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REVIEW ARTICLE

Geographical distribution and population variation of *Apis mellifera jemenitica* Ruttner

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Summary

The races of *Apis mellifera* L. have evolved as a result of long periods of geographical isolation and ecological adaptation. Among these subspecies, *A. m. jemenitica* Ruttner 1976 (Rutter 1976c) is particularly interesting because it is the only race reported to occur naturally in both Africa and Asia. According to the literature, its natural distribution is extremely large, extending for 4,500 km from the Arabian Peninsula to West Africa. However, different populations of *A. m. jemenitica* exhibit a high degree of morphometric variation. Moreover, published classifications of the subspecies do not agree; different names, including *A. m. nubi, A. m. sudanensis,* and *A. m. bandasii* have been applied to different populations of *A. m. jemenitica.* Although African and Asian *A. m. jemenitica* are reported to be morphometrically similar, genetic data have not shown African *A. m. jemenitica* to be genetically closer to the Asian *A. m. jemenitica* than to adjacent, contiguous African subspecies like *A. m. litorea, A. m. adansonii* and *A. m. scutellata,* which exchange genes continuously. Moreover, the African and Asian groups differ in migratory, aggressive, and brood-rearing behaviours. Thus, categorizing the geographically-isolated Asian and the African groups of *A. m. jemenitica* as one honey bee race is questionable. The other important issue is that the present homelands of *A. m. jemenitica* (near East Asia and East Africa) have been suggested as the geographic origin of *A. mellifera.* The existence of close similar population in both continents may support the suggestion that either of these two regions as may be the centre of origin and diversification of *Apis mellifera.*

Distribución geográfica y la variación poblacional de *Apis mellifera jemenitica* Ruttner

Resumen

Las razas de *Apis mellifera* L. han evolucionado como consecuencia de largos períodos de aislamiento geográfico y de adaptación ecológica. Entre estas subespecies, *A. m. jemenitica* Ruttner 1976 (1976c) es particularmente interesante, ya que es la única raza reportado que ocurre de forma natural en África y Asia. De acuerdo con la literatura, su distribución natural es muy grande, y se extiende a lo largo de 4.500 km desde la Península Arábiga hasta África occidental. Sin embargo, las diferentes poblaciones de *A. m. jemenitica* exhiben un alto grado de variación morfométrica. Por otra parte, las clasificaciones publicadas de las subespecies no están de acuerdo; se han aplicado diferentes nombres, entre ellos *A. m. nubi*, *A. m. sudanensis* y *A. m. bandasii* a diferentes poblaciones de *A. m. jemenitica*. Aunque *A. m. jemenitica* de África y de Asia son similares morfométricamente, los datos genéticos no han demostrado que la *A. m. jemenitica* africana sea genéticamente más cercana a la *A. m. jemenitica* de Asia que a las subespecies africanas adyacentes, como *A. m. litorea*, *A. m. adansonii* y *A. m. scutellata*, con las que intercambia genes continuamente. Por otra parte, los grupos africanos y asiáticos difieren en comportamientos de migración, agresividad y crianza de la cría. Por lo tanto, la categorización de los geográficamente aislados grupos africanos y asiáticos de *A. m. jemenitica* como una raza de abejas es cuestionable. La otra cuestión importante es que los actuales países de origen de *A. m. jemenitica* (cerca de Asia y África Orientales) se han sugerido como el origen geográfico de *A. mellifera*. La existencia de una población similar en ambos continentes puede apoyar la idea de que cualquiera de estas dos regiones pudieran ser el centro de origen y diversificación de *Apis mellifera*.

Keywords: *Apis mellifera jemenitica*, geographical distribution, population variability, morphometrics, behaviour, Africa, Asia

Introduction

Honey bees, *Apis mellifera,* occur naturally over vast and varied geographical areas, extending from Scandinavia in the north to the Cape of Good Hope in the south, and from Dakar in the west to Oman in the east. Different populations are adapted to a very wide range of climatic conditions (e.g., Ruttner *et al.,* 1978). *Apis mellifera* colonies are found from sea level to 1,000 m above sea level (a.s.l.) in temperate zones and from sea level to 3,700 m a.s.l. in the tropics. They also survive in the hot and arid zones of Oman at 200 m a.s.l. (Dutton *et al.,* 1981). A distribution over vast areas with extremely different climates has led to the diversification of honey bee morphology and behaviour, and, along with possible episodes of geographic isolation, has resulted in the many lineages and subspecies of *A. mellifera*. The different races of *A. mellifera* have evolved as a result of long periods of geographical isolation and ecological adaptation (e.g. Ruttner *et al*., 1978).

Based on morphometric studies, four lineages of *Apis mellifera* (A, M, C and O) have been recognized (Ruttner *et al.,* 1978; Ruttner, 1988). Analyses using microsatellites (Franck *et al*., 2001), and mitochondrial DNA (mtDNA; Franck *et al*., 2000, Palmer *et al.,* 2000) confirmed the existence of these four lineages and further reported a fifth 'Y' lineage (Franck *et al.,* 2001). A great deal of geographical variation is recognized among and within these lineages, ranging from slight differences among local populations to well-defined and distinct geographical races (Ruttner, 1988; Cornuet and Garnery, 1991). Analysis of this variability is the basis for the characterization of the present geographical races of *Apis mellifera*. Rothenbuhler *et al.* (1968) reported 25 races of *A. mellifera*. Later, Ruttner (1988) recognized 24 distinct taxonomic groups or geographical races, based on a now-standard biometry developed by Ruttner *et al.* (1978): seven in the Near East, 10 in Africa and seven in north and southeast Europe. Engel (1999) revised these names and brought them into compliance (as far as possible) with rules of zoological nomenclature.

Among these subspecies, *Apis mellifera jemenitica* is both important and interesting. The presence of small, yellow bees in Yemen was first reported by Alpatov (1935) and then by Guiglia (1964), but they were not treated as a taxonomic unit (race) of *A. mellifera* until 1976 (Ruttner, 1976c). *Apis mellifera jemenitica* is extreme both in its morphometric variability and its ecological distribution. It is well adapted to high temperatures of 27-40°C and irregular and low rainfall of 50-300 mm/annum in the semi-desert parts of its distribution and can survive a year or more without rain (Ruttner, 1988).

In this review article we have tried to summarize the current state of knowledge of the taxonomy of *Apis mellifera jemenitica* including its geographical distribution, variation in morphometric values, major biological and behavioural aspects and the existing ambiguities in the classification of the subspecies. Among the ambiguities is a particularly pressing issue - whether the far-flung populations attributed to *A. m. jemenitica* constitute a single cohesive subspecies, or are a collection of two or more distinct populations, each of which has converged on a morphology adapted to hot, arid conditions.

Moreover we have tried to suggest further research needed to fill the gaps and get a clear picture of the subspecies. In this regard it is important to determine *Apis mellifera jemenitica*'s relationship to other races, to better understand the phylogeography of *Apis mellifera* subspecies.

Geographical distribution of *Apis mellifera jemenitica*

Apis mellifera jemenitica is the only race of *A. mellifera* that is reported to occur naturally in both Africa and Asia. In Africa, *A. m. jemenitica* is mainly distributed in the Sahel, a dry tropical ecological-climatic zone south of the Sahara and north of the wetter, tropical Africa (Ruttner, 1988; Hepburn and Radloff, 1998). The Asian populations occupy the Arabian Peninsula (Fig. 1). The reported distribution of *A. m. jemenitica* is extremely large, extending 4,500 km from east to west, including Oman (Dutton *et al.,* 1981), Yemen (Ruttner, 1976a, 1976b), Saudi Arabia (Ruttner, 1988), Somalia (Ruttner, 1988), the northern parts of Ethiopia (Radloff and Hepburn, 1997, 1998), eastern and north-eastern parts of Ethiopia (Amssalu *et al.,* 2004), Sudan (Ruttner, 1976a, 1976b; Rashad and El-Sarrag, 1980), Chad (Gadbin *et al.,* 1979), Cameroon (Meixner *et al*., 1989; Radloff and Hepburn, 1997) and Mali (Hepburn and Radloff, 1998).

Many questions remain concerning the geographic distribution of *A. m. jemenitica.* For example, Radloff and Hepburn (1997) reported the presence of three honey bee races in Ethiopia: *A. m. bandasii, A. m. sudanensis* and *A. m. jemenitica,* but later (Hepburn and Radloff, 1998) suggested that the former two subspecies were probably local populations of *A. m. jemenitica.* Amssalu *et al.'s* (2004) morphometric analysis of honey bees of Ethiopia recognized *A. m. jemenitica* and four other subspecies in Ethiopia: *A. m. scutellata*, *A. m. monticola*, and two less widely recognized subspecies, *A. m. bandesii* and *A. m. woyi-gambell.* It should be noted that Engel (1999) listed *Apis mellifera sudanensis* and *Apis mellifera bandasii* as "*nomina nuda*," that is, names without adequate published description of the organisms. Meixner *et al.* (2011) carried out morphometric analysis of samples from essentially the same regions in Ethiopia and came to a different conclusion: they recognized a single subspecies (which they named *Apis mellifera simensis* Meixner, Leta, N. Koeniger & Fuchs 2011) with clinal variation related to altitude. They concluded there was no evidence for other subspecies (including *A. m. jemenitica*) in Ethiopia.

The honey bees of Sudan (Rashad and El-Sarrag, 1978, 1980; Mohamed, 1982; Mogga, 1988) were named as *A. m. nubica* Ruttner 1976 (Rutter 1976c), but later Ruttner (1988) argued that these bees were morphometrically indistinguishable from *A. m. jemenitica* of the Arabian Peninsula. However, Ruttner (1988) recognized the presence of several different populations of *A. m. jemenitica* in the region. These

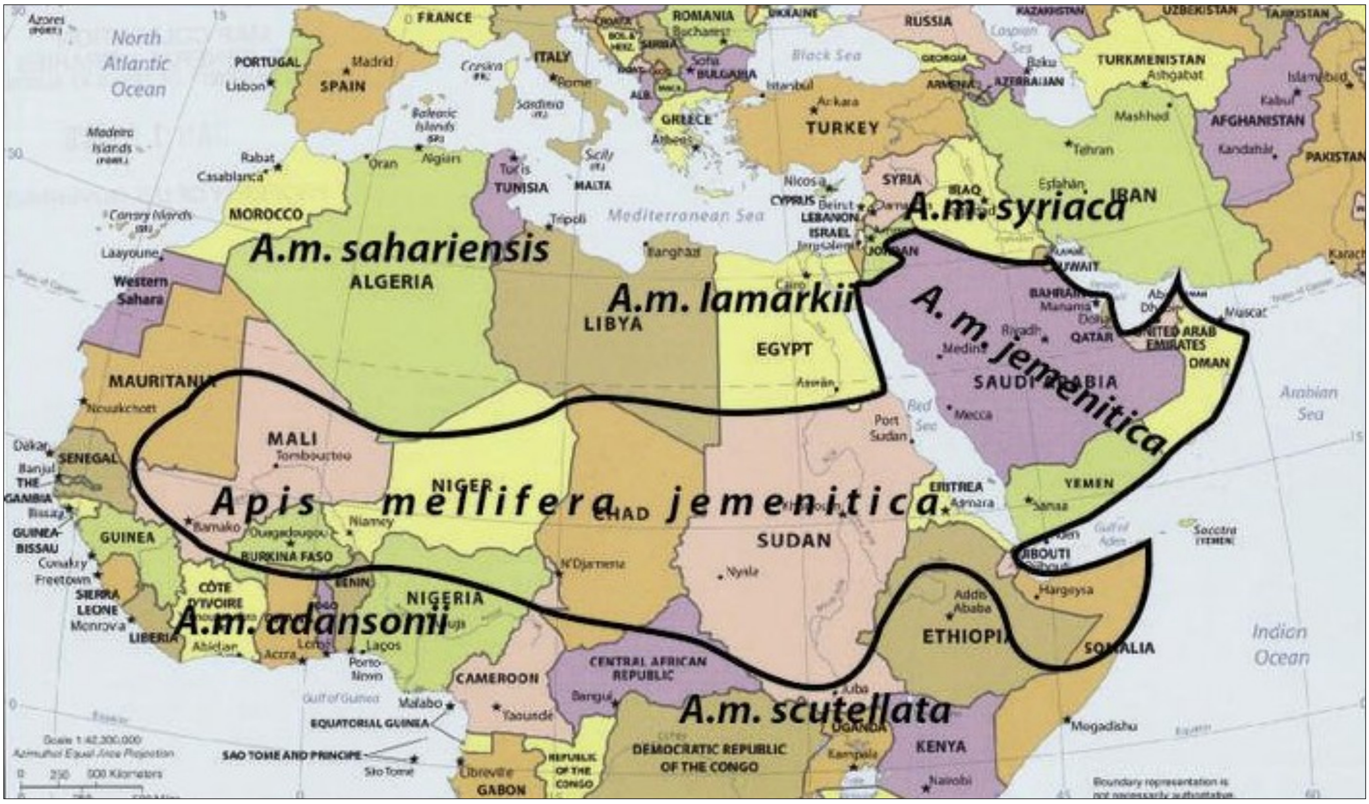

Fig. 1. The distribution of *Apis mellifera jemenitica* in Africa and Asia (all areas within bold line) based on published reports (Ruttner, 1988; Hepburn & Radloff, 1998).

populations vary considerably in many characters related to body size, hair length and intensity of colour (Table 1). Moreover, El-Sarrag, *et al.* (1992) reported the presence of two different races in Sudan: *A. m. sudanensis* and *A. m. nubica,* but did not comment on whether *A. m. jemenitica* occurred in that country.

The identity of the honey bees of Saudi Arabia is also under investigation: they may prove to be a distinct subspecies, or an ecotype of the *A. m. jemenitica* found in Oman and Yemen. As the density of sampling across Africa and the Arabian Peninsula increases, it is likely there will continue to be changes and improvements in our assessment of the identity and distribution of *A. mellifera* subspecies.

Morphometric values of *Apis mellifera jemenitica*

Morphometrically, *Apis mellifera jemenitica* is the smallest of all races of *A. mellifera* both in body size and hair length (Ruttner, 1988). Even though all the honey bee populations of the above mentioned geographical areas are considered to be *A. m. jemenitica,* local populations across its wide distribution have distinct morphometric values. Ruttner (1988) recognized five populations of *Apis mellifera jemenitica* (Saudi Arabia, Oman-Yemen, Somalia, Sudan and Chad) with considerable morphometric variation among them (Table 1).The *Apis mellifera jemenitica* of the Arabian Peninsula differ from those of Africa in both body size and colour. The colour of the *A. m. jemenitica* of Africa is a more intense yellow (pigmentation of tergite 4) than that of *A. m. jemenitica* of the Arabian Peninsula (Table 1). For example, Amssalu *et al.* (2004) reported more intense yellow pigmentation values for *A. m. jemenitica* populations from Ethiopia than from the Arabian Peninsula. Worker honey bees with entirely yellow abdomens without any bands and drones with yellow abdomens were observed in the *A. m. jemenitica* population of Ethiopia (Nuru, 2002). Moreover, Hepburn and Radloff (1998) recognized morphometric variation among the populations of *A. m. jemenitica* of East and West Africa (Table 2). In addition, the morphometric values of *A. m. jemenitica* of Ethiopia (Amssalu *et al.*, 2004) differ considerably from those reported for *A. m. jemenitica* from West and East Africa, particularly in pigmentation and hair length (Table 2).

Variation is also observed among the *A. m. jemenitica* of the Arabian Peninsula and adjoining islands. Dutton *et al.* (1981) observed the presence of two widely separated populations of *A. m. jemenitica* in the mountains of northern and southern Oman based on morphometric values. They also compared morphometric values of the Omani and Yemeni populations and found that the mean values of characters related to body size were higher in the Omani population. In terms of colour, reports on the Omani and Yemeni populations are contradictory. Dutton *et al.* (1981) reported that the Omani population were intensely yellow bees, with values of 5.6 to 8 on the colour scale for tergite 3 and the scutellum, while Karpowicz (1989) reported that the same bees varied from dark brown to very dark grey to almost black. Aqlan (1999) showed that the morphometric and colour values of

Table 1. Morphometric values (mean ± standard deviation) of five populations of *Apis mellifera jemenitica* (from Ruttner, 1988).

Population	No.	Length of tergites 3 & 4 (mm)	Proboscis length (mm)	Forewing length (mm)	Hind leg length (mm)	Hair length (mm)	Cubital vein 1 (mm)	Angle J 16 (degrees)	Tergite 4 colour
Saudi Arabia	6	3.748 ± 0.153	5.277 ± 0.210	7.868 ± 0.224	6.916 ± 0.259	0.172 ± 0.021	2.28 ± 0.25	89.94 ± 2.90	4.60 ± 0.99
Yemen & Oman	30	3.937 ± 0.137	5.481 ± 0.132	8.135 ± 0.192	7.120 ± 0.219	0.195 ± 0.020	2.20 ± 0.40	91.09 ± 4.16	4.52 ± 1.27
Somalia	9	3.981 ± 0.121	5.552 ± 0.120	8.214 ± 0.179	7.207 ± 0.203	0.213 ± 0.017	2.27 ± 0.36	99.33 ± 8.03	7.75 ± 1.03
Sudan	5	3.965 ± 0.180	5.450 ± 0.187	8.219 ± 0.214	7.214 ± 0.245	0.193 ± 0.033	2.45 ± 0.42	92.60 ± 3.49	6.38 ± 1.15
Chad	8	3.914 ± 0.121	5.356 ± 0.187	8.136 ± 0.141	7.175 ± 0.265	0.211 ± 0.019	2.39 ± 0.38	95.90 ± 3.96	5.36 ± 1.11

Table 2. Morphometric values (mean ± standard deviation) of West African and North East African *Apis mellifera jemenitica* populations.

Population	Hair (1)	Sternite 3 length (11)	Wax plates of sternite 3 width (13)	(22) Wing angle B4	(30) Wing angle N23	(31) Wing angle O26	(32) Pigment of tergite 2	(35) Scutellum colour	(36) Scutellar plate colour (B,K)
West Africa (Hepburn & Radloff, 1998)	0.20 ± 0.02	2.43 ± 0.07	1.98 ± 0.06	101.88 ± 4.16	89.78 ± 2.24	38.55 ± 2.49	8.72 ± 0.63	6.75 ± 0.94	2.97 ± 1.76
North East Africa (Hepburn & Radloff, 1998)	0.21 ± 0.02	2.48 ± 0.07	2.07 ± 0.06	106.45 ± 6.61	89.85 ± 3.32	37.55 ± 2.44	8.83 ± 0.24	5.87 ± 1.96	2.42 ± 1.19
Ethiopia (Amssalu *et al.*, 2004)	0.17 ± 0.02	2.48 ± 0.06	2.05 ± 0.06	104.9 ± 3.33	89.11 ± 2.23	37.07 ± 1.96	6.88 ± 1.70	4.39 ± 1.93	1.94 ± 1.19

Apis mellifera jemenitica from different localities in Yemen (Sana'a, Ibb, Taiz, Mareb, Hajh, and Hhodieda) were variable. Larger and darker bees were found at higher altitudes and smaller bees with lighter colour in the coastal areas. Moreover, Khanbash (1990, 2002) reported a high degree of variability, both in body size and pigmentation, in Yemeni honey bee populations, observing completely grey and yellow *A. m. jemenitica* in different ecological areas of Yemen.

Al-Gamdi (2006) also studied morphological and histological characters of some glands of the Saudi Arabian *Apis mellifera jemenitica*. The mean values of some morphometric characters, like width of the wax gland mirror on sternite 3 (1.95 mm) reported for this population differs from the values (2.05 ± 0.06 mm) reported for the *A. m. jemenitica* of Ethiopia (Amssalu *et al.*, 2004).

Overall, there appears to be a high degree of variation in morphometric values among the different populations of *A. m. jemenitica,* particularly between populations of Africa and the Arabian Peninsula. The pooled mean morphometric values of body size, hair length and pigmentation of the African and Asian populations show differences between the two populations (Fig. 2).

Behavioural aspects of *Apis mellifera jemenitica*

Management of *Apis mellifera jemenitica* in box hives

Beekeeping with *Apis mellifera jemenitica* is widely practiced in most areas of its distribution, both in Africa and Asia. Most colonies are kept in traditional hives, so that their commercial value when kept in box hives has not been established. In a study of the Saudi Arabian population, (Al-Ghamdi, 2005b), *A. m. jemenitica* colonies transferred from traditional hives to box hives with beeswax foundation and supplementary feeding were observed to establish successfully. This helped to debunk the belief of many beekeepers that *A. m. jemenitica* does not adapt to box hives, which is a common challenge for most African beekeepers. The study further demonstrated that colonies with beeswax foundation sheets are able to rear more brood and store more honey and pollen per season than colonies without beeswax foundation, indicating a good potential for the race in commercial beekeeping.

Resistance to *Varroa* mites by *Apis mellifera jemenitica*

Khanbash (2002) studied grooming behaviour in *Apis mellifera jemenitica* and reported a high level of cleaning out mites. Moreover, he noticed that the average duration of the worker bee pupal stage of some Yemeni populations is shorter than others by 11 h. A short capped brood period is reported to be very important in minimizing *Varroa* mite infestations. Indeed, for every 1 h reduction of the capped brood period, there is a reduction in the infestation level of *Varroa* mites by 8.7% (Buchler and Drescher, 1990). Bayaqhob *et al.* (2010) demonstrated well-developed hygienic behaviour in some populations of *A. m. jemenitica* in Yemen in that the bees remove all dead brood within 12 h, which indicates the potential of this race to protect itself against *Varroa* mites.

However, in most of the Arabian Peninsula countries where *A. m. jemenitica* naturally occurs, there is a high potential threat from the large-scale importation of other races of honey bees, such as *A. m. carnica* and *A. m. ligustica,* because interbreeding could dilute the genetic composition of the local honey bee populations, making

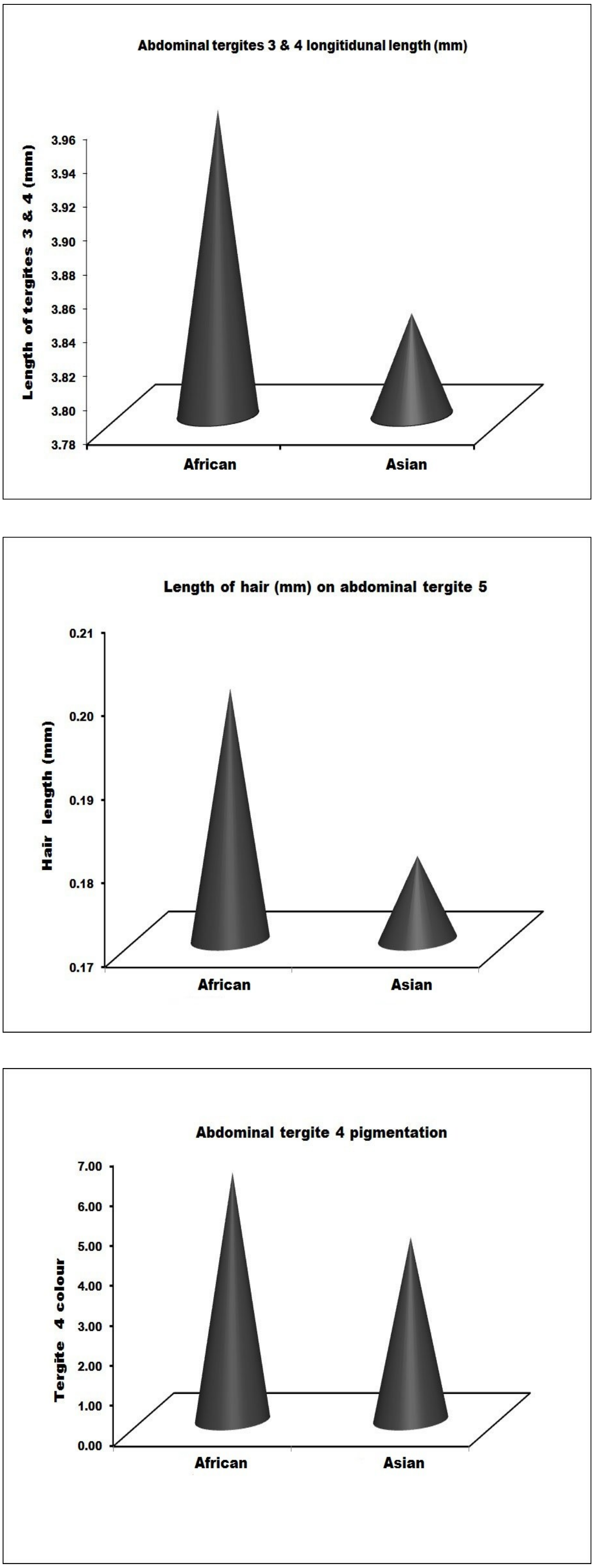

Fig. 2. The mean values of some morphometric characters of African and Asian populations of *Apis mellifera jemenitca.*

them more susceptible to various honey bee diseases and parasites. Imported races are generally poorly adapted to conditions in the Arabian Peninsula; more than 70% of imported bees perish every year because they are unable to withstand the environmental conditions of the region. Thus large numbers of colonies are imported each year, which also increases the risk of introduced diseases and pests. A policy of intervention is very necessary to conserve the local genetic resources.

Brood-rearing and colony growth

Generally, *Apis mellifera jemenitica* can quickly increase colony size, an important adaptive feature in a semi-arid habitat where rainfall and flowering periods are very short (Chandler, 1976). Because of their small body size, the average numbers of natural worker cells are relatively high, at 1,025 cells/dm^2 (Gadbin *et al.*, 1979; Dutton, *et al., 1981*; Karpowicz, 1989; Woyke 1993). Moreover, Al-Ghamdi (2005a) reported that natural combs built by the *A. m. jemenitica* population of Saudi Arabia contained on average 25% more cells/dm^2 than combs built on embossed European wax foundation sheets. As a result, the number of bees that can be raised per unit area in a given period of time is relatively high compared to European bees. The fast colony growth of *A. m. jemenitica* could be a positive trait in commercial, and especially migratory, beekeeping. Khanbash (1995) reported that during the peak brood-rearing period, queens of the Yemeni population of *Apis mellifera jemenitica* lay an average of 856 eggs/day and may reach a peak of 1,212 eggs/day and the African race may reach peak rate of 2,500 eggs/day (Fletcher, 1978).

Phenology of *Apis mellifera jemenitica*

The phenology of brood-rearing and reproductive swarming in *Apis mellifera jemenitica* differs among regions. In Oman, maximum brood-rearing and swarming were reported for the months of January –February and June–August, following the monsoon rains (Hussein, 1992). In Saudi Arabia, peak pollen collection and brood-rearing seasons were reported to take place between March–June (major period) and October–November (minor) (Alqarni, 1995). Alqarni (1995) reported a higher tendency for reproductive swarming in the *A. m. jemenitica* population of Saudi Arabia than in the imported Carniolan bees, and a maximum of 16 queen cells/colony was reported for the month of October for the local population.

Migration

The African ecotypes of *Apis mellifera jemenitica* are reported to have a relatively high incidence of migration in sub-Saharan Chad and Sudan (Gadbin, 1976; Rashad and El-Sarrag, 1978; Rashad and El-Sarrag, 1980; Paterson, 1985; Sawadogo, 1993; Woyke, 1993; Hepburn and Radloff, 1998). Moreover, in the northwestern parts of Ethiopia, *A. m. jemenitica* is adapted to a migratory way of life to exploit the seasonally available resources in different ecological habitats (Nuru, *et al.,* 2002). However, *Apis mellifera jemenitica* is reported not to migrate in north Oman and Yemen (Ruttner, 1988); likewise, the absence of annual migration of these bees in Saudi Arabia has been reported (Alqarni, 1995). The bees are reported to over-winter by maintaining a reduced colony density and relatively high stores of honey and pollen (Alqarni, 1995), much like temperate races of *A. mellifera.* These differences could well have a genetic basis.

Temperament

Apis mellifera jemenitica is reported to be docile in very hot North Oman and North Yemen (Dutton *et al*., 1981), and in Saudi Arabia it is reported to be so gentle that it does not sting even after provocation (Alqarni, 1995). As a result, honey bees of Saudi Arabia may be examined and manipulated at any time of day by workers with minimum protective clothing or equipment. On other hand, the *A. m. jemenitica* of Sudan and Chad are reported to be very aggressive (Gadbin, 1976; Rashad and El-Sarrag, 1980; Field, 1980). In Ethiopia, *A. m. jemenitica* were reported to be more aggressive than other subspecies (Nuru, 2002). Behaviourally, the African and Asian populations of *A. m. jemenitica* are distinctly different.

Genetic aspects

The genetic relationship between African and Arabian Peninsula *Apis mellifera jemenitica* populations, and their relationships to other surrounding subspecies have not been conclusively addressed. The available mitochondrial DNA (mtDNA) studies indicate that several different mtDNA haplotypes are found in populations referred to as *Apis mellifera jemenitica*. Ethiopian samples referred to as *Apis mellifera jemenitica* (n = 16 colonies from 3 sites) were reported to possess a new mitochondrial lineage "Y" which differs from the "O" lineage of Near East Asia and "A" lineage of Africa (Franck *et al.,* 2001). The honey bees of Sudan are classified as *Apis mellifera jemenitica* based on morphometrics (Ruttner, 1988), but mtDNA analysis did not confirm the presence of "Y" lineage (El-Niweiri and Moritz, 2008). Likewise, preliminary studies of *A. m. jemenitica* from Saudi Arabia (8 colonies) and Yemen (Socotra Island, 7 colonies) revealed the presence of O and A lineage haplotypes, but did not detect any Y lineage mitochondrial sequences (Smith, unpublished data). These results are consistent with the contention of Meixner *et al*. (2011) that *A. m. simensis* of Ethiopia is distinct from *A. m. jemenitica*.

This situation seems analogous to that of *A. m. monticola*. *Apis mellifera* populations in different high mountain areas of Africa have been grouped together as *Apis mellifera monticola* on the basis of morphometric similarity (Meixner *et al.,* 1989); this suggested that these were relicts of a once larger population that occupied lower elevations at times when the climate was cooler. However, a later mtDNA study (Hepburn *et al.,* 2000) did not support the idea of a monophyletic group of relictual populations occupying an archipelago of high altitude habitat islands. On the basis of mtDNA evidence, they concluded that the populations on different mountains should be regarded as ecotypically differentiated populations, each derived from the populations surrounding their particular mountain and convergent on morphology adapted to high altitude habitats (Hepburn and Radloff, 1998).

A similar situation may pertain to *A. m. jemenitica*. The morphometrically similar African and Asian populations currently called "*Apis mellifera jemenitica"* could comprise a single monophyletic lineage, adapted to hot, arid conditions. Alternatively, *A. m. jemenitica* could comprise several different, genetically distinct populations that differentiated from their respective neighbouring populations and converged on similar physical characteristics along with adaptation to similar hot arid habitats. These populations might also experience gene flow from other neighbouring populations, leading to the introduction and spread of mtDNA haplotypes characteristic of their neighbours. In this regard Franck *et al.* (2001) particularly suggested the importance of surveying microsatellites or other nuclear markers of the honey bee subspecies from Eastern Africa and the Middle East, to better understand their phylogeography.

The African and Asian *Apis mellifera jemenitica* have been geographically isolated from one another for several thousands of years, and the occurrence of independent evolutionary changes as a result of long-term geographical isolation has been well stated (Avise *et al.,* 1987; Smith 1991a, 1991b; Smith 2002). The newly described *A. m. simensis* in Ethiopia indicates that much additional survey of African and Arabian populations is needed before the diversity and distribution of *A. m. jemenitica* can be described with certainty.

Ambiguities in the classification of *Apis mellifera jemenitica*

The three major views on the observed geographical variation among populations of honey bees consider them as: (1) subspecies or geographical races (e.g. Ruttner, 1988), (2) adaptive ecotypes derived from adjacent populations (Kerr, 1992), or (3) products of asynchronous gene fluctuations within a contiguous metapopulation for which the term "subspecies" may not be appropriate (Hepburn and Crewe, 1990; Hepburn and Radloff, 1998). However, none of these views satisfactorily match with the classification of the *Apis mellifera jemenitica* populations of Asia and Africa into a single race.

In their classification of African honey bee races, Kerr and Portugal-Araújo (1958) and Kerr (1992) recognized only five subspecies (*capensis, scutellata, unicolor, lamarckii,* and *intermissa*). Their major considerations for the classification of different African races were geographical and reproductive isolation and (in the case of *Apis mellifera capensis*) biological variations. Both Ruttner (1988) and Hepburn and Radloff (1998) recognized ten subspecies or morphoclusters of African *A. mellifera*: *intermissa* and *sahariensis* in northwest Africa; *lamarckii* in Egypt; *jemenitica, adansonii, scutellata, litorea, monticola* and *capensis* in sub-Saharan Africa and *unicolor* in Madagascar. In Hepburn and Radloff's (1998) analyses, *A. m. jemenitica* extends from the Horn of Africa in the east, across the Sahel, to the west coast of Africa. More recently *A. m. simensis* has been proposed as a name for all

Ethiopian bees formerly identified as *A. m. jemenitica* (Meixner *et al.,* 2011). Practical challenges to infra-specific classifications arise from inconsistent morphometric reports. The differences among reports are due to many factors: natural variability of the bee populations of different regions; lack of uniformity in samples sizes; types of characters chosen and subjective variation in the measurement of sizes of body parts and classification of pigments, among others.

A second and fundamental problem in recognition of honey bee subspecies is that the term "subspecies" is ambiguous. Historically, honey bee subspecies have been recognized on the basis of geographic distribution and morphometric measurements, though some authors have also made note of behavioural and physiological differences among geographic populations. Ruttner (1988 and works cited there-in) created a standardized set of morphometric measurements by which subspecies could be described and compared.

For some authors, the subspecies is primarily a descriptive term indicating a morphologically recognizable population, usually occurring in a defined geographic location. The study of honey bee subspecies began long before it was possible to directly assay genetic polymorphisms in honey bees; but with a strictly morphometric definition of subspecies, there was no necessary reason to expect morphometric, nuclear DNA and mtDNA data to show congruent patterns. Nonetheless, there was an implicit expectation that most morphological characteristics had a genetic underpinning, and thus, that morphometric similarity could be used to infer genetic similarity and evolutionary relationships.

For other researchers, the use of a Linnaean trinomial implies a monophyletic linage that has diverged from other conspecific populations; in this case, one would expect data from mtDNA, nuclear DNA, and morphometrics to be largely congruent. However, morphometric and genetic characters may not be congruent for a number of reasons. For example, lineage sorting may be incomplete, particularly for recently diverged populations. When geographically isolated subspecies come into secondary contact, gene flow between them is then possible and subspecies boundaries can become blurred by hybridization. The continued existence of a subspecies then may depend on the fitness of hybrids, the continued existence of the habitat to which they are best adapted, mate choice, and the relative size of the two hybridizing populations, among other factors.

Although honey bees from the Arabian Peninsula, North-East Africa and parts of West Africa are considered to be *Apis mellifera jemenitica*, there is a high degree of variation and morphologically differentiated local populations are well recognized within the subspecies (Ruttner, 1976a, 1976b; Dutton and Free, 1979; Dutton *et al.*, 1981; Karpowicz, 1989; 1990; Radloff and Hepburn, 1997; Aqlan, 1999). Moreover, *Apis mellifera jemenitica* is reported to hybridize with adjacent races, like *A. m. adansonii* in West Africa (Hepburn and Radloff, 1998) and with *A. m. bandasii* in East Africa (Amssalu, *et al.*, 2004) further increasing diversity among populations normally assigned to *Apis mellifera jemenitica.* Hybridization with the adjacent *A. m. syriaca* has not yet been reported. Thus, for many reasons, the classification of *Apis mellifera jemenitica* has remained more ambiguous than that of any other race of *A. mellifera* because, first, the various available morphometric reports were not in agreement. Second, the genetic similarity of African *A. m. jemenitica,* with the Asian population which is geographically isolated, has not been substantiated or compared with the levels of similarity among other adjacent populations which have continuous exchange and homogenization of genes, like with subspecies *litorea, adansonii* and *scutellata*. Third, the African and Asian *A. m. jemenitica* are distinctively different behaviourally, particularly in respect to annual migration and temperament. In contrast, *Apis mellifera scutellata* and *A. m. capensis* are not geographically isolated and have little significant variation in morphometric values but are nonetheless considered to be separate races based on various non-morphometric characters (Ruttner, 1977a, 1977b; Hepburn and Crewe, 1990).

On other hand, the existence of a single race of honey bee (*A. m. jemenitica)* across isolated geographical locations after thousands of years of geographical and reproduction isolation would be very interesting. Such a situation would demonstrate that environmentally-induced morphometric factors could be more important than genetic factors in the classification used to describe honey bee races, since the bees of the two regions are reported to be morphologically close but may well be genetically distinct.

Besides geographical isolation and significant behavioural differences between African and Asian populations, the limited mtDNA studies available for *Apis mellifera jemenitica* of Ethiopia, Sudan and the Arabian Peninsula do not support each other (Franck *et al.,* 2001; El-Niweiri and Moritz, 2008; Smith unpublished data). Does this sub-species belong to the "O" lineage of Near East Asia (Franck, *et al.*, 2001; Palmer *et al.*, 2000), the "Y" lineage of the Horn of Africa (Franck *et al.*, 2001), or the "A" lineage of Africa (Ruttner *et al.*, 1978; Ruttner, 1988; Franck *et al.*, 2001)? It is likely that the answer will be different depending on which population is examined.

Discussion

The different populations of *Apis mellifera jemenitica* are generally considered to be a single race based on shared morphometric characters. Nevertheless, the categorization of the Asian and the African populations of *A. m. jemenitica* — which have been geographically isolated for thousands of years without exchanges of genes and which occur under different ecological conditions — as one honey bee race is questionable. In addition to the geographical isolation of the bees of these regions, there are significant differences in their behavioural characteristic (temperament, migration and swarming) and the distribution of mtDNA haplotypes. In this regard, categorizing honey bees with such disparate distributions into one subspecies, without considering the genetic relationships, behavioural variations and geographical isolation between them seems unwarranted.

Another important issue is that the original homeland of the *Apis mellifera* species is thought to be the Near East, Asia or Africa. In this regard, Ruttner *et al*. (1978) based on morphometric studies and Whitfield *et al.* (2006) based on single nucleotide polymorphisms data suggested that Africa was the probable centre of the origin for *A. mellifera*. Alternatively, Franck *et al.* (2001) suggested that *A. mellifera* originated in Asia and colonized Africa via the Rift Valley in the Horn of Africa. *Apis mellifera jemenitica* is important to this debate because its present homeland, stretching from Asia to Africa, has been suggested as the origin of *A. mellifera* by both sets of authors. In either case, one of the populations currently called "*Apis mellifera jemenitica*" could be the basal race within the *A. mellifera* phylogeny.

This leaves several questions to be resolved: is *Apis mellifera jemenitica* of the two regions one race or two? Are the African and Asian *Apis mellifera jemenitica* more closely related to one another or to the other sympatric races found in their respective regions? Is *A. m. jemenitica* basal within the *Apis mellifera* phylogeny? Is it possible that secondary contact and gene flow between formerly isolated subspecies has created a population with unique characteristics, different from either parental subspecies? These questions are essential in further research and the region is a hot spot for evaluating questions about *Apis mellifera* as a species in general and *Apis mellifera jemenitica* in particular. Hence holistic approaches that include all possible data, such as morphometric, biological, behavioural and genetic characters, and covering all its areas of distribution, would be essential to resolve the classification of *Apis mellifera jemenitica* and to understand more about origin and diversification of *Apis mellifera*.

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