

Multivariate morphometric analysis of honeybees (*Apis mellifera*) in the Ethiopian region

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Abstract – Honeybees sampled from 285 colonies at 57 localities were morphometrically analysed. The multivariate analysis established five statistically separable morphoclusters occupying ecologically different areas: *Apis mellifera jemenitica* in the northwest and eastern arid and semi-arid lowlands; *A. m. scutellata* in the west, south and southwest humid midlands; *A. m. bandasii*, in the central moist highlands; *A. m. monticola* from the northern mountainous highlands; and *A.m.woyi-gambell* in south western semi-arid to sub-humid lowland parts of the country. Moreover some areas with high inter and intracolony variances were noted, suggesting introgression among these defined honeybee populations.

Apis mellifera / morphometry / race / introgression / Ethiopia

1. INTRODUCTION

Ethiopia is physiographically and climatologically diverse, varying from arid, lowland plains to moist Afroalpine conditions (Van Chi-Bonnardel, 1973; Mammo, 1976). This complexity is reflected in a considerably diverse flora and fauna, including honeybees. In the early days of classification of the honeybees of Africa, Smith (1961) reported *A. m. monticola* from the Ethiopian plateaus and later, Ruttner (1975) the presence of *A. m. scutellata* and *A. m. jemenitica*. More recently Radloff and Hepburn (1997a) recorded *A. m. jemenitica*, *A. m. bandasii* and *A. m. sudanensis* from Ethiopia.

However, these findings are conflicting so that the picture of honeybee populations of the country remains blurred. In addition, pheromone analyses of the honeybee populations showed those of Ethiopia to differ from the rest of Africa (Radloff and Hepburn, 1997b). Moreover, microsatellite and mitochondrial DNA

analyses established that the greatest genetic diversity in Africa actually occurs in the honeybees of Ethiopia (Franck et al., 2000), which constitute a 5th lineage of *A. mellifera*.

Thus, to refine our understanding of the honeybee populations of Ethiopia, a more detailed study, geographically broader in scope and with a finer sampling distance resolution, was undertaken to determine the occurrence of morphoclusters, their biogeography, the magnitude of differences between the populations and their ecological distributions and where possible to resolve conflicts in the literature.

2. MATERIALS AND METHODS

2.1. Sampling and measurement

285 honeybee samples of 20 worker honeybees per colony were collected from each of five traditional hives at 57 localities with an average interlocality distance of 100 km (Fig. 1, Tab. I).

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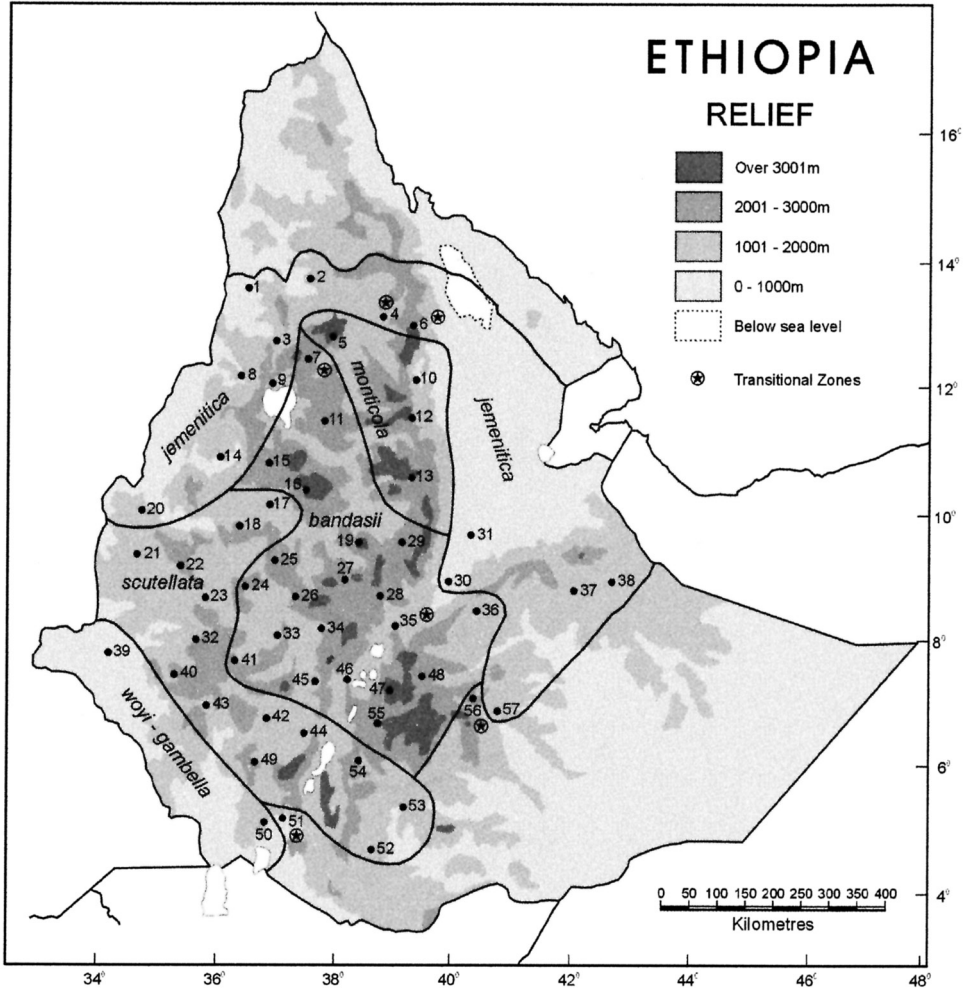


Figure 1. Physiography, sampling localities and distribution of five morphoclusters of honeybees in Ethiopia. Names of localities are given in Table I.

2.2. Morphometric analysis

Even though Ruttner (1988) used 36 morphometric characters in the discrimination of world honeybee groups, Crewe et al. (1994), Radloff and Hepburn (1997a,b) and Hepburn and Radloff (1998) successfully classified the honeybees of Africa using 9–11 morphometric characters. In the present study due to larger variations in size and pigmentation in the honeybee populations of Ethiopia (Radloff and Hepburn, 1997a) four more (2 related to size and 2 to pigmentation) morphological characters were included. Thus thirteen morphometric characters were measured and are designated by their Ruttner (1988) numbers. These include four categories of characters: hair, pigmentation, size,

and forewing venation angles: length of hair on abdominal tergite 5 (1), pigmentation of scutellum (35), pigmentation of scutellar plate (36), pigmentation of abdominal tergite 2 (32), pigmentation of abdominal tergite 3 (33), pigmentation of abdominal tergite 4 (34), tergite 3 longitudinal (9), tergite 4 longitudinal (10), sternite 3 longitudinal (11), transverse of wax plate on sternite 3 (13), wing angle B4 (22), wing angle N23 (30) and wing angle O26 (31).

2.3. Multivariate analyses

A principal components analysis using colony mean data was used to detect the presence of possible clusters of colonies among the scatter scores from a

Table I. Localities, altitudes and coordinates of study areas in Ethiopia.

1. Humera 600 m, 14.17N, 36.36E;	30. Melka Sedi 770 m, 9.15N, 40.07E;
2. Shiraro 1100 m, 14.19N, 37.43E;	31. Gewane 587 m, 9.58N, 40.32E;
3. Angereb 910 m, 13.13N, 37.08E;	32. Gechi 1516 m, 8.21N, 35.51E;
4. Abi Adi 1800 m, 13.37N, 38.59E;	33. Boter Bacho 2958 m, 8.21N, 37.16E;
5. Debark 3000 m, 13.23N, 39.30E;	34. Roge 2194 m, 8.30N, 37.59E;
6. Mekele 2025 m, 13.31N, 39.30E;	35. Nazrieth 1699 m, 8.32N, 39.17E;
7. Dabat 2656 m, 12.59N, 37.43E;	36. Boke Tiko 1575 m, 8.43N, 40.38E;
8. Wohni 1000 m, 12.39N, 36.41E;	37. Deriri Arba 1450 m, 9.79N, 42.23E;
9. Aykel 2230 m, 12.32N, 37.03E;	38. Dudi Affi 1559 m, 9.12N, 42.57E;
10. Korem 2600 m, 12.34N, 39.32E;	39. Itang 456 m, 8.11N, 34.16E;
11. Debre Tabor 2450 m, 11.54N, 37.57E;	40. Masha 2110 m, 7.46N, 35.28E;
12. Woldeya 2400 m, 11.53N, 39.26E;	41. Effo Yachi 1877 m, 7.57N, 36.30E;
13. Gugufu 3600 m, 10.55N, 39.27E;	42. Waka 1719 m, 7.44N, 37.11E;
14. Manbuk 1230 m, 11.17N, 36.14E;	43. Woshi 1750 m, 7.19N, 36.12E;
15. Dangla 2060 m, 11.12N, 36.51E;	44. Sodo 1759 m, 6.49N, 37.43E;
16. Feres Bet 3000 m, 10.46N, 37.38E;	45. Hosaina 2276 m, 7.33N, 37.53E;
17. Bir Sheleko 1545 m, 10.33N, 37.10E;	46. Alage 1830 m, 7.36N, 38.24E;
18. Hinde 2195 m, 10.08N, 36.27E;	47. Mararo 2869 m, 7.24N, 39.14E;
19. Salayish 2248 m, 9.50N, 38.54E;	48. Gado Lama 2121 m, 7.40N, 39.46E;
20. Menge 1000 m, 10.22N, 34.45E;	49. Sawla 2087 m, 6.18N, 36.52E;
21. Bambis 1460 m, 9.44N, 34.43E;	50. Woyito 921 m, 5.16N, 37.33E;
22. Nejo 1890 m, 9.30N, 35.29E;	51. Konso 1436 m, 5.20N, 37.25E;
23. Dedessa 1320 m, 9.01N, 36.01E;	52. Arero 1483 m, 4.49N, 38.52E;
24. Nekemte 2166 m, 9.05N, 36.33E;	53. Har Kalo 1427 m, 5.33N, 39.23E;
25. Shambu 2570 m, 9.00N, 37.27E;	54. Eshido Aliyo 2158 m, 6.17N, 38.39E;
26. Gedo 2517 m, 9.00N, 37.27E;	55. Serofta 2377 m, 6.51N, 39.15E;
27. Inchini 2650 m, 9.20N, 38.21E;	56. Woltae Atote 2051 m, 7.15N, 40.34E;
28. Sendafa 2500 m, 9.04N, 38.54E;	57. Karre Tule 1194 m, 7.34N, 41.45E.
29. Deneba 2670 m, 9.47N, 39.12E;	

plotted plane graph of the first two high loading factors. Stepwise discriminant analysis using the principal components clusters was carried out to determine the most discriminatory variables to enter into the discriminant functions. The discriminant functions were used to classify the colonies and to determine the percentages of correctly classified colonies and the highest posterior probability of each colony being in any cluster was computed. Wilks' lambda statistic was used to test for significant differences in the cluster vector of means of each character used in the discriminant function (Johnson and Wichern, 1998). Mahalanobis distances between each cluster group were determined (Cornuet, 1982).

Intra and intercolonial variances were computed based on factor analysis procedures, using the first unrotated factor scores of each bee and colony means for each morphometric character, respectively. The homogeneity of the intercolonial and intracolonial variances at each locality was tested using Levene's F-statistic. Correlation analysis was also carried out

to determine correlations within morphometric characters and with environmental factors (altitude, rainfall and temperature). The Bonferroni adjustment to the level of significance was used to ensure that the overall level of significance did not exceed 0.05.

3. RESULTS

In a principal components analysis using colony means of 13 morphometric characters of 5700 worker honeybees comprising 74 100 measurements from 285 colonies at 57 localities, four factors with eigenvalues greater than one were extracted: factor 1 includes length of hairs on the fifth abdominal tergite (1), width of abdominal tergite 3 (9), width of tergite 4 (10), sternite 3 longitudinal (11), and transverse of wax plate on

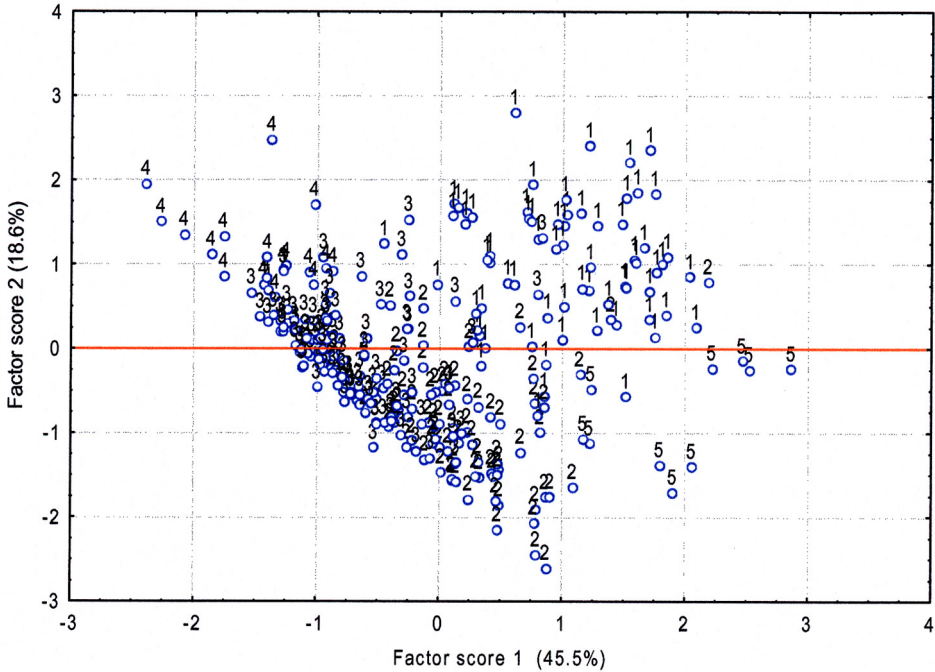


Figure 2. Factor analysis plot using the colony means of the morphological characters. Numbers represent the five statistically separable morphoclusters.

sternite 3 (13); factor 2 comprises pigmentation of scutellum (35), pigmentation of tergite 2 (32), pigmentation of tergite 3 (33) and pigmentation of tergite 4 (34); factor 3 includes forewing venation angle N23 (23) and O26 (31) and factor 4 includes angle B4 (22) and pigmentation of scutellar plate (36). These factors accounted for 82.1% of the total variance in the data. Factor 1, which is entirely associated with body size, and factor 2, which is associated with pigmentation accounted for 45.5% and 18.6% of the total variance in the data respectively.

The factor loadings of each of the characters had absolute values greater than 0.68. The scatter plot was obtained using factor 1 and factor 2, which had high eigenvalues and revealed the formation of 5 statistically separable but not distinct morphoclusters (Fig. 2). Honeybee colonies from localities Nos. 1-3, 8-9, 14, 20, 30-31, 37-38, 57 (Figs. 1 and 2) formed group 1 in the upper right-hand quadrant of the plot. Colonies from localities Nos. 17-18, 21-23, 32, 40, 42-44, 49, 52-54 formed

group 2 in the lower mid-quadrant of the plot (Figs. 1 and 2).

Colonies from localities Nos. 11, 15-16, 19, 24-29, 33-34, 36, 41, 45-48, 55 formed group 3 in the left mid-quadrant plot (Figs. 1 and 2). Colonies from localities Nos. 5, 10, 12, 13 formed group 4 in the upper left-hand quadrant of the plot (Figs. 1 and 2) and colonies from localities Nos. 39 and 50 formed group 5 in the lower right-hand quadrant (Figs. 1 and 2). Thirty colonies from localities Nos. 4, 6-7, 35, 51, and 56 were spread among the other groups (Figs. 1 and 2).

In the stepwise discriminant analysis all the 3 forewing venation angles and pigmentation of tergite 3 morphometric characters did not enter the discriminant functions due to lack of discriminatory power in these characters for the discrimination of honeybees of the Ethiopian region. The nine morphometric characters that entered into the linear discriminant functions in order of their discriminatory power are given in Table II. About 91% of the colonies were correctly classified into 5 groups (Tab. III). The

Table II. Morphometrical characters entered into the discriminant functions ranked according to their discriminatory power.

Characters entered	F-statistic	df	P-values
Pigmentation tergite 2 (32)	273.54	4, 250	< 0.00001
Width of tergite 3 (9)	108.22	4, 249	< 0.00001
Sternite 3 long (11)	11.86	4, 248	< 0.00001
Width of tergite 4 (10)	6.75	4, 247	0.00004
Pigmentation plate (36)	6.65	4, 246	0.00003
Width of wax plate (13)	3.63	4, 245	0.00680
Pigmentation scutellum (35)	2.88	4, 244	0.02331
Pigmentation tergite 4 (34)	2.32	4, 243	0.05759
Hair length (1)	2.16	4, 242	0.07412

Table III. Classification matrix and Mahalanobis distances (D^2) between Ethiopian honeybee groups.

Groups	Percent of correct classification	Group 1		Group 2		Group 3		Group 4		Group 5	
		$P = 0.2352$	D^2	$P = 0.2745$	D^2	$P = 0.3726$	D^2	$P = 0.0784$	D^2	$P = 0.0392$	D^2
1	93.33	56	0.00	3	20.83	0	30.11	0	44.30	1	15.33
2	85.71	1		60	0.00	9	8.03	0	27.84	0	28.20
3	93.68	2		4		89	0.00	0	8.39	0	51.82
4	85.00	0		0		3		17	0.00	0	84.74
5	100.00	0		0		0		0		10	0.00
Total	90.98	59		67		101		17		11	

Mahalanobis distances between the groups varied from $D^2 = 8.03$ for group 2 and group 3 to $D^2 = 84.74$ for group 4 and group 5 (Tab. III). The linear discriminant functions classified 93.33% of colonies from localities 1-3, 8-9, 14, 20, 31-32, 37-38 and 57 (Fig. 2) correctly into group 1 with posterior probabilities, $P = 0.82$ – 1.00 for 52 colonies and $P = 0.55$ – 0.77 for 4 colonies while 4 colonies were misclassified. 85.71% of the colonies from localities 17-18, 21-23, 32, 40, 42-44, 49, and 52-54 (Fig. 2) were correctly classified in group 2 with posterior probabilities, $P = 0.80$ – 1.00 for 54 colonies and $P = 0.55$ – 0.78 for 6 colonies while 10 colonies were misclassified. 93.68% of colonies from localities 11, 15-16, 19, 24-29, 33-34, 36, 41, 45-48, and 55 (Fig. 2) were correctly classified in group 3 with posterior probabilities, $P = 0.80$ – 1.00 for 77 colonies and $P = 0.52$ – 0.79 for 12 colonies while 6 colonies were misclassified. 85% of colonies from localities 5, 10, and 12 (Fig. 2) were correctly classified in group 4 with posterior probabilities, $P = 0.83$ – 1.00 for 14 colonies and $P =$

0.63 – 0.76 for 3 colonies while 3 colonies were misclassified. All the colonies from localities 39 and 50 (Fig. 2) were correctly classified in group 5 with posterior probabilities, $P = 0.83$ – 1.00 for 8 colonies and $P = 0.46$ – 0.64 for 2 colonies.

Wilks' lambda value approximated by the F-statistic ($\Lambda = 0.04$, $F(36,908) = 34.84$, $P < 0.00001$) indicated that there was a highly significant difference among the means of morphometric characters for the 5 groups entered into the discriminant functions. The group means and standard deviations of the morphometric characters are given in Table IV.

To test for the homogeneity of the variances, the first principal components coefficients of the morphometric characters were used to determine the factor scores of colonies at each locality and the variances of these scores were tested for homogeneity of inter-colonial variances at each locality. Accordingly, significant differences were found (Levene's test $F(56, 228) = 1.87$, $P = 0.0007$). Similarly,

Table IV. The means and standard deviations (SD) of discriminant morphometric characters (n is the number of colonies).

Characters	Group 1 n = 60		Group 2 n = 70		Group 3 n = 95		Group 4 n = 20		Group 5 n = 10	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Scutellum (35)	4.39	1.93	0.71	0.71	0.41	0.76	0.73	0.58	4.22	2.11
Plate (36)	1.04	1.19	0.81	0.68	0.39	0.53	0.63	0.81	0.04	0.07
Hair (1)	0.17	0.02	0.18	0.02	0.21	0.02	0.23	0.03	0.13	0.01
Tergite 2 (32)	6.88	1.70	1.12	1.06	0.47	1.17	0.74	1.04	6.44	1.96
Tergite 3 (33)	6.78	1.66	1.44	1.08	0.62	1.22	0.77	1.10	6.43	2.00
Tergite 4 (34)	5.38	1.78	1.12	0.97	0.43	0.84	0.46	0.73	4.95	1.70
Width tergite 3 (9)	2.02	0.04	2.00	0.04	2.10	0.04	2.17	0.04	1.92	0.05
Width tergite 4 (10)	1.97	0.05	1.94	0.04	2.03	0.04	2.12	0.04	1.84	0.05
Sternite 3 (11)	2.48	0.06	2.47	0.06	2.58	0.05	2.70	0.03	2.35	0.04
Sternite 3 (13)	2.05	0.06	2.04	0.06	2.13	0.06	2.23	0.06	1.93	0.05
Angle B4 (22)	104.90	3.33	104.30	2.99	104.70	3.10	105.20	2.30	104.50	4.46
Angle N23 (30)	89.11	2.23	88.82	2.23	88.48	2.45	90.35	2.31	86.97	1.21
Angle O26 (31)	37.07	1.96	37.87	1.71	37.29	1.69	37.72	1.66	38.17	1.43

the intracolony variances were determined using the individual honeybee values and significant differences among the localities were found ($F(56, 5643) = 29.82, P < 0.0001$). These results revealed that the intra and inter-colony variances obtained from localities 3-4, 6-7, 9, 14-15, 30, 35, 38-39, 46, 48-49, 51 and 56-57 (Fig. 1) were significantly higher than the other localities, suggesting that these localities are transitional zones between the morphoclusters.

Morphometric characters associated with pigmentation were positively significantly correlated to each other ($0.50 < r < 0.99, P < 0.001$) and weakly negatively correlated to those of body size ($-0.30 < r < -0.47, P < 0.01$). Strong positive correlations were found among the morphometric characters associated with body size ($0.78 < r < 0.99, P < 0.001$). However, forewing venation angles showed no strong correlation among themselves or to either body size or pigmentation ($-0.06 < r < 0.33, P > 0.05$).

All pigmentation characters were positively significantly correlated to temperature ($0.24 < r < 0.71, P < 0.001$) (except the scutellar plate), and all were negatively significantly correlated to both altitude ($-0.21 < r < -0.71, P < 0.001$) and rainfall ($-0.51 < r < -0.56,$

$P < 0.001$). Moreover, morphometric characters related to body size and hair length were significantly negatively correlated to temperature and significantly positively correlated to altitude ($-0.49 < r < -0.56$ and $0.35 < r < 0.66, P < 0.001$ respectively, the Bonferroni adjustment to level of $\alpha = 0.05/3 = 0.0166$ used).

Data on the climatological and physio-graphical regions of the morphoclusters are shown in Table V and Figure 1. The morphocluster 1 region consists predominantly of tropical woodland and thorny bush and semi-desert steppe vegetation below 2000 m with annual temperatures between 20 °C–25 °C and rainfall between 400 mm–1000 mm. Grasslands and forest are predominant in the morphocluster 2 area situated between 1000 m–2000 m with a temperature range of 18 °C to 20 °C and an annual rainfall of 1400 mm to 2300 mm. The areas of morphoclusters 3 and 4 both consist mainly of grassland vegetation between 1000 m and 3000 m with an annual temperature range of 16 °C to 18 °C. Small areas 6% and 14% respectively of both morphoclusters occur above 3000 m. The vegetation in the area of morphocluster 5 comprises tropical woodland and thorny bush, grassland and savannah, two-thirds of which is below 1000 m and one-third between 1000 m and

Table V. Climatological, vegetation and physiographical regions of the five morphoclusters of Ethiopian honeybees*.

Climatological / Physiography	Cluster 1 <i>jemenitica</i>		Cluster 2 <i>scutellata</i>		Cluster 3 <i>bandasii</i>		Cluster 4 <i>monticola</i>		Cluster 5 <i>woyi-gambella</i>	
	km ²	%	km ²	%	km ²	%	km ²	%	km ²	%
1. Vegetation										
Tropical wood land and thorny bush	147301	47.1	31187	18.7	164319	7.5	2109	4.1	32686	49.6
Grass land	64139	20.5	93880	56.2	177396	80.7	41601	80.3	18230	27.7
Savannah	5882	1.9	4076	2.4					14969	22.7
Semi desert steppe	955552	30.5								
Forest land			37903	22.7	17179	7.8				
Altimontane scrub steppe					8952	4.1	8116	15.7		
2. Altitude (m)										
< 1000	142014	45.4							43649	66.3
1000–2000	152526	48.8	141421	84.7	101423	46.1	26390	50.9	22236	33.8
2000–3000	18335	5.9	25625	15.3	106064	48.2	17958	34.7		
3000–4000					12472	5.7	7479	14.4		
3. Temperature (°C)										
16–18					219958	100.0	51826	100		
18–20	73181	23.4	167045	100					21960	33.3
20–25	148209	47.4							33470	50.8
25–30	914856	29.2							10456	15.9
4. Rainfall (mm)										
100–400	90640	29.0								
400–1000	199020	63.6								
600–900							23887	46.1		
600–1000			31304	18.7					17690	26.9
700–1300					102545	46.6				
1000–1300	23215	7.4	22785	13.6					39702	60.3
1000–1500							27940	53.9		
1400–1700					177414	53.4				
1400–1800									8493	13.0
1400–2300			112956	67.6						

Climatological and physiographic data compiled from Mesfin (1970).

2000 m. Here the annual temperature and rainfall range from 18 °C–25 °C and 600 mm–1800 mm respectively.

4. DISCUSSION

Multivariate morphometric analyses of Ethiopian honeybees demonstrated a high

degree of variability in size and pigmentation. Mixed black and yellow bees in a single colony and predominantly black or yellow colonies occur in the same localities. Generally Ethiopian honeybees are darker than those of neighbouring Sudan, Somalia and Kenya. Such variability both in colour and size in Ethiopian honeybees (Hepburn and Radloff, 1998; Radloff and Hepburn, 1997a) and in

Table VI. Mahalanobis distances (D^2) between five Ethiopian honeybee groups and previously designated *A. m. jemenitica*, *A. m. scutellata*, *A. m. bandasii*, and *A. m. monticola* subspecies*.

Groups	<i>A. m. jemenitica</i>	<i>A. m. scutellata</i>	<i>A. m. bandasii</i>	<i>A. m. monticola</i>
1	5.83	8.16	24.99	16.97
2	18.37	12.91	13.12	16.73
3	19.05	13.84	2.92	16.69
4	27.20	23.85	3.85	26.73
5	19.39	25.59	45.95	37.19

* Data from Ruttner/Oberursel (Ruttner, 1988) and Radloff and Hepburn (1997a, b) databases.

Sudanese honeybees (Rashad and El-Sarrag, 1978, 1980; Mohamed, 1982; Saeed, 1981; Mogga, 1988; El-Sarrag et al., 1992) has been noted previously. The morphometric characters associated with size and pigmentation were significantly positively and negatively correlated to altitude respectively. There is a gradual increase in size and change in pigmentation from yellow to black with increasing altitude (Tab. V); thus, the highland honeybees are larger and darker than the lowland ones. These results also confirm the findings of Radloff and Hepburn (1997a).

Principal components analysis of honeybees from 285 colonies from 57 localities in Ethiopia revealed the existence of 5 statistically separable morphometric groups. Honeybees from the eastern and northwestern parts of the country (morphocluster 1) were light in colour, relatively small and with short hairs, characteristics very similar to *A. m. jemenitica* Ruttner, of the semi-desert parts of Sudan, Somalia and northwestern Ethiopia (Mogga, 1988; Ruttner, 1988; Radloff and Hepburn, 1997a; Hepburn and Radloff, 1998). The mean values of the morphometric characters [(1), (11), (13) and (22)] fell within the range of the mean values of *A. m. jemenitica* previously recorded by Ruttner (1988) and Radloff and Hepburn (1997a, b). The shortest Mahalanobis distance was found between morphocluster 1 and *A. m. jemenitica* (Tab. VI, $D^2 = 5.83$). Group 1 bees occupy arid and semi-arid areas with high temperatures and low precipitation (Tab. V), which are ecologically similar to those of *A. m. jemenitica*. Hence, on the grounds of morphometric and ecological similarity these bees are classified as *A. m. jemenitica*. This is in agreement with the results of Radloff and Hepburn (1997a).

Morphometrically the honeybees from southern and western, wet tropical areas of the country (morphocluster 2), closely match *A. m. scutellata* Lapeletier of east Africa (Hepburn and Radloff, 1998; Radloff and Hepburn, 1997a; Ruttner, 1988). The mean values of the morphometric characters [(1), (11), (13), (22), (31), (35) and (36)] fell within the range of the mean values of *A. m. scutellata* previously recorded by Hepburn and Radloff (1998) and Radloff and Hepburn (1997a). The shortest Mahalanobis distance was found between morphocluster 2 and *A. m. scutellata* (Tab. VI, $D^2 = 12.91$). In east Africa, *A. m. scutellata* occurs at 500 m–2400 m, in rich savannah and semi-evergreen deciduous forest (Smith, 1961), which corresponds to the area of morphocluster 2 in Ethiopia (Tab. V). As a result of morphometric and ecological similarity, morphocluster 2 is classified as *A. m. scutellata*. Radloff and Hepburn (1997a) initially regarded these honeybees as *A. m. sudanensis*, but subsequently suggested they could actually be *A. m. scutellata* (Hepburn and Radloff, 1998) and this now resolves this difference.

Morphocluster 3 honeybees occur in the central, moist grasslands of the highlands (Tab. V). The mean values of the morphometric characters of this group [(1), (11), (13) and (22)] are very close to those of *A. m. bandasii* (Radloff and Hepburn, 1997a). The shortest Mahalanobis distance was found between morphocluster 3 and *A. m. bandasii* (Tab. VI, $D^2 = 2.92$). Moreover these honeybees are morphometrically intermediate between *A. m. scutellata* and *A. m. monticola* Smith. But, the principal components analysis clearly showed that they are a statistically separable group, the morphometric values for which closely resemble *A. m. bandasii* (Radloff and Hepburn,

1997a; Mogga, 1988). Hence, this morphocluster is classified as *A. m. bandasii*. This concurred with the results of Radloff and Hepburn (1997a).

Honeybees from the mountainous regions of northern Ethiopia (morphocluster 4) were found similar to others of the east African mountains; the bees are long-haired and larger than those of all other morphoclusters. The mean values of the morphometric characters of morphocluster 4 bees [(1), (11) and (13)] correspond with those of *A. m. monticola* (Hepburn and Radloff, 1998; Ruttner, 1988). These bees are, however, darker than those of the east African mountains. This pigmentation difference resulted in a large Mahalanobis distance between morphocluster 4 and *A. m. monticola* (Tab. VI, $D^2 = 37.19$). Ecologically this group occupies cool, high altitude areas (Tab. V) (2400 m–3600 m), very similar to those of Kenya and Tanzania from where *A. m. monticola* was first described (Smith, 1961). Based on morphometric and ecological similarities, this group is classified as *A. m. monticola* or “monticola-like” as reported by Hepburn and Radloff (1998).

In the western and southern semi-arid to sub-moist lowlands of Ethiopia, a very small honeybee group was detected (morphocluster 5), whose body size characteristics do not match any of the other African honeybees. It is distributed below the area of *A. m. scutellata* in the southwest of Ethiopia. Even though these bees are slightly closer in colour to *A. m. jemenitica*, they are smaller. The shortest Mahalanobis distance was found between morphocluster 5 and *A. m. jemenitica* (Tab. VI, $D^2 = 19.39$). Hence, the morphocluster is given the name *A. m. woyi-gambella*. This name derived from a contraction of two localities Woyito and Gambella (Itang) as is customary in the Amaharic language.

High intra and intercolonial variances were observed in all of the honeybee groups, and in the areas of transition between the ecological zones of the groups. Honeybee colonies from Nazrieth, Konso, Mekele, Woltae Atote, Abi Adi and Dabat showed high variances and were distributed among all the morphoclusters, indicating probable introgression among statistically defined honeybee groups. This could be attributed principally to swarming and migration (Nuru et al., unpublished data), purchase of colonies and transhumance, which

may greatly affect gene flow among the honeybee groups.

Résumé – Analyse morphométrique multivariée des abeilles de la région éthiopienne. L'Éthiopie, région complexe du point de vue de la physiogéographie et de la climatologie, renferme une flore et une faune extrêmement diverse, y compris en ce qui concerne les abeilles *Apis mellifera*. Il y a bien eu des tentatives de classification des abeilles d'Éthiopie mais les résultats étaient contradictoires et décousus, donnant une image confuse.

Pour déterminer les groupes morphologiques (« morphoclusters »), leur biogéographie, leur répartition écologique et l'étendue des différences entre les populations et pour résoudre les conflits de la littérature, 285 échantillons d'abeilles de 20 ouvrières ont été prélevés dans 57 localités à raison de 5 ruches paniers traditionnelles par localité (Fig. 1, Tab. I). La distance moyenne entre localités était de 100 km. Treize caractères morphométriques (5 relatifs à la taille y compris la pilosité, 5 à la pigmentation et 3 angles de la véneration de l'aile antérieure) ont été analysés à l'aide des méthodes multivariées.

Dans l'analyse en composantes principales qui a porté sur les moyennes par colonie des 13 caractères morphométriques des 5700 ouvrières, 4 facteurs ayant une valeur propre >1 ont été extraits : le facteur 1 comprend les caractères morphométriques liés à la taille corporelle, le facteur 2 les caractères liés à la pigmentation, le facteur 3 les angles de véneration alaire et le facteur 4 l'angle B4 et la pigmentation du scutellum. Ces facteurs rendent compte d'environ 82,1 % de la variation des données, parmi lesquels 64,1 % sont dus à la variance de la taille corporelle (facteur 1) et de la pigmentation (facteur 2). Sur les 13 caractères morphométriques utilisés pour discriminer les abeilles d'Éthiopie, seuls 9 d'entre eux ont été entrés dans les fonctions discriminantes ; les 3 angles de la véneration de l'aile antérieure et la pigmentation du tergite 3 ne l'ont pas été en raison de leur manque de pouvoir discriminatif (Tab. II).

L'analyse en composantes principales et l'analyse discriminante pas à pas ont déterminé 5 morphoclusters statistiquement séparables et occupant des axes différents du point de vue écologique : *A. mellifera jemenitica* dans les basses plaines arides et semi-arides du nord-ouest et de l'est ; *A. m. scutellata* dans les plaines centrales humides de l'ouest, du sud et du sud-ouest ; *A. m. bandasii*, dans les montagnes humides du centre ; *A. m. monticola* dans les montagnes du nord et *A. m. « woyi-gambella »* dans les parties basses semi-arides à sub-humides du sud-ouest du pays (Fig. 1 ; Tab. V).

Environ 91 % des colonies ont été classées correctement dans les 5 morphoclusters (Tab. III). En raison de variances inter-colonies élevées, les colonies des localités n° 4, 6, 7, 35, 51 et 56 (Fig. 1) se sont réparties entre les différents morphoclusters. Dans certaines régions des morphoclusters, on a

également noté de fortes variances intra-colonies, suggérant des régions d'introgession entre les morphoclusters.

Les caractères morphométriques associés à la pigmentation ont montré des corrélations fortement positives entre eux et faiblement négatives avec les caractères liés à la taille corporelle. Ceux-ci avaient entre eux des corrélations fortement positives, tandis que les angles de vénation alaire n'ont montré de fortes corrélations positives ni entre eux ni avec les autres caractères. Tous les caractères de pigmentation, sauf pour le scutellum, étaient significativement corrélés de façon positive aux températures et de façon négative à l'altitude et aux précipitations. En outre, les caractères liés à la taille corporelle et à la pilosité étaient négativement corrélés à la température et positivement à l'altitude.

Apis mellifera / morphométrie / race / introgession / Éthiopie

Zusammenfassung – Multivariate morphometrische Analyse von Honigbienen aus der Region Äthiopien. Äthiopien weist eine große physiographische und klimatische Vielfalt auf und beherbergt eine diverse Flora und Fauna, darunter Honigbienen. Es gab zwar einige Ansätze zur Klassifikation der Honigbienen von Äthiopien, die Ergebnisse waren aber widersprüchlich und Zusammenhangslos und ergaben nur ein unscharfes Bild der äthiopischen Bienen.

Um die Morphocluster und ihre Biogeographie, ihre ökologische Verbreitung und die Stärke der Unterschiede zu erfassen sowie die Widersprüche in der Literatur zu klären, wurden 285 Honigbienenproben mit 20 Arbeiterinnen aus jeweils 5 traditionellen Korbbeuten an 57 Sammelorten mit einem durchschnittlichen Abstand von 100 km zwischen den Sammelorten genommen (Tab. I, Abb. 1). Von diesen wurden 13 morphometrische Merkmale (5 Größenmerkmale unter Einschluss der Haarlänge, 5 Farbmerkmale und 3 Flügelwinkel des Vorderflügels) gemessen und mit multivariaten Methoden analysiert.

In der Hauptkomponentenanalyse der Koloniemittelwerte der 13 morphometrischen Merkmale von 5700 Arbeiterinnen wurden vier Faktoren mit Eigenwerten >1 extrahiert: Faktor 1 umschloss die Größenmerkmale, Faktor 2 die Färbungsmerkmale, Faktor 3 die Flügelwinkel und Faktor 4 den Winkel B4 sowie die Pigmentierung des Scutellums. Diese Faktoren erfassten 82,1 % der Datenvariation, hiervon entfiel 64,1 % auf die Größenvarianz (Faktor 1) und die Färbung (Faktor 2). Von den 13 zur Unterscheidung der äthiopischen Bienen verwendeten Merkmale gingen nur 9 in die Diskriminanzfunktionen ein, da die drei Flügelwinkel und die Pigmentierung des 3. Tergites zu geringe Unterscheidungskraft zur Differenzierung der äthiopischen Bienen hatten (Tab. II).

Beide Hauptkomponenten sowie die schrittweise Diskriminanzanalyse ergaben 5 statistisch trennbare Morphokluster aus ökologisch unterschiedlichen Arealen. Dies waren *Apis mellifera jemenitica* im norwestlichen und östlichen trockenen und halbtrockenen Tiefland; *A. m. scutellata* in dem westlichen, südlichen und südwestlichen feuchten Mittelland; *A. m. bandasii* in dem zentralen und feuchten Hochland; *A. m. monticola* in dem nördlichen gebirgigen Hochland und "*woyi-gambella*" in den südwestlichen halbtrockenen bis niedrigfeuchten südwestlichen Tieflandteilen des Landes (Abb. 1; Tab. V).

Etwa 91 % der Völker wurden korrekt den fünf Morphoklustern zugeordnet (Tab. III). Die Orte 4, 6, 7, 35, 51 und 56 (Abb. 1) wurden auf Grund der hohen Varianzen zwischen den Völkern zwischen die unterschiedlichen Morphokluster eingeordnet. Auch innerhalb der Morphokluster wurde bei einigen Probenorten hohe Varianzen gefunden, die auf Bereiche mit Introgessionen zwischen den Morphokluster hindeuten.

Die mit der Färbung verbundenen Merkmale zeigten untereinander eine starke positive Korrelation sowie eine schwache negative zu den Merkmalen der Körpergröße, die ihrerseits ebenfalls stark positiv korreliert waren. Dagegen waren die Flügelwinkel weder untereinander noch mit den anderen Merkmalen korreliert. Alle Färbungsmerkmale mit Ausnahmen des Scutellums zeigten eine signifikante positive Korrelation zur Temperatur und eine negative mit der Höhe und der Niederschlagsmenge. Darüber hinaus waren die auf die Körpergröße und der Behaarung bezogenen Merkmale negativ mit der Temperatur und positiv mit der Höhe korreliert.

Apis mellifera / Morphometrie / Introgession / Äthiopien

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