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Marina Meixner, Messele Leta, Nikolaus Koeniger, Stefan Fuchs. The honey bees of Ethiopia represent a new subspecies of *Apis mellifera*—*Apis mellifera simensis* n. ssp.. *Apidologie*, 2011, 42 (3), pp.425-437. 10.1007/s13592-011-0007-y . hal-01003606

**HAL Id: hal-01003606**

**<https://hal.science/hal-01003606>**

Submitted on 11 May 2020

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# The honey bees of Ethiopia represent a new subspecies of *Apis mellifera*—*Apis mellifera simensis* n. ssp.

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Received 28 May 2010 – Revised 28 July 2010 – Accepted 2 August 2010

**Abstract** – Honey bees endemic to the volcanic dome system of Ethiopia are described as a new subspecies, *Apis mellifera simensis*, on the basis of morphometrical analyses. Principal component and discriminant analyses show that the Ethiopian bees are clearly distinct and statistically separable from honey bees belonging to neighboring subspecies in eastern Africa. Considerable variation of morphological characters in relation to altitude is present in the samples under analysis, but there are no statistically separable subgroups within this population. There is no indication for the presence of more than one subspecies of honey bee in Ethiopia.

**Ethiopia / *Apis mellifera simensis* / subspecies / morphometrics / Africa**

## 1. INTRODUCTION

In the biogeographic context of the African continent, the Ethiopian mountain system is an unusual region, geologically dominated by its vast volcanic dome that occupies most of the country's area and reaches elevations of more than 4,000 m, harboring a distinctive flora and fauna. Its isolation and unique climate support a high rate of endemism of animals and plants (Kingdon 1989; Yalden and Lagen 1992; Sillero-Zubiri and Gotelli 1994) brought about by the geographical isolation and the unique

climate of the Ethiopian massifs, as results of the last Ice Age (Kingdon 1989).

Likewise, the honey bee fauna of Ethiopia has long been recognized as particular within the African context, and has been subjected to several studies leading to controversial interpretations. Based on early reports (Mammo 1976) and the comparatively few samples available at that time, Ruttner (1976, 1988, 1992) assumed the bees of Ethiopia to be disjunctive populations of *Apis mellifera monticola* Smith 1961, the subspecies described from the mountains of Kenya and Tanzania, mainly because of their similarity in pigmentation and pilosity. In later analyses, however, Radloff and Hepburn (1997a) suggested to divide the bees of Ethiopia among three different subspecies: *Apis mellifera jemenitica* Ruttner 1976 in the North, *Apis mellifera scutellata* Lepeletier, 1836 in the South, and “*Apis mellifera bandasii*” Mogga 1988 in the central mountains. In a later publication, however, five different subspecies were identified in this region (Amssalu et al. 2004).

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Messele Abebe Leta—deceased

**Electronic supplementary material** The online version of this article (doi:[10.1007/s13592-011-0007-y](https://doi.org/10.1007/s13592-011-0007-y)) contains supplementary material, which is available to authorized users.

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Manuscript editor: Klaus Hartfelder

The results of recent research have moved the honey bees of Ethiopia into the focus of attention, suggesting that they may have a unique status and play a distinctive role in general honey bee phylogeography. Based on morphometric data, Ruttner (1988) had first described the geographic structure of the species as consisting of the four different evolutionary branches “A” (Africa), “M” (northern and western Europe), “C” (south-eastern Europe), and “O” (Near East and western Asia). Later, this hypothesis was largely supported by several studies investigating variation of molecular markers (Garnery et al. 1992; Arias and Sheppard 1996; Whitfield et al. 2006); however, in an analysis of mitochondrial DNA, honey bees from Ethiopia deviated substantially from the known lineages and were grouped in a separate molecular lineage termed Y (Franck et al. 2001). The appearance of a new lineage in this region is of particular interest as new analyses based on genetic data strongly indicate that the species started its radiation in Africa (Whitfield et al. 2006), probably about 1 Ma ago (Ruttner 1988; Cornuet and Garnery 1991; Arias and Sheppard 1996), contradicting the previous hypothesis of Ruttner et al. (1978) and Ruttner (1988) who assumed the geographic origin of *Apis mellifera* somewhere between north-eastern Africa and western Asia.

In this paper, we aim to resolve the controversial question of Ethiopian honey bee microtaxonomy and present a comprehensive morphometric analysis based on samples from throughout Ethiopia within the context of neighboring bee populations in eastern Africa.

## 2. MATERIALS AND METHODS

### 2.1. Collection of bee samples and morphometric analysis

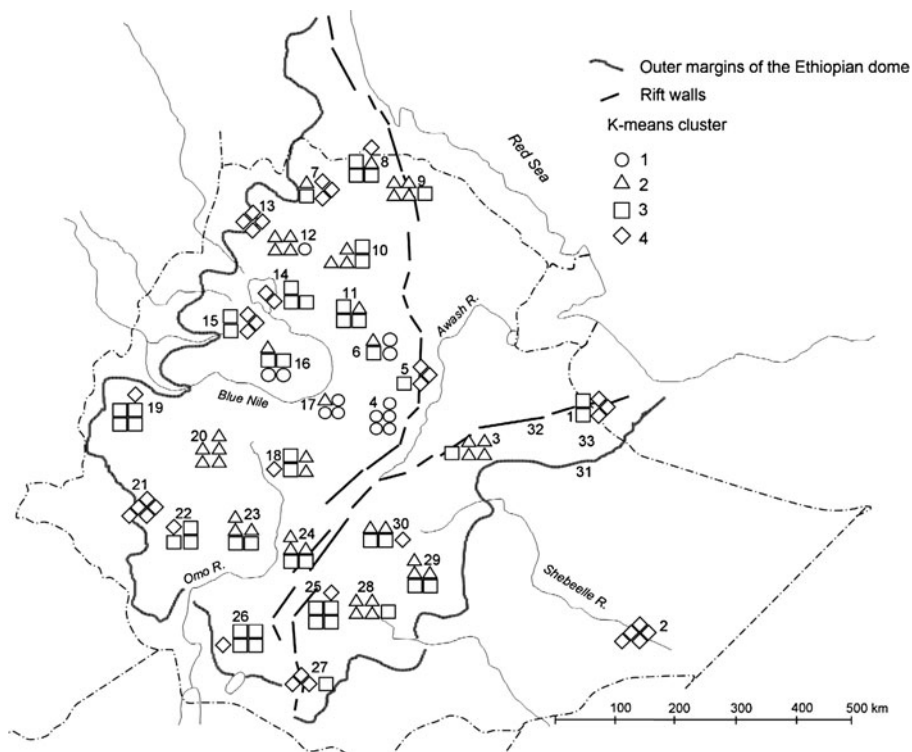
Honey bee samples were collected from a total of 33 locations throughout Ethiopia (Figure 1 and Table in the [Electronic supplementary material](#)); either from natural nests or from traditional hives. Most sampling locations were situated inside the volcanic dome

system of Ethiopia, but several of the peripheral sites were located on the rim or on the walls of the East African rift valley. The altitude of sampling localities ranged from 325 to 3,000 m above sea level. Each location is represented by five samples, with each sample containing about 30 worker bees from one colony. Bees were killed and stored in 70% ethanol prior to analysis.

Fifteen worker bees of each sample were dissected and 38 morphometric characters were measured according to methods described in Ruttner (1988). Measurements of size and wing venation were performed using a stereo microscope and a computer-aided measuring system based on a video system and measuring program (Meixner 1994). For measurements of pilosity and color scaling a stereo microscope was used.

### 2.2. Statistical analysis of the data

Colony sample means, standard deviation, and standard error were computed for each character of each sample and subsequently used as representative estimates for the colony. Reference samples of the following subspecies from the morphometric data base in Oberursel were included: *A. mellifera scutellata* (50), *A. mellifera monticola* (27), *A. mellifera jemenitica* (48), and *Apis mellifera litorea* Smith 1961 (9). The data were submitted to factor analysis and sample scores were plotted on principal component coordinates for visualization. Discriminant analysis was used to perform reallocation of samples to their respective groups, based on the results of the factor analysis. To detect variation between the samples and to identify morphologically homogeneous groups, *k*-means clustering procedures were performed with increasing numbers of clusters, starting with two groups. To determine the number of clusters within Ethiopia that best reflected the structure of the morphological variation, a goodness-of-fit statistics was calculated for each number of clusters. To further analyze variation within Ethiopia, a discriminant analysis was performed using the *k*-means membership of the samples as group identifiers. Calculations were performed using the SPSS (2003) for Windows 12.0 and Systat 9.0 (2000) statistical packages.



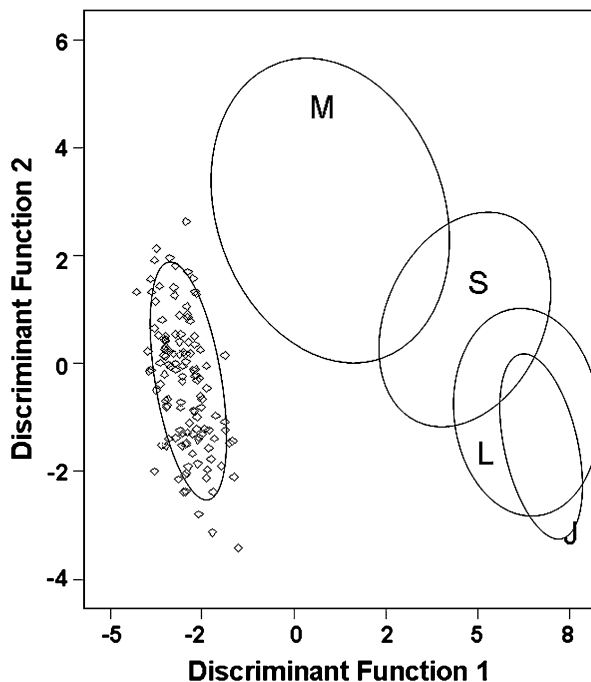
**Figure 1.** Sampling locations in Ethiopia. The map was redrawn and modified after Kingdon (1989). Each symbol represents one colony. The figure shows a plot of the geographical sample distribution allocated to four *k*-means clusters. Samples assigned to cluster one (circles) are concentrated at high elevations in the centre of the Ethiopian dome, with samples of clusters two (triangles), three (squares) and four (diamonds) forming concentric circles of distribution towards lower elevations in the periphery. The geographic coordinates of each location are given in the Table in the [Electronic supplementary material](#).

### 3. RESULTS

#### 3.1. The bees of Ethiopia in relation to the surrounding subspecies

In an initial factor analysis including reference samples from the adjacent subspecies *A. mellifera monticola*, *A. mellifera scutellata*, *A. mellifera litorea*, and *A. mellifera jemenitica*, the samples from all five groups fell into overlapping, yet discernible groups. The bees from Ethiopia only partially overlapped with samples from reference groups, but were concentrated in a different plot area (see Figure in the [Electronic supplementary material](#)).

The distinctiveness of the Ethiopian bees was confirmed by a discriminant analysis where all samples from the study area were reassigned to their group of origin, and where the Ethiopian bees were entered as group of their own. In this analysis (Figure 2), the bees from Ethiopia form a distinct and very tight cluster that does not overlap with any of the reference groups. All samples from Ethiopia were allocated to this group with probabilities of  $0.99 < P < 1.00$ . In addition, 12 Ethiopian samples that were not part of the current study, but were collected earlier and obtained from the morphometric database, were unambiguously allocated to this cluster when entered as “ungrouped” into the



**Figure 2.** Positions of the samples studied in a discriminant analysis. Abscissa, discriminant function 1 and ordinate, discriminant function 2. The ellipses of confidence (75%) calculated from classified reference samples are given. To improve the readability of the figure, positions of individual reference samples are omitted and only the 75% ellipses of confidence are shown. *M* *Apis mellifera monticola*, *S* *Apis mellifera scutellata*, *L* *Apis mellifera litorea*, *J* *Apis mellifera jemenitica*.

discriminant analysis ( $P=1.00$ , all). The statistical differences (multiple  $F$  values) between the group centroids of the Ethiopian cluster and the reference groups in the analysis ranged between 35.4 (Ethiopia—*A. mellifera monticola*) and 222.72 (Ethiopia—*A. mellifera jemenitica*) (Table 1). Thus, they were larger than the differences between the centroids of all reference groups, with the exception of the distance between *A. mellifera monticola* and *A. mellifera jemenitica* (56.18). The statistical differences between group centroids were significant in all cases ( $P<0.001$ ).

### 3.2. Morphological variation within Ethiopia

To investigate the morphological variability within Ethiopia,  $k$ -means cluster analyses were carried out with increasing numbers of groups,

starting with two groups and increasing to ten groups. The goodness-of-fit  $F$ -statistics improved in a linear trend with each added group without reaching an optimum (two groups:  $F=1.11$ ,  $P=0.30$ ; four groups:  $F=2.50$ ,  $P<0.001$ ; ten groups:  $F=4.45$ ,  $P<0.001$ ). As this did not indicate a particular number of groups as best fit, we arbitrarily resolved to present the results obtained by a  $k$ -means analysis with four groups in Figure 1, showing a plot of the geographical sample distribution allocated to the four  $k$ -means clusters. This shows, that samples assigned to cluster one are concentrated at high elevations in the centre of the Ethiopian dome, with samples of clusters two, three and four forming concentric circles of distribution towards lower elevations in the periphery. The altitudinal distribution of the four clusters was significantly different from each other, with cluster one at the highest, and cluster four at

**Table I.** Differences (multiple *F* values) between the group centroids of the Ethiopian bees and the reference groups.

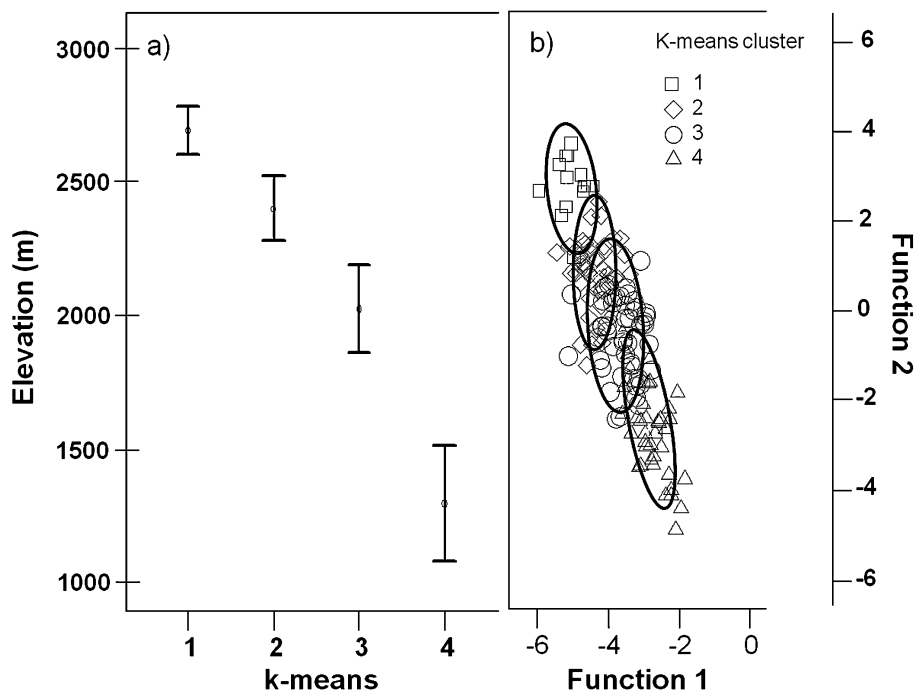
	<i>A. m. jemenitica</i>	<i>A. m. litorea</i>	<i>A. m. scutellata</i>	<i>A. m. monticola</i>
<i>A. m. jemenitica</i>				
<i>A. m. litorea</i>	4.376*			
<i>A. m. scutellata</i>	18.906*	5.684*		
<i>A. m. monticola</i>	56.178*	20.245*	23.863*	
<i>A. m. simensis</i>	222.721*	49.546*	146.219*	35.395*

\**P*<0.01

the lowest elevations (*F*=38.9, *P*<0.001; Figure 3a).

To statistically test the amount of differentiation among the groups defined by the *k*-means analysis, a further discriminant analysis was performed, where each *k*-means cluster was entered as a separate group (Figure 3b). In this plot, the Ethiopian samples are positioned at

increasing values of function 2 in the sequence of their elevation, with samples from *k*-means cluster 1 (highest elevation) at high values, and *k*-means cluster 4 (lowest elevations) at low values of function 2. In particular, *k*-means clusters positioned next to each other in this sequence show considerable overlap of confidence ellipses and lack clear separation. Ac-



**Figure 3.** **a** Altitudinal distribution of the samples assigned to the respective *k*-means clusters with *N*=4. Mean and the 95% confidence interval of each *k*-means cluster are given. **b** Positions of the Ethiopian samples in a discriminant analysis, based on their assignment to one of four *k*-means clusters. Abscissa, discriminant function 1 and ordinate, discriminant function 2.

cordingly, the classification result for most samples (88%) remained ambiguous ( $P < 0.99$ ), with 6% of the samples being misclassified. Only 5% of the samples were classified to their correct  $k$ -means cluster with a probability of  $P > 0.99$ . In this analysis, the statistical differences between the Ethiopian subgroups, represented by the  $k$ -means clusters 1 to 4, albeit significant, fell into a distinctively lower range than the differences between the reference subspecies (Table II).

To test for indications of hybridization between the bees of the geographically most peripheral  $k$ -means cluster 4 and the adjacent *A. mellifera jemenitica* and *A. mellifera scutellata*, a discriminant analysis was performed where the  $k$ -means 4 samples were entered as “ungrouped”. In this analysis, none of the  $k$ -means 4 samples was assigned to any of the adjacent reference groups, but instead they were all classified as  $k$ -means 3, in the majority of cases (21/31) with a probability of  $P > 0.99$ . In all ten cases with probabilities of  $P < 0.99$ , the second highest group was cluster  $k$ -means 2 (plot not shown).

To elucidate changes in the morphological characters in relation to elevation, a regression analysis of hair length, wing length, pigmentation of tergum and pigmentation of scutellum was performed, resulting in significant coefficients for all four characters (hair:  $F = 150.30$ ,  $P < 0.001$ ; forewing:  $F = 150.92$ ,  $P < 0.001$ ; pig-

ment tergum:  $F = 73.53$ ,  $P < 0.001$ ; scutellum:  $F = 54.90$ ,  $P < 0.001$ ). In Figure 4a–d, the results of this analysis are shown for both the Ethiopian bees and for the reference groups. While the regression lines of the characters wing length and length of hair were not different in the Ethiopian bees and the reference groups, the regression lines for pigmentation of scutellum ( $t = 26.22$ ,  $df = 200$ ,  $P < 0.0001$ ) and pigmentation of tergum 2 ( $t = 29.44$ ,  $df = 200$ ,  $P < 0.0001$ ) vary significantly less with elevation in the Ethiopian bees than in the reference groups. Obviously, Ethiopian bees are much darker and more uniformly so, than mountain bees from other regions in East Africa.

Based on the distinctiveness of the Ethiopian honey bees from the surrounding subspecies and the demonstrable morphological coherence of our samples, we conclude that the honey bees of Ethiopia deserve subspecific rank and propose the name *Apis mellifera simensis*.

### 3.3. Description of *A. mellifera simensis*

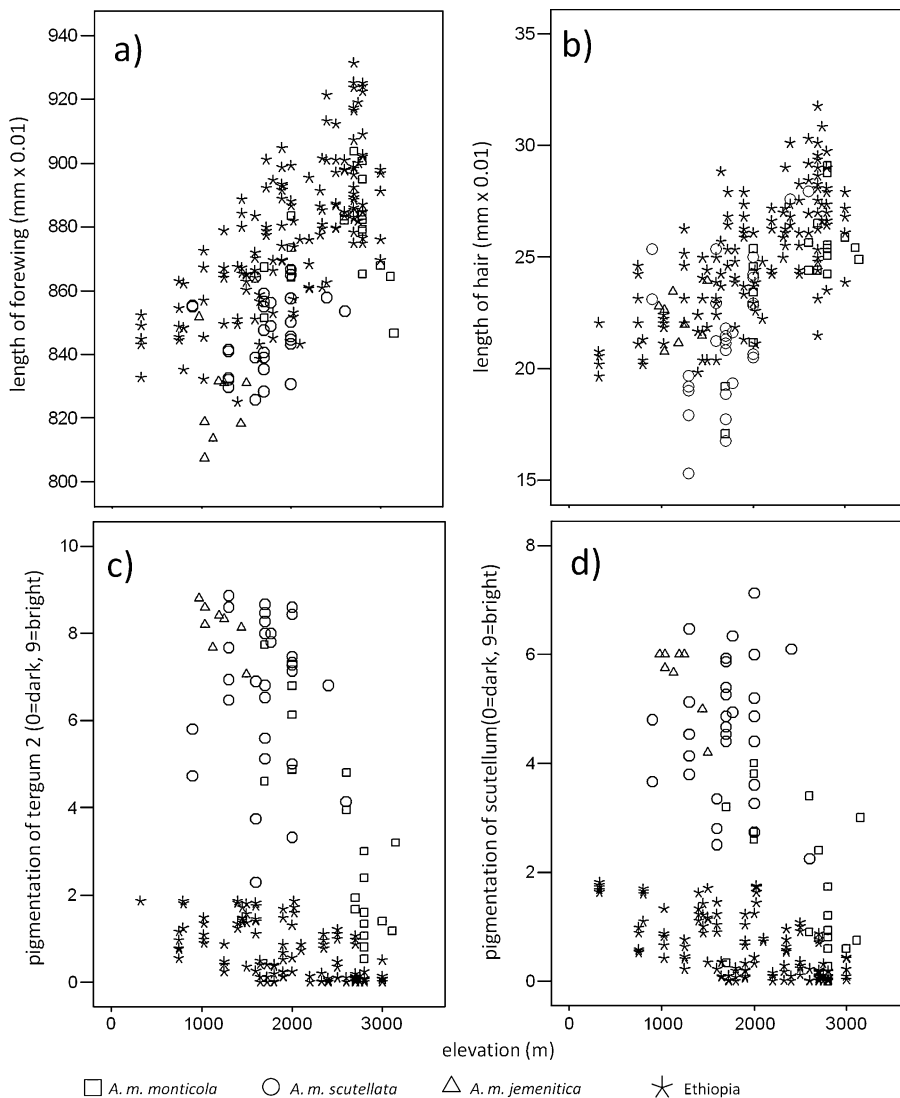
#### 3.3.1 *A. mellifera simensis* n. ssp.

*Holotype* Worker bee; Ethiopia, Haro Wonchi, 8°50' N, 37°49' E, elevation 3,000 m; leg. Messele Abebe Leta (1998). Oberursel honey bee collection, sample number 2709.

**Table II.** Statistical differences (multiple  $F$  values) between the Ethiopian subgroups, represented by the  $k$ -means clusters 1 to 4 and the reference subspecies.

	$k$ -means 1	$k$ -means 2	$k$ -means 3	$k$ -means 4	<i>A. m.</i> <i>jemenitica</i>	<i>A. m.</i> <i>litorea</i>	<i>A. m.</i> <i>scutellata</i>
$k$ -means 1							
$k$ -means 2	4.72**						
$k$ -means 3	20.15**	10.78**					
$k$ -means 4	23.97**	15.56**	3.17*				
<i>A. m. jemenitica</i>	137.75**	177.97**	137.42**	78.22**			
<i>A. m. litorea</i>	68.09**	71.10**	61.11**	44.53**	6.13**		
<i>A. m. scutellata</i>	105.86**	161.68**	127.26**	65.84**	22.71**	7.79**	
<i>A. m. monticola</i>	32.22**	41.94**	40.45**	30.06**	71.16**	29.73**	37.72**

\* $P < 0.05$ ; \*\* $P < 0.01$



**Figure 4. a–d** Values of four different morphometric characters of Ethiopian bees and reference groups in relation to altitude.

*Paratypes* Several worker bees, same data as holotype.

Hepburn and Radloff 1997, 1998; Amssalu et al. 2004).

*Etymology* The name refers to the Simen mountains as a typical geographical feature of the volcanic dome system of Ethiopia. We decided not to validate one of the *nomina nuda* used in earlier publications (Mogga 1988 unpublished data; Radloff and Hepburn 1997a;

### 3.3.2 Diagnosis and description

The body size of worker bees from Ethiopia ranges at the high end of all African subspecies of honey bees. They are larger than the east



African mountain bee, *A. mellifera monticola*, and only slightly smaller than the bees of Egypt, *Apis mellifera lamarckii*; however, with much longer and broader wings. Compared with other honey bees of Africa including *A. mellifera monticola*, their appearance is very dark, although characters of pigmentation can appear variable in some samples. The cover hair on tergum 5 is of comparable length to *A. mellifera monticola*. Selected morphometric characters of *A. mellifera simensis* in comparison to surrounding African honey bee subspecies are presented in Table III. The queen and drones of this subspecies remain still unknown.

*Type locality* Western slopes of Mt. Wonchi, about 7 km northwest of Lake Wonchi in Ethiopia.

*Distribution* The subspecies is distributed in the mountain systems of Ethiopia.

#### 4. DISCUSSION

The results of our morphometric analysis show that the honey bees of Ethiopia form a population of their own that is distinct and well separated from the honey bees of neighboring areas of Africa. They further show that the considerable range of morphological variation within Ethiopia predominantly follows a clinal pattern that is closely linked to elevation. Within the samples studied, we found no indication for the existence of statistically separable subgroups. The distinctness and homogeneity of the Ethiopian honey bees support their classification as a new subspecies, *A. mellifera simensis*.

##### 4.1. The bees of Ethiopia in relation to the surrounding subspecies

The discriminant analysis clearly separated the Ethiopian bees from the four adjacent subspecies *A. mellifera monticola*, *A. mellifera scutellata*, *A. mellifera litorea*, and *A. mellifera*

*jemenitica*. The samples from Ethiopia were grouped in a distinct and very tight cluster, forming a narrow band and extending over a considerable range in the coordinate system of discriminant functions 1 and 2 (Figure 2). This cluster did not overlap with any of the reference groups, and its ellipse of confidence was clearly separate from all of them. Although the Ethiopian cluster lay in the vicinity of *A. mellifera monticola* at one end of its extension, it was clearly separate from this reference group, while the distances to *A. mellifera scutellata*, *A. mellifera litorea* and *A. mellifera jemenitica* were even greater. As demonstrated by the statistical differences in Table I, with the exception of the pair *A. mellifera monticola* - *A. mellifera jemenitica*, the reference groups appeared to be morphometrically more similar to each other than the Ethiopian bees were to any of the reference groups. Our results are corroborated by samples from the morphometric data bank collected much earlier (between 1969 and 1995) from different ecological zones of the country, which were unambiguously assigned to the Ethiopian cluster when included in the discriminant analysis.

##### 4.2. Morphological variation within Ethiopia

Despite their obvious separation and clear distinctness from other honey bee populations of eastern Africa, Ethiopian bees displayed a considerable degree of morphological variation within the country. However, none of our analyses provided any indication for the existence of further subdivisions within the collection area. Therefore, the samples were allocated into a variable number of predefined clusters by a *k*-means cluster analysis, where the optimum number of groups can be identified via goodness-of-fit statistics. However, when applied to our data, the goodness-of-fit statistic continued to increase with the number of groups, without settling for an optimum. Thus, no statistical evidence for a superior fit of a specific limited number of existing clusters was provided.

**Table III.** Comparative characteristics of *Apis mellifera lamarckii*, *Apis mellifera jemenitica*, *Apis mellifera litorea*, *Apis mellifera scutellata*, *Apis mellifera monticola*, and *Apis mellifera simensis*.

	<i>A. m. lamarckii</i> (N=24)	<i>A. m. jemenitica</i> (N=48)	<i>A. m. litorea</i> (N=9)	<i>A. m. scutellata</i> (N=50)	<i>A. m. monticola</i> (N=27)	<i>A. m. simensis</i> (N=144)
Body size	419.41±12.13	394.99±8.88	387.85±8.75	400.56±13.13	405.21±16.00	414.78±11.13
Length forewing	819.65±17.42	823.44±14.70	830.28±14.81	850.24±14.15	877.56±18.06	878.20±22.48
Width forewing	276.50±5.21	284.41±6.76	285.66±4.99	295.92±6.12	300.61±6.66	305.26±7.90
Length of hind leg	738.09±16.53	717.71±15.90	728.44±7.55	741.01±23.07	751.49±22.97	747.99±19.99
Stermite 6 index	87.05±3.13	86.34±2.26	86.33±2.39	85.50±3.11	85.96±3.44	86.92±2.16
Cubital index	2.33±0.15	2.32±0.18	2.40±0.26	2.36±0.26	2.31±0.21	2.24±0.20
Body size/leg	56.82±0.91	55.04±0.71	53.24±0.97	54.07±1.49	53.93±1.69	55.46±0.91
Hair length	21.49±2.57	20.88±1.66	22.92±1.89	22.55±2.80	25.33±3.26	25.04±2.77
Pigmentation tergite 2	8.44±0.47	8.61±0.63	7.39±1.05	6.71±1.79	3.20±2.15	0.64±0.66
Pigmentation tergite 3	7.07±0.49	8.36±0.83	7.29±1.11	6.20±1.59	3.17±1.98	1.58±1.61
Pigmentation tergite 4	3.72±0.32	5.35±1.59	4.46±0.94	3.54±1.12	1.90±1.26	1.42±1.59
Pigmentation of scutellum 1	6.06±0.60	6.56±0.96	6.51±1.00	4.93±1.42	1.67±1.49	0.55±0.57
Pigmentation of scutellum 2	3.93±1.15	2.89±1.67	2.47±1.09	1.79±1.20	1.40±1.15	1.02±1.45
Wing angle J16	98.42±2.75	95.62±4.32	93.05±1.39	90.55±4.06	89.17±5.93	93.40±2.04

Values are means and standard deviations of samples; each sample representing one colony. Measurements of size are in units of 1:100 mm; wing venation angles are in degrees. Characters of pigmentation: 0=completely dark, 9=completely bright (yellow). Measurements were taken according to Ruttner (1988)  
 N number of sampled colonies

When investigating the sample distribution using the arbitrary number of four *k*-means clusters, these four groups were arranged according to the elevation range of the collecting sites, with increasing statistical distances between the clusters from the lowest to the highest elevations. A discriminant analysis performed on these clusters resulted in overlapping ellipses of confidence between clusters with neighboring elevation ranges, with numerous misclassifications and ambiguous classifications. Thus, the sequential distribution of clusters that were aligned according to elevation from the high centre of the sampling area to the periphery, with considerable overlap between the samples of each cluster, did not support the existence of separable subgroups. Instead, this result strongly suggested that the morphological variation of honey bees within Ethiopia follows clinal patterns from the highest elevations in the centre to the lowest in the periphery. Similar results were obtained when the number of *k*-means clusters was set to other values.

Across the elevation range sampled, the honey bees of Ethiopia show morphological adaptations in relation to ecological factors comparable to those known from bees of other mountain systems (Ruttner 1976, 1985; Meixner et al. 1989, 1994; Hepburn et al. 2000). The selective forces acting on wing length should strongly depend on altitude, since an increase of wing area, together with an increase in body mass, is known to be necessary to meet higher aerodynamic power requirements at higher altitudes, and to compensate for reduced lift (Hepburn et al. 1998, 1999). This is reflected in our data, where the gradation of wing length in Ethiopian bees exactly matches the slope observed in the reference samples from other regions in Africa. Likewise, the increase in hair length has been rather uniform in all populations, including Ethiopia, in our analyses. A dense and long hair cover is known to be of vital importance for both individual and social thermoregulation in social bees (Heinrich 1993; Southwick 1985; Stiles 1979). In our data set, the increase of hair length with altitude in Ethiopia was not statistically different from the reference samples.

In contrast, the slopes of the pigmentation characters differed considerably and significantly between these two groups, with the Ethiopian bees being on average darker at lower altitudes. A tendency towards darker pigmentation is common in mountain insects and has mainly been discussed as an adaptation to high proportions of UV light at higher altitudes (Mani 1968, 1991). However, several subspecies of *Apis mellifera* at low altitudes are also completely dark (e.g., *Apis mellifera intermissa*), so that a strict relation between elevation and dark pigmentation does not seem to exist. The comparatively dark appearance of the Ethiopian bees has also been mentioned by Amssalu et al. (2004).

#### 4.3. Comparison with previous results

Our results are in obvious disagreement with previously published analyses. They do not support the hypothesis that the honey bees of Ethiopia belong to the East African mountain subspecies, *A. mellifera monticola*, as first proposed by Smith (1961) and later by Ruttner (1976, 1988). *A. mellifera monticola* occurs in the mountain systems of Kenya and Tanzania to the south, at least 1,000 km away. Based on an apparent morphological similarity in regard to some characters, the bees of Ethiopia were thought to represent disjunct populations of this subspecies. According to this hypothesis, all East African mountain bees were considered relics of a Pleistocene bee population covering large areas of East Africa during more humid climatic conditions between 18,000 and 7,000 BC (Wickens 1975; Hamilton 1982; Nagel 1986). In our analyses, the bees of Ethiopia are clearly distinct from *A. mellifera monticola*; however, in comparison to the other reference subspecies, they still appear to resemble the East African mountain bee. Although morphometric data alone are not sufficient to disprove the previously hypothesized common origin of the East African and Ethiopian bee populations, a more parsimonious explanation for this resemblance is provided by similar selective pressures prevailing at higher elevations, lead-

ing to larger and darker colored bees, as it has been demonstrated for bee populations of other mountain systems (Meixner et al. 1989, 1994; Hepburn et al. 2000).

Our results also contradict the interpretations of later authors, who, again based on morphometric analyses, postulated the presence of up to five different subspecies of honey bees in Ethiopia. In a first analysis of samples from Ethiopia, Radloff and Hepburn (1997a) identified three statistically separable groups of bees, which they assigned to different subspecies on the basis of comparisons of single characters (such as hair length, cubital index, size and pigmentation) with published data. Thus, they attributed their samples from the north to *A. mellifera jemenitica*, those from central Ethiopia to "*A. mellifera bandasii*", and samples from the south to *A. mellifera scutellata*. However, in a different publication, the same authors describe samples collected along a north–south transect in Ethiopia as *A. mellifera jemenitica*, "*A. mellifera bandasii*" and "*Apis mellifera sudanensis*" (Hepburn and Radloff 1997).

Subsequently, Amssalu et al. (2004) conducted a morphometric study on a comprehensive sampling across Ethiopia, covering a wide geographical area and elevation range, and representing most of the ecological zones of the country. In addition to the three groups identified by Radloff and Hepburn (1997a), they recognized the presence of *A. mellifera monticola* in the northeast of Ethiopia and, based on data from two locations in the southwest, postulated the existence of a separate taxonomic entity that they named "*Apis mellifera woyigambella*". The conclusions of Amssalu et al. (2004) were based on the results of principal component and discriminant analyses of their sampling, which, according to their interpretation, yielded five separable morphoclusters. They also provide a comparison table with Mahalanobis distances between each of their five groups and published samples of *A. mellifera jemenitica*, *A. mellifera scutellata*, "*A. mellifera bandasii*", and *A. mellifera monticola* (Ruttner 1988; Radloff and Hepburn 1997a, b). However, presentations of the anal-

yses on which those values were based, including *P* values for the classification of their samples to these respective taxonomical units, were absent in this publication.

The geographic range covered by sampling in our study (4°53' to 14°16' N and 34°50' to 44°07' E) was comparable to the area studied by Amssalu et al. (2004) (4°49' to 14°19' N and 34°16' to 42°57' E). Although morphological variation was easily recognizable within the samples of our study, our analyses with inclusion of reference data did not support any of the allocations or subgroups proposed by Amssalu et al. (2004). Thus, our results did not give any indication for the presence of more than one subspecies of *A. mellifera* in Ethiopia. Instead, within the statistically distinct and clearly separate cluster of the Ethiopian samples, considerable clinal variation of morphological characters was observed. In particular, we did not find indications justifying the separation of a central high-elevation group from a northern mountain group ("*A. mellifera bandasii*" and *A. mellifera monticola*, respectively, as in Amssalu et al. 2004). The existence of clinal variation generally invites the postulation of subgroups, particularly if sampling coverage is incomplete. However, without any clear rationale for delineations this is bound to remain arbitrary. Considering the rather coherent and very distinct group that the bees of Ethiopia formed in all our analyses, we thus regard them as one population confined to the Ethiopian mountain dome. The limitation of their geographic range towards the west is also supported by the morphometric analysis of the honey bees of the Sudan by Omer (2007), which showed no resemblance to the Ethiopian bees.

#### 4.4. Naming of the new subspecies

Our results demonstrate morphometric separateness of the Ethiopian honey bees from adjacent subspecies of *A. mellifera*. This population possesses a clear geographic and ecological range connected to the volcanic dome of Ethiopia, with morphological variation through its elevation range, but without clear subgroups.

Thus, our results support the hypothesis that these bees are to be considered as a separate subspecies. The data provide clear evidence that these honey bees are not *A. mellifera monticola*. The question then remains whether they have to be regarded as "*A. mellifera bandasii*" (Mogga 1988) or "*A. mellifera woyi-gambella*" (Amssalu et al. 2004). According to the rules of the I.C.Z.N. (1999), both these names have to be considered invalid. As already stated by Engel (1999), the name "*A. mellifera bandasii*" has been proposed in the M. Sc. thesis of Mogga (1988), but was never published according to the rules of the I.C.Z.N. (1999) (*nomen nudum*).

The name "*A. mellifera woyi-gambella*" was introduced by Amssalu et al. (2004) to describe a small portion of the honey bee population of Ethiopia in the south-western corner of the country. It is lacking the designation of a holotype and a type locality; further, the name violates Art. 11.9.4 of the code and can therefore not be considered valid. Therefore, and to avoid further confusion, a new subspecies name for the honey bees of Ethiopia is introduced. We propose *A. mellifera simensis* with reference to the Simen mountains as a typical geographic feature of the geographic origin of these bees. The type locality of the new subspecies is the western slope of Mt. Wonchi.

## ACKNOWLEDGMENTS

We gratefully acknowledge Wolfgang Nässig for his help with all questions relating to the taxonomy and the application of the Code.

**Les abeilles d'Ethiopie représentent une nouvelle sous-espèce d' *Apis mellifera*—*Apis mellifera simensis* n. ssp.**

**Ethiopie / *Apis mellifera simensis* / Sous-espèce / Morphométrie / Afrique**

**Zusammenfassung—Die Honigbienen von Äthiopien repräsentieren eine neue Unterart von *Apis mellifera*—*Apis mellifera simensis* n. ssp.** Honigbienen aus den vulkanischen Gebirgssystemen von Äthiopien werden auf der Grundlage von multivariaten Analysen morphometrischer Merkmale als neue Unterart *Apis mellifera simensis* beschrieben.

Insgesamt 144 Proben von 33 Sammelorten aus verschiedenen Höhenlagen in allen Regionen Äthiopiens wurden morphometrisch analysiert. Die Ergebnisse von Hauptkomponenten- und Diskriminanzanalyse zeigten, dass diese Proben nicht als eine der anderen im östlichen Afrika vorkommenden Unterarten klassifiziert werden können, sondern einen eigenen, klar definierten und gut abgegrenzten Cluster bilden. Innerhalb der äthiopischen Bienen wurde erhebliche morphologische Variabilität in Korrelation mit der Höhenlage festgestellt, jedoch ohne dass dabei gegeneinander abgegrenzte Untergruppen nachgewiesen werden konnten. Die Variation der Merkmale Flügellänge und Haarlänge mit der Höhe stimmte dabei mit den Referenzproben von anderen Unterarten aus Afrika überein, während die Variabilität von Pigmentierungsmerkmalen bei den äthiopischen Bienen weit weniger ausgeprägt war. Im Vergleich zu anderen afrikanischen Unterarten der Honigbiene ist *Apis mellifera simensis* eine große Biene mit langen und breiten Flügeln. Sie besitzt langes Überhaar und ist recht dunkel gefärbt. Mittelwerte und Standardabweichungen einiger morphometrischer Merkmale im Vergleich zu benachbarten Unterarten sind in Tabelle III zusammengefasst.

Die deutliche Verschiedenheit der äthiopischen Bienen von den benachbarten Unterarten sowie ihre morphologische Einheitlichkeit unterstützen ihre Klassifizierung als neue eigene Unterart *Apis mellifera simensis*. Der Name bezieht sich auf das Simen-Gebirge als typische geographische Formation des vulkanisch geprägten Gebirgssystems in Äthiopien.

**Äthiopien / *Apis mellifera simensis* / Unterart / Morphometrie / Afrika**

## REFERENCES

- Amssalu, B., Nuru, A., Radloff, S.E., Hepburn, H.R. (2004) Multivariate morphometric analysis of honeybees (*Apis mellifera*) in the Ethiopian region. *Apidologie* **35**, 71–81
- Arias, M.C., Sheppard, W.S. (1996) Molecular phylogenetics of honey bee subspecies (*Apis mellifera* L.) inferred from mitochondrial DNA sequence. *Mol. Phylogenet. Evol.* **5**, 557–566
- Cornuet, J.M., Garnery, L. (1991) Mitochondrial DNA variability in honeybees and its phylogeographical implications. *Apidologie* **22**, 627–642

- Engel, M.S. (1999) The taxonomy of recent and fossil honey bees (Hymenoptera: Apidae; Apis). *J. Hymenopt. Res.* **8**, 165–196
- Franck, P., Garnery, L., Loiseau, A., Oldroyd, B.P., Hepburn, H.R., Solignac, M., Cornuet, J.-M. (2001) Genetic diversity of the honeybee in Africa: microsatellite and mitochondrial data. *Heredity* **86**, 420–430
- Garnery, L., Cornuet, J.-M., Solignac, M. (1992) Evolutionary history of the honey bee *Apis mellifera* inferred from mitochondrial DNA analysis. *Mol. Ecol.* **1**, 145–154
- Hamilton, A.C. (1982) Environmental history of East Africa. A study of the quaternary. Academic, New York
- Heinrich, B. (1993) The hot-blooded insects, strategies and mechanisms of thermoregulation. Springer, Berlin
- Hepburn, H.R., Radloff, S.E. (1997) Biogeographical correlates of population variance in the honeybees (*Apis mellifera* L.) of Africa. *Apidologie* **28**, 243–258
- Hepburn, H.R., Radloff, S.E. (1998) Honeybees of Africa. Springer, Berlin
- Hepburn, H.R., Youthed, C., Illgner, P., Radloff, S.E., Brown, R.E. (1998) Production of aerodynamic power in mountain honey bees (*Apis mellifera*). *Naturwissenschaften* **85**, 389–390
- Hepburn, H.R., Radloff, S.E., Fuchs, S. (1999) Flight machinery dimensions of honey bees, *Apis mellifera*. *J. Comp. Physiol. B* **169**, 102–112
- Hepburn, H.R., Radloff, S.E., Oghiake, S. (2000) Mountain honeybees of Africa. *Apidologie* **31**, 205–221
- I.C.Z.N. (1999) International Code of Zoological Nomenclature, The International Trust for Zoological Nomenclature, 4th edn. Natural History Museum, London
- Kingdon, J. (1989) Island Africa. The evolution of Africa's rare animals and plants. Princeton University Press, Cambridge
- Mammo G. (1976) Practical aspects of bee management in Ethiopia, Proc. 1st Int. Conf. Apic. Trop. Climates, London. pp 69–78
- Mani, M.S. (1968) Ecology and biogeography of high altitude insects. Junk Publishers, The Hague
- Mani, M.S. (1991) Fundamentals of high altitude biology. Aspect Publications Ltd., London
- Meixner M.D. (1994) Analyse polymorpher Subspezies von *Apis mellifera* L.: Morphometrische und molekulare Untersuchungen an den europäischen Rassen *Apis mellifera carnica* und *ligustica* und den afrikanischen Rassen *Apis mellifera monticola* und *scutellata*. Ph.D. thesis, Johann-Wolfgang-Goethe-University, Frankfurt
- Meixner, M., Ruttner, F., Koeniger, N., Koeniger, G. (1989) The mountain bees of the Kilimanjaro region and their relationship to neighbouring bee populations. *Apidologie* **20**, 165–174
- Meixner, M.D., Sheppard, W.S., Dietz, A., Krell, R. (1994) Morphological and allozyme variability in honey bees from Kenya. *Apidologie* **25**, 188–202
- Mogga J.B. (1988) The taxonomy and geographical variability of the honeybee *Apis mellifera* L. in Sudan. M.Sc. thesis, Faculty of Agriculture, University of Khartoum, Sudan
- Nagel, P. (1986) Die Methode der Arealssystemanalyse als Beitrag zur Rekonstruktion der Landschaftsgenese im tropischen Afrika. *Geomethodica* **11**, 145–176
- Omer E.A. (2007) Studies on the taxonomy of honeybees in Sudan. Ph.D. thesis, Faculty of Agriculture, Khartoum, Sudan
- Radloff, S.E., Hepburn, H.R. (1997a) Multivariate analysis of honeybees, *Apis mellifera* L. (Hymenoptera: Apidae) on the horn of Africa. *Afr. Entomol.* **5**, 57–64
- Radloff, S.E., Hepburn, H.R. (1997b) Multivariate analysis of honeybees, *Apis mellifera* Linnaeus (Hymenoptera: Apidae) from western central Africa. *Afr. Entomol.* **5**, 195–204
- Ruttner F. (1976) African races of honeybees. In: Proc. Int. Beekeeping Congr. 25, Apimondia, Bucharest. pp 1–20
- Ruttner, F. (1985) Graded geographic variability in honey bees and environment. *Pszczel. Zesz. Nauk.* **29**, 81–92
- Ruttner, F. (1988) Biogeography and taxonomy of honeybees. Springer, Berlin
- Ruttner, F. (1992) Naturgeschichte der Honigbienen. Ehrenwirth, München
- Ruttner, F., Tassencourt, L., Louveaux, J. (1978) Biometrical-statistical analysis of the geographical variability of *Apis mellifera* L. *Apidologie* **9**, 363–381
- Sillero-Zubiri, C., Gotelli, D. (1994) *Canis simensis*. *Mamm. species.* **485**, 1–6
- Smith, F.G. (1961) The races of honeybees in Africa. *Bee. World.* **42**, 255–260
- Southwick, E.E. (1985) Bee hair structure and the effect of hair on metabolism at low temperature. *J. Apic. Res.* **24**, 144–149
- SPSS (2003) SPSS for Windows, release 12. SPSS Inc., Chicago
- Stiles, E.W. (1979) Evolution of color pattern and pubescence characteristics in male bumblebees: automimicry vs. thermoregulation. *Evolution* **33**, 941–957
- Systat 9.0 (2000) Systat software Inc., Chicago
- Whitfield, C.W., Behura, S.K., Berlocher, S.H., Clark, A. G., Johnston, J.S., Sheppard, W.S., Smith, D.R., Suarez, A.V., Weaver, D., Tsutsui, N.D. (2006) Thrice out of Africa: ancient and re-cent expansions of the honeybee, *Apis mellifera*. *Science* **314**, 642–645
- Wickens, G.E. (1975) Changes in the climate and vegetation of the Sudan since 20000 B.P. *Boissiera* **24**, 43–65
- Yalden, D.W., Lagen, M.J. (1992) The endemic mammals of Ethiopia. *Mamm. Rev.* **22**, 115–150