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HYBRIDIZATION BETWEEN *APIS MELLIFERA CAPENSIS* AND ADJACENT RACES OF *APIS MELLIFERA* *

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SUMMARY

The distribution of the Cape honeybee (*Apis mellifera capensis* Esch.) was analysed by biometrical methods. Characters separating *A.m. capensis* clearly from its adjacent races (spermathecal size, length of abdominal hairs, tergite colour) showed a high inter and intra colonial variation in the classical distribution area of the Cape honeybee. This high variance is typical for hybrid areas and implies that *A.m. capensis* is a race close to extinction.

INTRODUCTION

Two races of honeybees, *Apis mellifera capensis* and *A.m. adansonii* are described in Southern Africa by various authors (eg. SMITH, 1958, 1961 ; KERR and PORTUGAL-ARAUJO, 1958 ; ANDERSON, 1963 ; RUTTNER, 1976 a, 1976 b, 1976 c, 1977 ; FLETCHER, 1978). According to RUTTNER (1981) the adjacent race to *A.m. capensis* could be *A.m. scutellata* and not *A.m. adansonii* as discussed in previous papers. As the definition is yet not clear, we treat *A.m. adansonii* as adjacent race in this paper. Both races are easily distinguished by morphological and physiological features. Workers of the Cape honeybee *Apis mellifera capensis* have a spermatheca larger than 0.3 mm in diameter (RUTTNER, 1977), high numbers of ovarioles (at the average 19 to 20 ; ANDERSON, 1963 ; RUTTNER, 1977), queen substance in the mandibular glands (RUTTNER *et al.*, 1976 ; HEMMLING *et al.*, 1979 ; CREWE, 1982) and the ability of thelytokous parthenogenesis

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(ONIONS, 1912, 1914 ; RUTTNER, 1977 ; RUTTNER and HESSE, 1981 ; RUTTNER and VERMA, 1983). Workers of this race have a small or completely missing spermatheca. They have a bright yellow tergite coulour whereas *capensis* workers are usually black.

RUTTNER (1977) found that the typical *A.m. capensis* is abundant only in a rather small area of the Cape region. He estimated the total population size to be 20 000 colonies and proposed a sanctuary on the Cape peninsula in order to prevent extinction of this race. As there is no geographical isolation between the two races in southern Africa, a constant natural gene flow between the two populations is to be expected. In addition to the natural migration there is a larger gene flow caused by migratory bee keepers.

As the races are crossfertile, one would expect a large hybrid area between the two populations. This should result in a cline (SPERLICH, 1973) and a high inter and intra colonial variance for discriminating characters in the hybrid area. Specially large intra colonial variance between workers should document that the queen is mated with a highly variable set of drones. In a closed population of the « pure » race, variance of «typical » characters is expected to be rather small. Hence an analysis of variance-patterns and the continous change of certain characters (cline) which are different in both population should be a feasable way to locate hybridization zones.

We measured several morphological and anatomical characters of honeybees in this area in southern Africa to determine whether the Cape honeybee is really close to extinction or whether it is separated from *adansonii* by a clear cut hybridization zone.

METHODS

Worker bees from honeybee colonies (20 bees per colony) were collected at 24 locations in the Cape region of southern Africa, Namaqualand and Namibia (see map in Fig. 1). The bees were killed in hot water in order to obtain an extended proboscis and then fixed in Pampell's fixative (acetic acid 5.6 %, formaline 11.2 %, ethanol 28 %, distilled water 56 %). Forty-two morphological characters of each bee were measured according to RUTTNER *et al.* (1978). For each colony, the distance from the Cape peninsula, the hypothetical origin of the Cape honeybee (GUY, 1976 ; RUTTNER, 1977 ; TRIBE, 1983), was determined. A preliminary analysis revealed that few characters separated the northern honeybees from *A.m. capensis* clearly.

We included three well discriminating characters in our analysis, two of them being characteristically for *A.m. capensis* in its classical definition. There were : 1) The size of the spermatheca was determined by dissecting the bees and measuring the diameter of the organ ; 2) the length of the abdominal hairs at the fifth tergite was measured according to GOETZE (1940) ; and 3) the colour of the second tergite was classified according to the scheme of RUTTNER *et al.* (1978) and GOETZE (1940) ranging from 0 to 9 (black to bright yellow).

Variances and mean values were calculated for each colony. Inter- and intra-colonial variance was determined by a one way analysis of variance (ANOVA).

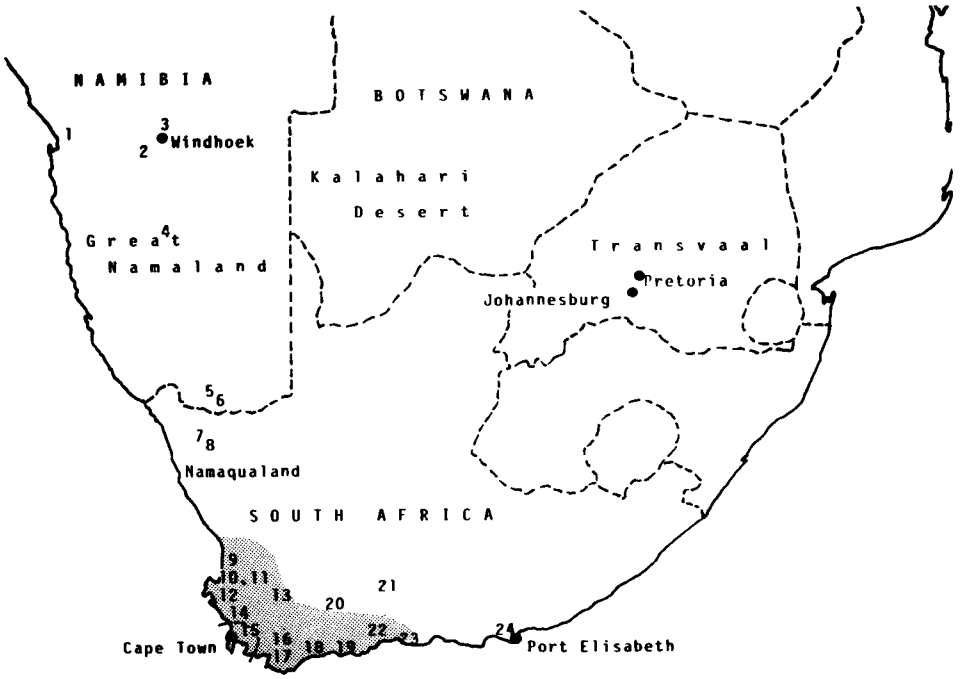

FIG. 1. — *Map of South Africa indicating the locations where bees have been collected (24 locations)*

Shaded area : Winter rain fall area and distribution region of *A.m. capensis* according to KERR and PORTUGAL-ARAUJO (1958).

Dotted line : Borderline of distribution area of *A.m. capensis* according to RUTTNER (1977).

RESULTS

The number of bees with large spermatheca was remarkebly low in our material. In only two samples were workers with *capensis* sized spermatheca (larger than 0.3 mm) found [60 % in Cape Town (15) ; 10 % in Stellenbosch (14)] (Fig. 2). The sizes of the spermathecae decreased rapidly when leaving the surroundings of Cape Town (Fig. 2). The average intra colonial variance in colonies in the « classical *capensis* area » is significantly larger than in the other colonies (Tab. 1 ; $F = 6.83$; $p \leq 0.01$). The spermatheca sizes measured in the « classical *capensis* area » (RUTTNER, 1977) were significantly smaller than the values obtained by RUTTNER (1977) seven years before our present study (Fig. 2. t-test : $t = 5.1$, $p \leq 0.01$).

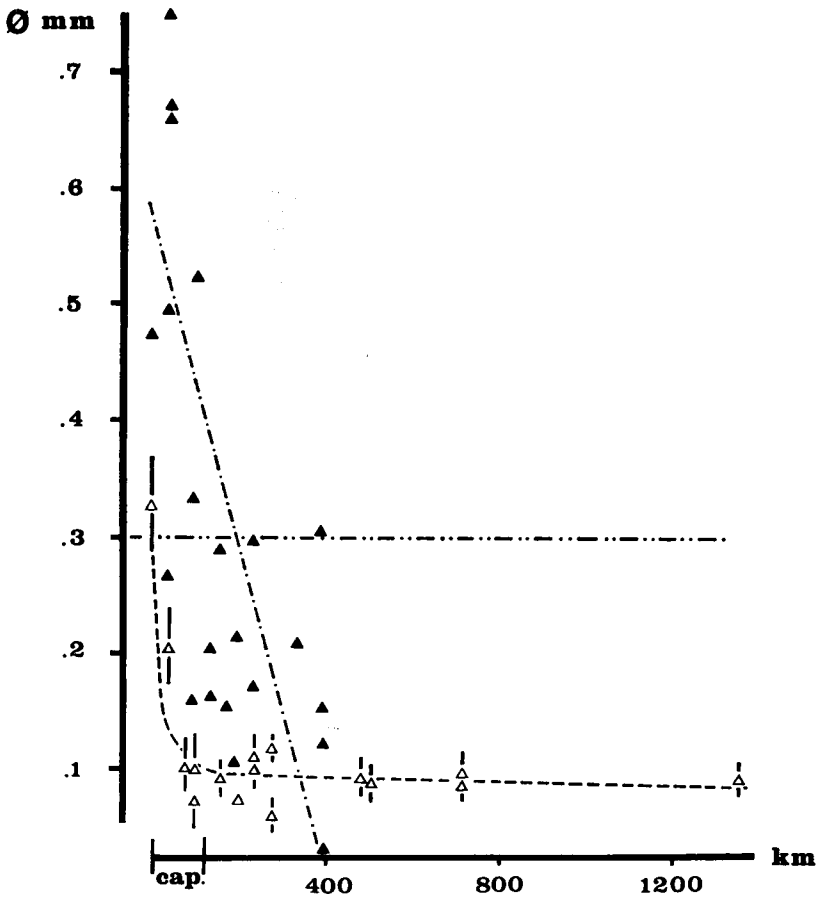

FIG. 2. — *The average size (diameter in mm) of the spermatheca (± S.D.) in worker bees (Y-axis) decreases rapidly with an increasing distance from Cape Town (in km ; X-axis) in our survey (open triangles, - - - - = regression curve)*

The intra colonial variance is significantly larger in samples close to Cape Town (« cap. »). RUTTNER (1977) found significantly larger spermatheca in this area seven years before our study (black triangles, — · — · = linear regression). « cap. » = distribution of classical *capensis* according to GUY, 1976 or RUTTNER, 1977. Horizontal line (· · — · · —) at 0.3 mm indicates the limit for *capensis* sized spermatheca.

TABL. 1. — *Variances between and within colonies for the measured characters*

Character	Between colonies			Between bees within colonies		
	Cape	South-west	F	Cape	South-west	F
Spermatheca	2.14	0.38	5.6*	0.41	0.06	6.8**
Tergite colour	1.14	0.21	5.4*	3.39	0.34	10.1**
Length of hair	0.82	0.2	4.1*	1.04	1.08	n.s.

« Cape » = Area with detectable cline for the according character (Hybrids). « South-west » = Area with no cline.

n.s. : not significant ; * : $p \leq 0.05$; ** : $p \leq 0.01$.

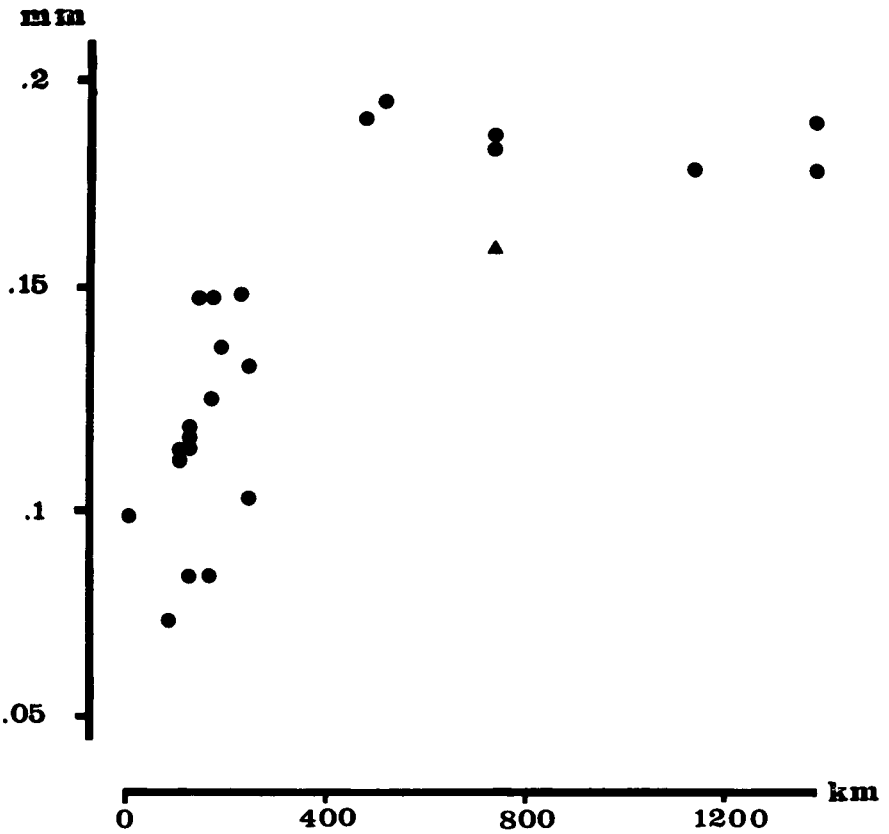

FIG. 3. — *The average length of the abdominal hairs (mm) at the fifth tergite (Y-axis) increases from south to north*

Samples from Port Elizabeth (triangle). X-axis : Distance from Cape Town in km.

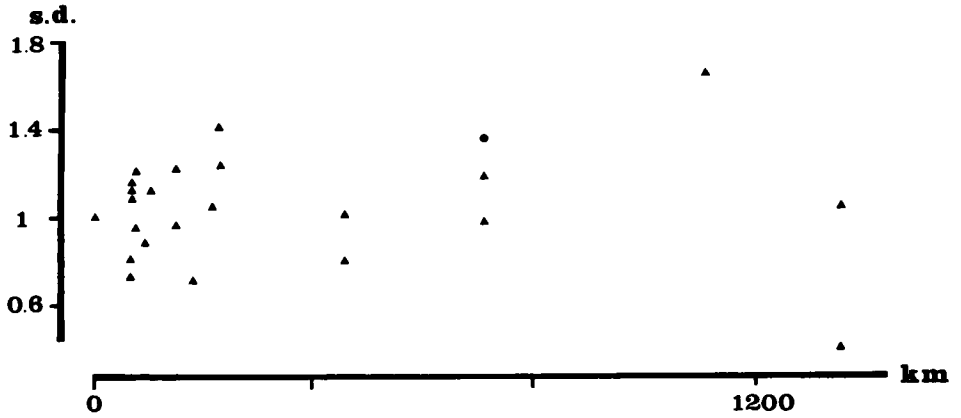

FIG. 4. — *The intra colonial variation (standard deviation) of the length of abdominal hairs at the fifth tergite (Y-axis) does not change significantly with the distance from Cape Town (X-axis in km)*

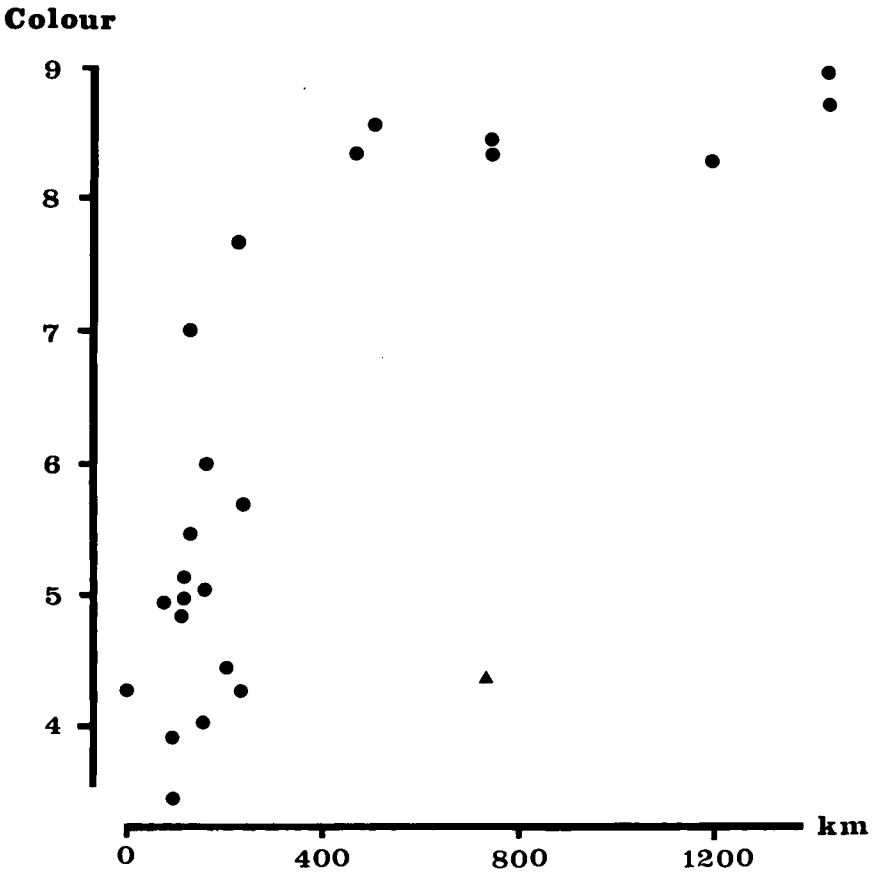

FIG. 5. — *The colour pattern of the second tergite (classes from 0 = black to 9 = bright yellow, Y-axis) changes from south to north.*

Bees in the north are almost completely yellow at the 2nd tergite. A sample from Port Elizabeth is marked with a triangle. X-axis : Distance from Cape Town in km.

The length of abdominal hairs at the 5th tergite shows a positive cline from south to north in an area from Cape Town to Clanwilliam (9). The colonies from Namaqualand and Namibia are rather uniform for this character (Fig. 3) and the variance between colonies is significantly smaller ($F = 4.1$, $p \leq 0.05$) than in the south. Honeybees from Port Elizabeth (24) are similar to those found close to Cape Town. Though there is a cline, there is no significant difference for the intra colonial variance of this character in our material (Fig. 4).

The colour of the second tergite also shows a positive cline from south to north (Fig. 5). Again the bees in the dry and arid areas north of Clanwilliam are very uniform (Fig. 6) whereas the inter colonial variance in the winter rain fall area is significantly larger ($F = 5.43$, $p \leq 0.05$). The intra colonial variance in this area is also significantly larger than in the northern regions ($F = 10.08$, $p \leq 0.01$). The samples from Port Elizabeth 680 km east of Cape Town have a high intra colonial variance and its values for the tergite colour are inbetween that of the Cape and Namibia.

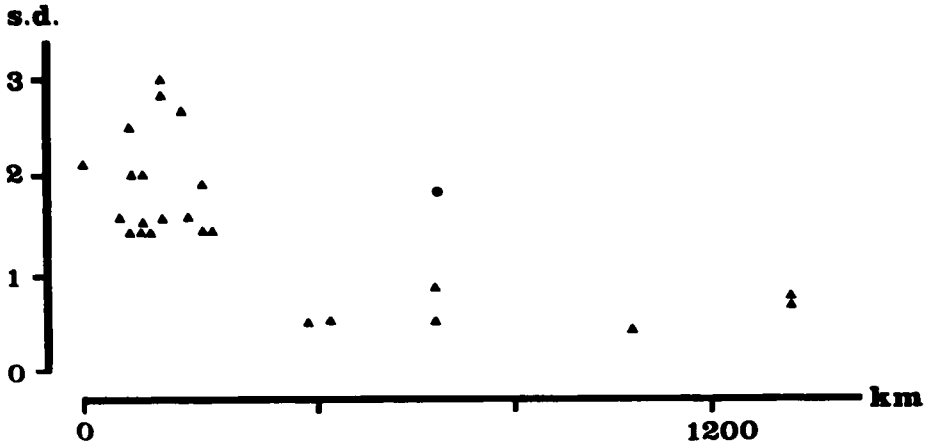

FIG. 6. — *The intra colonial variation (standard deviation) of the tergite colour (Y-axis) is significantly smaller in areas far north of the Cape*

Sample from Port Elizabeth is marked with a dot. X-axis : Distance from Cape Town in km.

DISCUSSION

There is considerably controversy over the actual distribution of the Cape honeybee. KERR and PORTUGAL-ARAUJO (1958) suggested that the winter rain fall area of southern Africa is the distribution zone of *capensis*. ANDERSON (1977) considers Lutzville and Prince Albert as forming a boundary line between the two races. TRIBE (1983) discusses the distribution of *Protea repens* as a biological indicator of the distribution of *A.m. capensis*.

In contrast to these reports, our results confirm the thesis of RUTTNER (1977) who states that the population of *capensis* is much smaller and in danger for extinction. In 1976 he could only find *capensis* [in the classical definition of ONIONS (1912, 1914)] in an area of about 50 km around Cape Town. In our analysis we could not find any discriminating line between *capensis* and *adansonii*. In contrast to RUTTNER's report (1977) however we could not find areas with « pure » *capensis* in our study seven years later. For all measured characters, a large variance was observed in the Cape area. The typical *capensis* spermathecae were especially variable in the area around Cape Town as well intra- as inter-colonial. Another typical *capensis* character, the tergite colour, varied widely. Colonies with exclusively black bees were found only occasionaly, and in general the workers of colonies in the Cape area showed a wide range of coloration. They were not as uniform as the bees form Namaqualand and Namibia which formed a clear definable population. This high variance and the steep cline in this region indicates that the *A.m. capensis* genome only excists in a hybrid zone with the adjacent race. This hybrid area may range from Clanwilliam and the Great Karoo in the north to at least Port Elizabeth in the east.

These results suggest that there is a constant migratory pressure of bees from the dry areas into the honeybee population of the winter rain fall area. In addition to natural migratory swarms, the effect of commercial migratory beekeeping may increase this pressure on the *capensis* population. Natural selection which kept a stable evolutionary balance between the two races may become less important as more artificial nesting sites become available. Well insulated bee hives may give *A.m. adansonii* swarms a chance to survive in the windy climate of the Cape (SCHULZE, 1974). The rough climate is very likely to be one of the major selective forces which favour thelytokous parthenogenesis of laying workers (MORITZ, 1984).

The lack of an area with pure *capensis* colonies strongly supports RUTTNER's (1977) thesis of the distribution of *A.m. capensis*. Our results show that this race is indeed very close to extinction, if not already extinct. The Cape honeybee seems to be highly important for pollination and for applied bee keeping in Southern Africa and needs to be protected. It is a well adapted race to the local flora and climate (TRIBE, 1983) and of large commercial interest because of its well known docileness (SMITH, 1961; RUTTNER, 1977). In an effort to preserve the Cape bee the, first promising steps have already been done by establishing *capensis* nature reserves at Cape Point and near Bredasdorp (CREWE, 1983). In order to prevent the extinction of this unique race on the long run, a selection program for pure *capensis* on one hand and a large scale sanctuary on the Cape peninsula as suggested by RUTTNER (1977) on the other may be feasable.

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RÉSUMÉ

HYBRIDATION D'*APIS MELLIFICA CAPENSIS* AVEC LES RACES D'ABEILLES LIMITROPHES

Deux races d'*Apis mellifica* ont été décrites pour la région d'Afrique du Sud : *A.m. capensis* et *A.m. adansonii*. RUTTNER (1981) a décrit une race propre à l'Afrique orientale, *A.m. scutellata*, qui doit être considérée comme une autre race sud-africaine. Jusqu'à présent la distinction entre *A.m. capensis* et les races limitrophes s'appuyait principalement sur la présence d'une spermathèque nettement visible (= 0,3 mm), d'un grand nombre d'ovarioles et d'une coloration foncée chez les abeilles *capensis* par rapport aux autres races africaines.

La région *capensis* décrite par RUTTNER (1977) (Cape Town et environs) a été récemment étudiée et on a utilisé des échantillons d'abeilles provenant de la région du nord-ouest (Namaqualand et Namibie) à titre de comparaison (Fig. 1). On a prélevé en 24 endroits des échantillons constitués chacun de 20 ouvrières et étudié divers caractères morphologiques ainsi que leur variabilité. Les 3 caractères suivants possèdent un bon pouvoir discriminant entre *A.m. capensis* et *A.m. adansonii* : 1) taille de la spermathèque, 2) pilosité du 5^{e} tergite et 3) couleur du 2^{e} tergite.

La taille de la spermathèque décroît au fur et à mesure que l'on s'éloigne de Cape Town (Fig. 2). Dans 2 échantillons seulement, on a trouvé une spermathèque supérieure à 0,3 mm (60 % à Cape Town, 10 % à Stellenbosch). L'analyse de variance (résultats dans le tableau 1) montre une faible variation de ce caractère à l'intérieur et entre les colonies du Namaqualand et de Namibie. Les variances dans la région du Cap sont significativement plus élevées.

La pilosité augmente lorsqu'on s'éloigne de Cape Town (Fig. 3). La variance de ce caractère aussi est plus faible entre les colonies du sud-ouest qu'entre celles de la région du Cap. La variance intra-colonie de ce caractère est relativement élevée dans toute la région étudiée et les différences ne sont pas significatives (Fig. 4).

De ces résultats nous concluons que la population *capensis* s'est encore plus réduite que ne l'indiquait RUTTNER (1977). Nous n'avons pas pu trouver de colonies « *capensis* » pures. Les caractères discriminants varient fortement dans la région du Cap, tandis que les échantillons provenant du sud-ouest ont une variabilité réduite et forment donc une population bien définie. Ceci montre qu'*A.m. capensis* n'existe plus aujourd'hui que dans une zone d'hybridation qui s'étend de Clanwilliam à l'ouest et de Karoo au nord jusqu'aux environs de Port Elizabeth à l'est. Nous soutenons par conséquent les efforts pour installer une grande réserve sur la péninsule du Cap et y développer un programme de sélection de *capensis*, afin de conserver cette race d'abeille, qui est importante aussi bien pour la science que pour l'apiculture locale (bonne adaptation à la flore et au climat et grande douceur).

ZUSAMMENFASSUNG

HYBRIDISIERUNG VON *APIS MELLIFERA CAPENSIS* MIT ANGRENZENDEN BIENENRASSEN

Zwei Rassen von *Apis mellifera* sind für die Region Südafrika beschrieben : *Apis mellifera capensis* und *Apis mellifera adansonii*. RUTTNER (1981) beschrieb für Ostafrika eine eigene Rasse, *Apis mellifera scutellata,* die folglich als weitere südafrikanische Rasse in Betracht gezogen werden müßte. Die Unterscheidung zwischen *A. m. capensis* und den angrenzenden Rassen fußte bislang besonders auf dem Vorhandensein einer deutliche sichtbaren Spermatheka ($\geq$ 0,3 mm), einer großen Zahl von Ovariolen und einer deutliche dunkleren Färbung von *capensis*-Bienen gegenüber den anderen afrikanischen Bienen.

Das von RUTTNER (1977) beschriebene *capensis*-Gebiet (Cape Town und Umgebung) wurde neu analysiert und zum Vergleich Bienenproben aus dem im Nordwesten anschließenden Gebiet (Namaqualand und Namibia) herangezogen (Fig. 1). Dazu wurden Proben (bestehend aus je 20 Arbeitsbienen) an 24 verschiedenen Orten gesammelt und verschiedene morphologische Merkmale und deren Variabilität untersucht. Drei Merkmale mit guten Diskriminierungseigenschaften zwischen Arbeiterinnen von *A.m. capensis* und *A.m. adansonii* waren : 1.) Spermatheka-Größe, 2.) Länge der Haare auf dem 5. Tergit und 3.) Farbe des 2. Tergits.

Die Spermatheka-Größe nimmt mit der Entfernung von Cape Town rapide ab (Fig. 2). Nur in zwei Proben wurden Spermatheken größer als 0,3 mm gefunden (bei Cape-Town 60 %, in Stellenbosch 10 %). Die Varianzanalyse (Ergebnisse in Tab. 1) ergab eine geringe Variation dieses Merkmals innerhalb und zwischen den Kolonien im Namaqualand und Namibia. Die Varianzen in der Kapregion waren signifikant größer.

Die Haarlänge nahm mit zunehmender Entfernung von Cape-Town zu (Fig. 3). Auch für dieses Merkmal war die Varianz zwischen den Völkern in Süd-West geringer als in der Kapregion. Die intrakoloniale Varianz dieses Merkmals war im gesamten Untersuchungsgebiet relativ groß und nicht signifikant voneinander verschieden (Fig. 4).

Die Farbe des 2. Tergits änderte sich von Süd (Kapregion) nach Nord (Namibia) ähnlich wie die Spermatheka-Größe. Die Bienen aus Namaqualand und Namibia sind einheitlich gelb (Fig. 5 ; 0 = dunkel, 9 = hell). Die Varianzanalyse zeigt, daß auch hier in der Kapregion große intra- und inter-koloniale Varianzen auftreten (Fig. 6).

Wir schließen aus unseren Ergebnissen, daß die *capensis* Population noch kleiner geworden ist als RUTTNER (1977) angab. Wir konnten keine « reinen » *capensis*-Völker mehr finden. Diskriminierende Merkmale variierten in der Kapregion stark, während die Proben aus dem Südwesten Afrikas wenig Variabilität zeigten und somit eine klar definierte Population bildeten. Dies zeigt, daß *A.m. capensis* heute nur noch in einer Hybridzone existiert, die sich von Clanwilliam (West) und der Karoo (Nord) bis in die Nähe von Port Elizabeth (Ost) erstreckt. Wir unterstützen daher Bestrebungen, ein großflächiges Schutzgebiet auf der Kap-Halbinsel einzurichten und dort ein gezieltes *capensis* Zuchtprogramm durchzuführen, um diese für die Wissenschaft und die lokale Bienenwirtschaft (gute Anpassung an Flora und Klima große Sanftmut) wichtige Bienenrasse zu erhalten.

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