merkmale der Größe und die Haarlänge zeigen eine deutliche Korrelation mit der Meereshöhe (Fig. 2). Die Rüssellänge (r = 0.114) und die Aderwinkel des Vorderflügels (z.B.J16; r = 0.044) sind jedoch nicht signifikant mit der Meereshöhe korreliert. Anhand des vorliegenden Materials konnte nicht entschieden werden, ob die Korrelationen mit der Höhe linear oder sprungförmig verlaufen, da die Funktionen in beiden Fällen voneinander nicht verschieden sind (Tabelle III).

Die Faktorenanalyse (PCA) ergibt jedoch zwei nicht überlappende Gruppen, eine mit Proben unterhalb 2 000 m, die andere oberhalb dieser Höhe (Fig. 3). Diese Gruppierung wird durch eine

Diskriminanzanalyse bestätigt (Fig. 4). Morphometrisch wie ökologisch entsprechen diese Gruppen der ostafrikanischen Savannenbiene A.m. scutellata Lep. und der Bergbiene A.m. monticola Sm. Zwischen den Bergbienen von Mt. Meru und Kilimanjaro bestehen konstante Unterschiede, aber nur in zwei Merkmalen (Länge von T4 und Aberwinkel J16), welche die richtige Einordnung jeder einzelnen Probe ermöglichen, selbst wenn diese schon vor 20 Jahren gesammelt wurden und in anderer Hinsicht verschieden sind (Fig. 5).

Diskussion. Die Unterschiede zwischen den Bienenpopulationen der Hochlandsavanne und des Bergwaldes stellen nicht einfache ökologische Anpassungen infolge unterschiedlicher klimatischer Bedingungen dar, sondern sie sind Merkmale zweier verschiedener geographischer Rassen, entstanden in einem spezifischen Evolutionsprozeß. Dies wird belegt durch den Vergleich mit tropischen Bergpopulationen aus Westafrika (Cameroun), die in den meisten Merkmalen Unterschiede zwischen Küsten- und Bergpopulationen vermissen lassen (Fig. 6). Die beiden ostafrikanischen Rassen scutellata und monticola gehen an den Berührungsgrenzen (Höhenstufe ca. 2 000 m) nicht gleitend ineinander über, sondern sie sind trotz Fehlens physischer Barrieren phänotypisch voneinander abgegrenzt. Innerhalb der beiden Rassen sind die Herkünfte nach ihrer Höhenstufe anscheinend regellos verteilt (Fig. 3). Als Isolierungsfaktoren können Verhaltensunterschiede (z.B. in der Reproduktion) vermutet werden.

Die zahlreichen monticola-Vorkommen in den isolierten Bergmassiven Ostafrikas sind vermutlich Refugial-Reste einer früher einheitlichen, sich über das ganze Hochland erstreckenden Population. Es liegen heute zahlreiche Belege von Wald- bzw. Steppenbiozönosen vor (Hamilton, 1982; Nagel, 1987), die zeigen, daß große Teile des ostafrikanischen Hochlandes bis hinunter in das Rift Valley bis 6 000 B.P. von einem geschlossenen Regenwald bedeckt waren. Diese Zeitangabe stimmt gut mit der Feststellung überein, daß die monticola-Populationen untereinander geringfügige, aber doch typische Unterschiede entwickelt haben, ohne aber das Niveau einer Subspezies zu erreichen.

Apis mellifera monticola — Apis mellifera scutellata — *Morphometrie — Afrika — Evolution*

Introduction

A race of honey bees is found in the humid mountain forests of East Africa from Rwanda Burundi to Ethiopia, which is clearly distinguished by size, darker pigmentation, and behavior from the yellow bee of the savanna, described by Smith (1961) as *Apis mellifera monticola.* As a second new subspecies of the region, Smith (1961) established the very small *A.m.litorea* from the coast of the Indian Ocean (Fig. 1). In between these extremes, geographically as well as in body size, *A.m.scutellata*, the generally distributed honey bee of the East and South African savanna (formerly known as *A.m.adansoni;* Ruttner and Kauhausen, 1985) is found at altitudes between 500 and 2 000 m.

This gradation (cline) of size comprises up to 63% of the total variability of the species (Ruttner, 1985; Ruttner and Kauhausen, 1985). The cline is most impressive in the Kilimanjaro region where the isolated volcanic cones of Mt. Meru and Kilimanjaro are situated only 300 km from the Indian Ocean; therefore, the succession of the three subspecies cited above becomes especially obvious. Important questions concerning the differentiation and isolation of taxonomic units are raised by this special pattern of distribution not generally found in honey bees. However, no data are available about the separation of the savanna bee and the mountain bee. Ecological factors were suggested (Ruttner and Kauhausen, 1985), but is there a zone of hybridization or is the limitation as abrupt as the transition between savanna and mountain forest ?

Another problem is the origin of the isolated populations of *A.m.monticola* in East African mountain forests which are situated like islands in a vast sea of the coherent *scutellata* population of the savanna. Is this situation a consequence of a local adaptive selection of tropical populations by temperatures decreasing with altitude, in conformity with Bergmann's rule, or is this the consequence of climatic changes resulting in disjunct refugia ?

In this paper the results of a morphometrical analysis of a series of samples from different altitudes in the Kilimanjaro region are presented, in order to find, at least, indications of the acting factors.

Materials and Methods

Sample collection

Twenty-two samples of local bees were collected in November 1984 in the vicinity of Arusha (Tanzania), on the slopes of Mount Meru (one series each in the east and one in the west, above Olmontoni) and of Kilimanjaro (above Marangu). Additionally, five samples were collected at Magugu, south of Lake Manyara (Table I). These bees live at an altitude of 800 m, whereas the highest site for bee colonies on Mount Meru and Kilimanjaro was 2 800 m. No bees were found at altitudes of 3 000 m. Four samples of *A.m.monticola* obtained from Kilimanjaro in 1965, were available as references for the study of the change over a period of time of one isolated population. The parameters of the Morphometric Data Bank Oberursel (Ruttner, 1988) were used to classify the populations investigated.
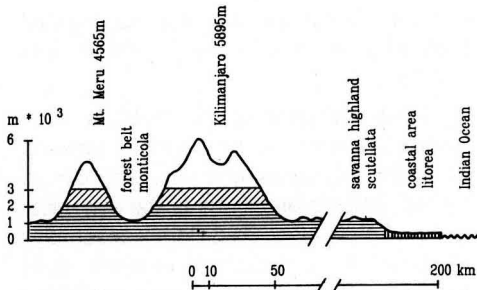
The honey bees were caught with nets from the entrance of traditional hives which were fixed to tree branches at a considerable height. The altitude of the location was measured by an altimeter, regularly adjusted at Arusha (1 350 m).

Selection of the discriminant characteristics and statistical analysis

For the morphometric analysis the standard method of Ruttner (1988) was applied. The 8 characteristics with the best discriminant effect were selected by means of 13 samples from Tanzania and Kenya that had been previously analyzed by stepwise discriminant analysis :

Table I. Source of analysed samples.

No. of sample	Location	Altitude	No. of sample	Location	Altitude
1270	Magugu	800	1247	Mount Meru West	2000
1271	Magugu	800	1246	Mount Meru West	2000
1272	Magugu	800	1245	Mount Meru West	2050
1273	Magugu	800	1244	Mount Meru West	2550
1274	Magugu	800	1243	Mount Meru West	2600
1241	Mbuguni	910	1259	Mount Meru West	2600
1242	Mbuguni	910	1260	Mount Meru West	2800
1239	Njiro	1280	1261	Mount Meru West	2800
1262	Njiro	1280	1251	Mount Meru East	2200
1249	Mount Meru East	1500	1250	Mount Meru East	2250
1248	Mount Meru East	1600	1252	Mount Meru East	2250
1240	Olmontoni	1630	1253	Kilimanjaro	2200
175	Kilimanjaro 1965	2800	1254	Kilimanjaro	2450
176	Kilimanjaro 1965	2800	1256	Kilimanjaro	2600
177	Kilimanjaro 1965	2800	1255	Kilimanjaro	2800
178	Kilimanjaro 1965				

Fig. 1. Diagram of Tanzania between Indian Ocean and Kilimanjaro with climatic zones and distribution of honey bee races. Shading : vertical — zone of *A.m. litorea*, horizontal — *A.m. scutellata*, oblique — *A.m. monticola*

length of proboscis; length of sternite 3; distance of wax plates; wing venation angles J16, K19, and O26; and pigmentation of scutellum (Table II). As the mountain bees were described as larger, darker, and with longer hair (Smith, 1961), nine additional characteristics were selected that were expected to show dependence on altitude : length of cover hair length of tergite 3 and 4 (T_{3+4}), length and width of sternite 6, length of forewing and pigmentation of tergites 2—4. Thus, a total of 17 characteristics were used for analysis. One sample consisted of 15 worker bees.

The relation of population variation with altitude was investigated by correlation analyses and adaptations of functions for the single characteristics. By means of the standardized individual values for bees, the following parameters were calculated: correlation coefficient *(r)*, the initial value *(a)* and slope *(b)* of the linear regression and the parameters (y_1) and (y_2) of a "step function". It was assumed that the values of a characteristic remain constant up to 2 000 m, then change abruptly and stay constant again. Finally the mean deviation of the single values from the values of the functions (s) was calculated.

To determine the relative positions among the samples, multivariate analyses (factor analysis, discriminant analysis) were applied. In these cases, means of samples, rather than individual values of bees, were used.

Results

Correlation of characteristics with altitude

The results are summarized in Table III. A significant correlation with altitude exists for most of the characteristics, especially T_{3+4} (which is taken as measurement of body length), length of forewing, and hair

Table II. Analysed characteristics.

Method of selection			
Discriminant analysis		Subjective choice	
No.	Characteristic	No.	Characteristic
4	Proboscis	1	Cover hair
11	Sternite 3, long.	9	tergite 3, long.
		10	tergite 4, long.
14	distance of wax plates	15	sternite 6, longit.
	Wing venation angles	16	sternite 6, transvers.
27	Angle J16	17	Fore wings, length
28	Angle K19	32	Pigmentation tergite 2
31	Angle O26	33	Pigmentation tergite 3
		34	Pigmentation tergite 4
		35	Pigmentation scutellum 1
		36	Pigmentation scutellum 2

length (Fig. 2). No correlation with altitude was found for proboscis length and wing venation angle J16.

The question of whether the correlation is linear or stepwise cannot be settled. The deviations of the single values of the two functions (S_{IR} and s_{sp}) do not differ (Table III). However, the hypothesis of linearity had to be rejected for all characteristics taken separately at a level of 5%.

Classification

A factor analysis (PCA) of all samples clearly results in two clusters (Fig. 3). The samples are marked with the altitude of their origin and it can easily be recognized that along the coordinate of factor 1 (which is determined mainly by characteristics of size and hair length), all samples from locations higher than 2 000 m are found on the right of point 0 of the coordinates, and those from lower locations on the left. The lower border line

of the mountain forest in the investigated area was found between 1 900 m and 2 000 m.

Within the clusters the distribution of samples seems to be random and no arrangement according to altitude is visible. The presentations of the canonical factors 1+2 and 1+3 are essentially identical. A discriminant analysis (DA) confirms these results : the total is divided into two groups; all samples of the highland bee (locations below 2 000 m) are correctly classified, whereas of the 15 samples of the mountain bees only one is found closer to the wrong cluster ($P < 0.01$; Fig. 4). Factor analysis and DA demonstrated separation of the samples according to their association with the geographical races *A.m.scutellata* and *A.m.monticola*. No true transitional types were found in intermediate altitudes (the single misclassified sample mentioned above was collected at an altitude of 2 800 m).

Table III. Analysis of the correlation of single characteristics with altitude : linear regression (IR) or stepwise function (sp) ? Linear regression : *a* constant increase of characters with altitude is assumed; correlation coefficient *(r)*, level of significance *(p)*, initial value *(a)*, gradient *(b)*, mean deviation (s_{IR}).
Stepwise function : Values are assumed to be constant up to an altitude of 2 000 m, then take a step, and remain constant again; values of an adapted step function (y_1, y_2), mean deviation (ssp).

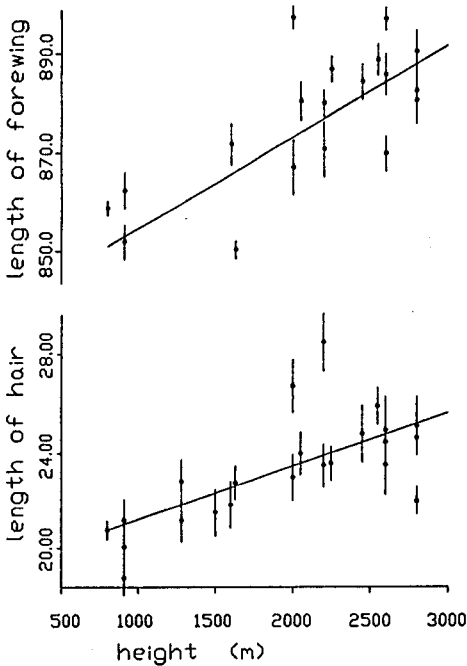| Character	n	Linear regression					Stepwise function		
		r	*p*	*a*	*b*	s_{IR}	y_1	y_2	s_{sp}
Hair length	400	0.385	0.001	18.99	0.22	3.79	21.13	24.48	3.76
Proboscis	242	0.114	n.s.	591.23	0.22	13.37	592.07	599.32	12.98
St 3, length	397	0.386	0.001	249.07	0.47	8.08	253.52	260.89	7.98
D wax plates	389	0.127	0.05	31.19	0.11	5.95	32.23	33.86	5.93
Fore wing L	399	0.594	0.001	835.92	1.86	18.21	853.02	883.35	16.87
Ven. angle J16	400	0.044	n.s.	94.58	− 0.03	4.01	94.14	94.11	4.01
Ven. angle K19	402	0.213	0.001	80.39	− 0.09	2.91	79.44	78.26	2.92
Ven. angle O26	401	0.127	0.01	36.04	0.07	3.75	36.91	37.52	3.77
T3+4 L	402	0.279	0.001	395.90	0.49	12.07	400.09	408.52	11.87
L/B St6	381	0.165	0.01	84.87	− 0.08	3.41	83.99	82.98	3.42

Fig. 2. Relation of measurements (in 1/100 mm) of length of fore wing (upper panel) and hair (lower panel) with altitude (in m). One circle represents the mean of 15 bees, the vertical line the standard error. For parameters see Table III.
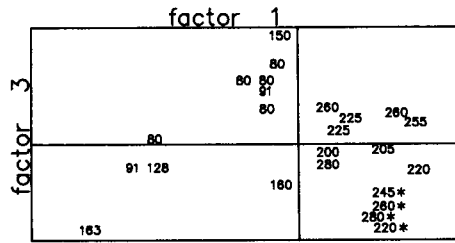

Fig. 3. Graph of a factor analysis (factor 1/3 of a PCA). The coordinates of the canonical variables are marked with the altitude of origin (given in meters divided by 10). Asterisk : samples from Kilimanjaro.
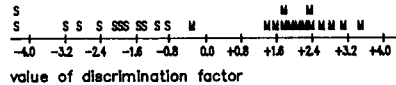

Fig. 4. Discriminant analysis of savanna (S) and mountain (M) bees.

Discrimination of isolated monticola populations

The four samples from Kilimanjaro are arranged in a subcluster separated from the samples of Mount Meru as shown in Fig. 3. By stepwise discriminant analysis the two *monticola* populations can be separated from each other by only two characteristics : the venation angle J16 and the length of tergite 4 (the bees of the Kilimanjaro population were smaller in all characteristics than those of Mount Meru).

Morphometric changes of the Kilimanjaro population in time

The four Kilimanjaro samples collected in 1965 offered the chance to compare samples from the same area after an interval of about 20 yr. The "old" Kilimanjaro bees were the largest among all *monticola* bees known, including the bees collected on Kilimanjaro in 1984, and somewhat separated in a joint factor analysis. However, they show the typical *monticola* and Kilimanjaro characteristics as demonstrated by a discriminant analysis : they are classified as group "Kilimanjaro" and not as group "Mount Meru" (Fig. 5).

Discussion

The concept of a linear gradation from the smallest and brightest coloured bee with the shortest body hair in the warmest climatic zone to the largest and darkest bee with the longest body hair in the coolest biotope was suggested by listing
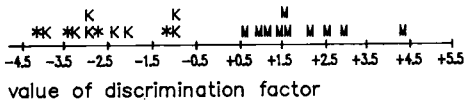
value of discrimination factor

Fig. 5. Discriminant analysis of the groups "Mount Meru" (M) and "Kilimanjaro" (K). Asterisk denotes : Kilimanjaro samples from 1965.

the characteristics of East African races of honey bees (Ruttner, 1985). In the present analysis, however, the measured characteristics show a variable and, in general, only slight correlation with altitude (Fig. 2a,b). More important is the observation that the samples are divided into two groups by multivariate analysis, in smaller bees below and in larger bees above 2 000 m of altitude. At first sight the variation within each group seems to be random and independent of altitude and is classified as "discontinuous horizontally-stepped cline" within a Formenkreis (Huxley, 1939). Our attempt to fit the data either to a linear regression or to a step function gave no result since both functions are identical (Table III). Therefore, for the single characteristics no decision can be made as to whether the increase with altitude is linear or stepwise. The outcome indicates that the data are inadequate to answer these questions (too few samples from different populations) and that a larger, more homogeneous series has to be analyzed in the future in order to obtain valid results.

It can be concluded, nevertheless, that the variation of characteristics cannot be a continuum because when all characteristics are investigated together, both factor analysis and discriminant analysis result in the division of the 27 samples from different altitudes of Mount Meru and Kilimanjaro and the neighbouring highlands into two different
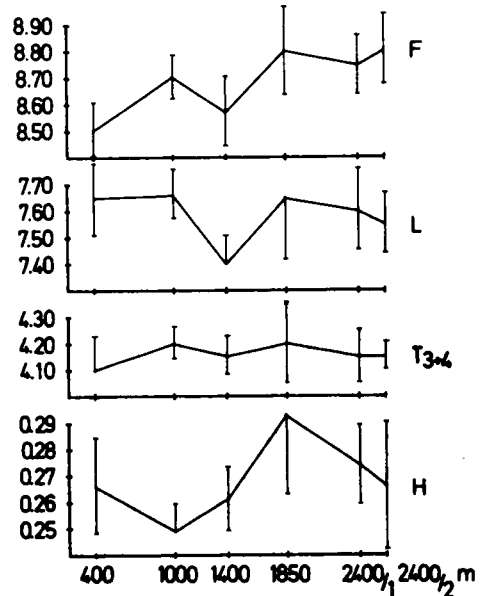

Fig. 6. Relation of morphometric data of bees from Cameroon with altitude. Abscissa — Altitude in m. Ordinate — scale in mm. F length of fore wing, L length of hind leg, T3+4 length of tergite 3 and 4, H hair length (scale 0.1 mm).

groups : the bee of the highland savanna, *A.m.scutellata,* and the bee of the mountain forest, *A.m.monticola.* Both groups are clearly differentiated from each other by size, length of hair and pigmentation.

With this result the discussion is shifted from the subject of straightforward ecological adaptation to subspecies (= geographic race). Subspecies are characterized by a multitude of morphological, ethological, ecological, and chorological features, originating with evolution. Every subspecies can be considered to be the result of a specific historic sequence, as shown for honey bees (Ruttner, 1988). Thus, a simple correlation of phenotypes with the present ecological data would be inappropriate as the starting point of an explanation of phenotypic variation. This is demonstrated

by comparing the bees from East Africa with an analogous series from the mountains of Cameroon, that is from a similar geographic latitude (5N) on the African west coast. The data comprise six samples collected in the coastal rain forest (altitude 400 m), the central highland (altitude 1 000 m), and at Mount Cameroun and Mount Oku (altitudes of 1 400, 1 850, and 2 400 m). In this series no gradation of characteristics was found except for forewing length (Fig. 6). Even the length of hair, closely correlated with altitude in East Africa, is the same near the western coast and in the mountain forest. The difference from East Africa is the minor extension of high elevations and only slight climatic changes during the Pleistocene, reducing the possibility for the evolution of individual subspecies.

In East Africa important climatic changes occurred during the cold phases of the Pleistocene. In the major part of the highland, between 1 000 m and 2 000 m altitude, conditions prevailed that were similar to those of the present habitat of *A.m.monticola*. It is concluded that the disjunct *monticola* areas of today represent the refugia of a former much larger coherent distribution across all of the highlands of East Africa (Ruttner, 1988). The quarternary history of East African climate and biota are well known (review see Hamilton, 1982; Nagel, 1987). During the peak of maximum glaciation in Europe (24 000—18 000 B.P.), the moraines of the East African glaciers were deposited at altitudes of about 3 500 m (that is 1 000 m lower than today). This period, however, was rather dry and unfavourable for the growth of forests. Later, a warmer, distinctly more humid period with a substantial expansion of forests followed. At the peak of the humid period, about 9 000 years B.P., virtually all of Uganda and even the floor of the Rift Valley were covered by forests. The

crucial factors of the *monticola* habitat are not yet known (whether it is mainly low temperature or also humidity favouring the growth of forests); thus both conditions, cool and dry or humid, could have enhanced the expansion of the mountain bee at the expense of the steppe bee, *A.m.scutellata*.

An even more convincing testimony than the search for remnants of a forest biotope such as trees, birds, and mammals (Hamilton, 1982) is the check-test, the study of elements of the African savanna. Nagel (1987) investigated the Paussinae, a myrmecophilic subfamily of the Carabidae (Coleoptera) which is strictly bound to the savanna. On the basis of the present distribution, the author concludes that in East Africa only restricted refugial areas of savanna remained during the humid period (*e.g.* one in northern Tanzania, one in southern Kenya). Areas of certain species were split into two by forest zones, resulting in pairs of semi-species, such as : *Paussus sphaerocerus* and *P. dissimulator,* and *P. cilipes* and *P. hirsutus.* During this period, the *Apis* subspecies *monticola* could have evolved and occurred in all of the widespread forests of the East African highland. The separation of the present isolated *monticola* populations must have started at about 6 000 years B.P. when the forests retreated. This explains the rather slight modifications of the individual populations.

The clean separation of the clusters *scutellata* and *monticola* (Fig. 3) may indicate a certain degree of reproductive isolation of neighbouring populations of the two subspecies. The reason for this observation is not easy to explain. Though colonies are reported to dwindle and to die if transferred from the mountain forest to the savanna in Ethiopia (Gebreyesus, 1976) and also in Mulala, Mount Meru (Mollel, personnel commu-

nication), the lack of hybrids is astonishing, considering the close contact of both populations. Again, it is noteworthy that the behavioral characteristics of these subspecies are only superficially known; differences in mating behaviour have to be considered as possible isolating factors.

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