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Review

A revision of subspecies structure of western honey bee *Apis mellifera*

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ABSTRACT

The taxonomy of honey bee *A. mellifera* contains a lot of issues due to the specificity of population structure, features of biology and resolutions of honey bee subspecies discrimination methods. There are a lot of transition zones between ranges of subspecies which led to the gradual changes of characteristics among neighbor subspecies. The modern taxonomic pattern of honey bee *Apis mellifera* is given in this paper. Thirty-three distinct honey bee subspecies are distributed across all Africa (11 subspecies), Western Asia and the Middle East (9 subspecies), and Europe (13 subspecies). All honey bee subspecies are subdivided into 5 evolutionary lineages: lineage A (10 subspecies) and its sublineage Z (3 subspecies), lineage M (3 subspecies), lineage C (10 subspecies), lineage O (3 subspecies), lineage Y (1 subspecies), lineage C or O (3 subspecies).

Contents

1. Introduction

The honey bee species *Apis mellifera* Linnaeus, 1758 is distributed in a wide range with various climatic conditions and is subdivided into numerous subspecies Ruttner, 1988; Sheppard et al., 1997; Engel, 1999). Different taxonomic revisions described 20–30 subspecies for the *A. mellifera* (Buttel-Reepen, 1906; Enderlein, 1906; Skorikov, 1929a, 1929b; Maa, 1953; Ruttner, 1988; Engel, 1999). The taxonomy of honey bee *A. mellifera* is contradictory and remains a number of errors and issues. Some honey bee subspecies described only by morphometry without any molecular proves (Maa, 1953; Ruttner, 1988; Arias and Sheppard, 1996; Franck et al., 2000; Smith, 2002; Kandemir et al., 2011).

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The subspecies composition of the evolutionary lineages A (+Z), M, C, O, Y has not yet been resolved and need in comprehensive molecular evidence (Smith, 1991; Smith et al., 1997; Garnery et al., 1992; Kandemir and Kence, 1995; Alburaki et al., 2011, 2013).

Since the honey bee subspecies are described as geographic races the confusion in their geographical localization and genes distribution are observed in Africa (Ruttner, 1992; Hepburn and Radloff, 1998; Dukku, 2016), in Europe (Ruttner, 1988; Cornuet and Garnery, 1991; Smith, 1991; Franck et al., 1998), and in Near East (Franck et al., 2000; Kandemir et al., 2006; Alburaki et al., 2011, 2013). The clarification of all confusions in honey bee *Apis mellifera* taxonomy is the main aim of this paper. Here we described all new, old, synonymic, and misspelled taxonomic names of honey bees *A. mellifera*.

2. The approaches to identify the taxonomic affiliation of the honey bee *A. Mellifera*

The methods of identification of the taxonomic affiliation of honey bee *A. mellifera* based on morphometry are subdivided into two groups: 1. the body parts measurement; 2. the wing shapes analysis. For discrimination of honey bee subspecies, the classical morphometry uses the measurement of 36 characters of body parts (Ruttner, 1988). Other popular morphometrical approaches for identification of the taxonomic affiliation of honey bee colonies based on analysis wing shapes. There are three different wing morphometry based approaches for discrimination of honey bee subspecies: classical wing morphometry (DuPraw, 1965), the DAWINO (Discriminant Analysis with Numerical Output) (www.beedol.cz) and geometric morphometry (Bookstein, 1991). Classical wing morphometry captures variation in wing shape by calculating 11 angles between 18 junctions in the wing venation, which constitute a subset of a suite of 17 angles. The DAWINO method consists of the full set of DuPraw's angles, supplemented by 7 linear measurements, 5 indices, and one area. The geometric morphometry uses DuPraw's coordinates of points called landmarks which is analyzed by multivariate statistical methods (Miguel et al., 2011).

The allozyme based method of identifying the taxonomic affiliation of honey bees based on the variability of isoenzymes. In honey bees six enzymes are polymorphic: malate dehydrogenase MDH1 (EC 1.1.1.37) (7 alleles) (Smith and Glenn, 1995); malik-enzyme ME (EC 1.1.1.40) (4 alleles) (Sheppard and Berlocher, 1984); esterase EST-3 (EC 3.1.1) (8 alleles) (Ivanova et al., 2010); alkaline phosphatase ALP (EC 3.1.3.1) (3 alleles) (Ivanova et al., 2010); phosphoglucomutase PGM (EC 5.4.2.2) (5 alleles) (Ivanova et al., 2010); hexokinase HK (EC 2.7.1.1) (5 alleles) (Del Lama et al., 1990).

The mitochondrial DNA (mtDNA) based methods of identification the taxonomic affiliation of honey bees based on its nucleotide polymorphism. There are three main directions of mtDNA based discrimination of honey bees: 1. Restriction Fragment Length Polymorphisms by restriction enzymes (RFLP) (Smith and Brown, 1988; Smith et al., 1989; Smith, 1991; Garnery et al., 1992) and RFLP of fragments amplified by PCR (PCR-RFLP) (Hall and Smith, 1991; Arias and Sheppard, 2005; Stevanovic et al., 2010; Ivanova et al., 2010); 2. Polymorphism of PCR products with specific (Arias and Sheppard, 2005) or random primers – Random amplified polymorphic DNA (RAPD) amplification (Hunt and Page, 1994; Suazo et al., 1998; Tunca and Kence, 2011); 3. Sequencing of the mtDNA with the quest of single nucleotide polymorphisms (SNPs) (Arias and Sheppard, 1996, 2005; Franck et al., 1998, 2000, 2001; Franck et al., 2001; Collet et al., 2006; Shaibi et al., 2009; Pinto et al., 2012; Pinto et al., 2014; Ilyasov et al., 2016, 2019). The study of mtDNA was based on the analysis of complete or partial mitochondrial genome or intergenic sequences IGS. The most polymorphic IGS is the region located between genes COX1 and COX2 of mtDNA (Hall and Smith, 1991; Crozier et al., 1991; Arias and Sheppard, 1996; Jensen et al., 2005; Ilyasov et al., 2007, 2011, 2016, 2019; Cánovas et al., 2008; Muli et al., 2014).

The nuclear DNA (nDNA) based methods of identification of the taxonomic affiliation of honey bees focused on its nucleotide polymorphism. The polymorphism of nDNA can be detected by three main approaches: 1. Polymorphism of PCR products with specific (Arias and Sheppard, 2005; Il'yasov et al., 2015; Kent et al., 2011, 2012) or random RAPD primers amplification (Hunt and Page, 1994; Waldschmidt et al., 2002; Kumar and Khan, 2014); 3. Sequencing of the mtDNA with the quest of single nucleotide polymorphisms (SNPs) (Chapman et al., 2015, 2016, Harpur et al., 2014, 2015; Henriques et al., 2018; Il'yasov et al., 2015; Ilyasov et al., 2016; Pinto et al., 2014; Wallberg et al., 2014, 2019; Whitfield et al., 2006); 4. Whole-genome sequencing by NGS methods (Weinstock et al., 2007; Whitfield et al., 2006; Wallberg et al., 2014, 2019). The most polymorphic nDNA loci are microsatellite repeats – Short Tandem Repeats (STR) that are detected by PCR with specific primers (De La Rúa et al., 2001; Estoup et al., 1995; Franck et al., 2000, 2001; Garnery et al., 1998; Il'yasov et al., 2015; Ilyasov et al., 2016; Miguel et al., 2011; Solignac et al., 2003).

3. The current taxonomic pattern of the honey bee *A. Mellifera*

The taxonomy of honey bee *Apis mellifera* Linnaeus, 1758 (synonym: *Apis mellifica* Linnaeus, 1761, *Apis gregaria* Geoffroy, 1762, *Apis cerifera* Scopoli, 1770, *Apis daurica* Fischer von Waldheim, 1843) has a lot of unsolved issues. The number of honey bee subspecies and their subdivision on evolutionary lineages is not well clear yet (Smith 1991; Smith et al., 1997; Garnery et al., 1992; Kandemir and Kence, 1995; Alburaki et al., 2011, 2013).

The subspecies of honey bee *A. mellifera* were divided into three lineages (A, M, C) by morphometry firstly (about 20 subspecies) (Ruttner et al., 1978; Moritz et al., 1986; Smith and Brown, 1988; Smith, 1991; Garnery et al., 1992; Estoup et al., 1995), into four lineages (A, M, C, O) by morphometry and molecular data later (about 25 subspecies) (Ruttner, 1988; Smith and Brown, 1988; Cornuet et al., 1988; Lebdigrissa et al., 1991; Cornuet and Garnery, 1991; Smith 1991; Estoup et al., 1995; Arias and Sheppard, 1996; Franck et al., 1998; Palmer et al., 2000) and five lineages (A (+sublineage Z), M, C, O, Y) by molecular data finally (about 30 subspecies) (Franck et al., 2001; Alburaki et al., 2011, 2013; Meixner et al., 2013).

The greatest problem in the discrimination of subspecies was the presence of transition zones between the area of subspecies which led to gradient changes in morphometric and molecular features. Transition is observed between 8 subspecies (*A. m. adansonii – A. m. jemenitica*, *A. m. sahariensis – A. m. intermissa*, *A. m. intermissa – A. m. major*, *A. m. intermissa – A. m. scutellata*, *A. m. capensis – A. m. unicolor*) in Africa (Ruttner, 1992; Hepburn and Radloff, 1998; Dukku, 2016); between 3 subspecies (*A. m. intermissa – A. m. iberiensis*, *A. m. iberiensis – A. m. mellifera*) in Europe (Ruttner, 1988; Cornuet and Garnery, 1991; Smith, 1991; Franck et al., 1998); between 4 subspecies (*A. m. meda – A. m. anatoliaca*, *A. m. anatoliaca – A. m. syriaca*, *A. m. syriaca – A. m. lamarckii*) in Near East (Franck et al., 2000; Kandemir et al., 2006; Alburaki et al., 2011, 2013).

The honey bee subspecies can be affiliated variously by different methods. The subspecies *A. m. adansonii*, *A. m. monticola*, *A. m. scutellata*, *A. m. capensis* and *A. m. unicolor* cannot to be discriminated by morphometry (Ruttner et al., 1978), by mtDNA (Garnery et al., 1995; Sheppard et al., 1996), but can be discriminated by

Table 1
The current taxonomy of the honey bee *Apis mellifera*.

No	Subspecies name	Common Name	Lineage	Distribution
Africa (11 subspecies)				
	Apis mellifera lamarckii Cockerell 1906	The Egyptian honey bee	O	Egypt, Sudan
	Apis mellifera litorea Smith 1961	The East African coastal honey bee	A	Kenya
	Apis mellifera adansonii Latreille 1804	The West African honey bee	A	Nigeria, Burkina Faso, Uganda, Tanzania, Zambia, Senegal, Sudan
	Apis mellifera scutellata Lepeletier de Saint Fargeau, 1836	The African honey bee	A	Kenya, Tanzania, Uganda, Republic of South Africa, Somalia
	Apis mellifera monticola Smith 1961	The East African Mountain honey bee	A	Mountains of Kenya, Tanzania
	Apis mellifera capensis Escholtz 1822	The Cape honey bee	A	Cape region in the Republic of South Africa
	Apis mellifera unicolor Latreille 1804	The Madagascar honey bee	A	Madagascar
	Apis mellifera simensis Meixner et al., 2011	The Ethiopian honey bee	A	Ethiopia
	Apis mellifera sahariensis Baldensperger 1932	The Saharan honey bee	A	Morocco, Algeria, Tunisia, Libya, Mauritania, Western Sahara
	Apis mellifera intermissa Maa 1953 (synonym: *A. m. major* Ruttner et al., 1978) (Kerr, 1992; Hepburn and Radloff, 1998)	The Tellian honey bee	A	Morocco, Libya, Tunisia
	Apis mellifera jemenitica Ruttner 1976 (synonyms: Apis mellifera yemenitica Ruttner, 1988, *Apis mellifera nubica* Ruttner, 1976, *Apis mellifera sudanensis* Ruttner, 1988, *Apis mellifera bandasii* Radloff and Hepburn, 1997, and *Apis mellifera woyi-gambell* Amssalu et al., 2004) (Hepburn and Radloff, 1998; Amssalu et al., 2004; Meixner et al., 2011)	The Arabian honey bee	Y	Arabian Peninsula, Chad, Saudi Arabia, Somalia, Sudan, Uganda, Yemen
Western Asia and the Middle East (9 subspecies)				
	Apis mellifera ruttneri Sheppard et al., 1997	The Maltese honey bee	A	Malta
	Apis mellifera syriaca Skorikov 1929b	The Syrian honey bee	A (Z)	Syria, Israel, Lebanon, Palestine, Jordan
	Apis mellifera mellifera Linnaeus 1758 (synonyms: *Apis mellifica germanica* Pollmann, 1879, *Apis mellifica nigrita* Lucas, 1882, *Apis mellifica mellifica lehzeni* Buttel-Reepen, 1906, *Apis mellifica mellifica silvarum* Goetze, 1964)	The European dark honey bee	M	France, United Kingdom, Switzerland, European part of Russia, Poland, Denmark, Norway, Sweden, Ireland
	Apis mellifera pomonella Sheppard and Meixner 2003	The Tian Shan honey bee	O	Tian Shan mountains of Kazakhstan, Kyrgyzstan
	Apis mellifera sinisxinyuan Chen et al., 2016	The Xinyuan honey bee	M	Uygur Autonomous Region of China
	Apis mellifera meda Skorikov 1929b	The Persian honey bee	A (Z)	Iran, Iraq, Syria, Turkey
	Apis mellifera caucasia Pollmann 1889	The Caucasian honey bee	C	South Russia, Turkey, Georgia
	Apis mellifera remipes Gerstäcker1862 (synonym: *Apis mellifera armeniaca* Skorikov 1929b) (Hepburn and Radloff, 1998)	The Armenian honey bee	O	South Russia, Armenia, Iran, Georgia
	Apis mellifera anatoliaca Maa 1953	The Anatolian honey bee	A (Z)	Iran, Armenia, Syria, Turkey
Europe (13 subspecies)				
	Apis mellifera iberiensis Engel 1999 (new name for *Apis mellifera iberica* Ruttner 1988, preoccupied, nec Skorikov 1929)	The Spanish honey bee	M	Spain, Portugal
	Apis mellifera macedonica Ruttner, 1988	The Macedonian honey bee	C	Bulgaria, Greece, Macedonia, Ukraine
	Apis mellifera ligustica Spinola 1806	The Italian honey bee	C	Italia
	Apis mellifera carnica Pollman 1879 (synonyms: *Apis mellifica hymettea* Pollmann 1879, *Apis mellifera carniolica* Koschevnikov 1900, *Apis mellifica banatica* Grozdanic 1926, *Apis mellifera banata* Skorikov 1929b) (Hepburn and Radloff, 1998)	The Carniolan honey bee	C	Slovenia, Bulgaria, Poland, Austria, Croatia, Bosnia and Herzegovina, Serbia, Hungary, Romania
	Apis mellifera carpathica Foti 1965	The Carpathian honey bee	C	Ukraine, Bulgaria, Romania, Moldova
	Apis mellifera rodopica Petrov 1991	The Bulgarian honey bee	C	Bulgaria
	Apis mellifera cecropia Kiesenweiter 1860	The Greek honey bee	C	Greece
	Apis mellifera siciliana Dalla Torre 1896 (synonym: *Apis mellifera sicula* Montagano 1911) (Hepburn and Radloff, 1998)	The Sicilian honey bee	C	Sicily
	Apis mellifera adami Ruttner, 1975	The Cretan honey bee	C	Crete
	Apis mellifera cypria Pollman 1879	The Cyprus honey bee	C	Cyprus
	Apis mellifera artemisia Engel 1999 (new name for preoccupied: *Apis mellifera acervorum* Skorikov 1929b)	The Russian steppe honey bee	C or O	South Russia, Ukraine

(*continued on next page*)

Table 1 (*continued*)

No	Subspecies name	Common Name	Lineage	Distribution
	Apis mellifera sossimai Engel 1999 (new name for preoccupied: *Apis mellifera cerifera* Gerstäcker 1862)	The Ukrainian honey bee	C or O	Crimea, South Russia, Ukraine
	Apis mellifera taurica Alpatov 1935	The Crimean Honey Bee	C or O	Crimea, South Russia, Ukraine

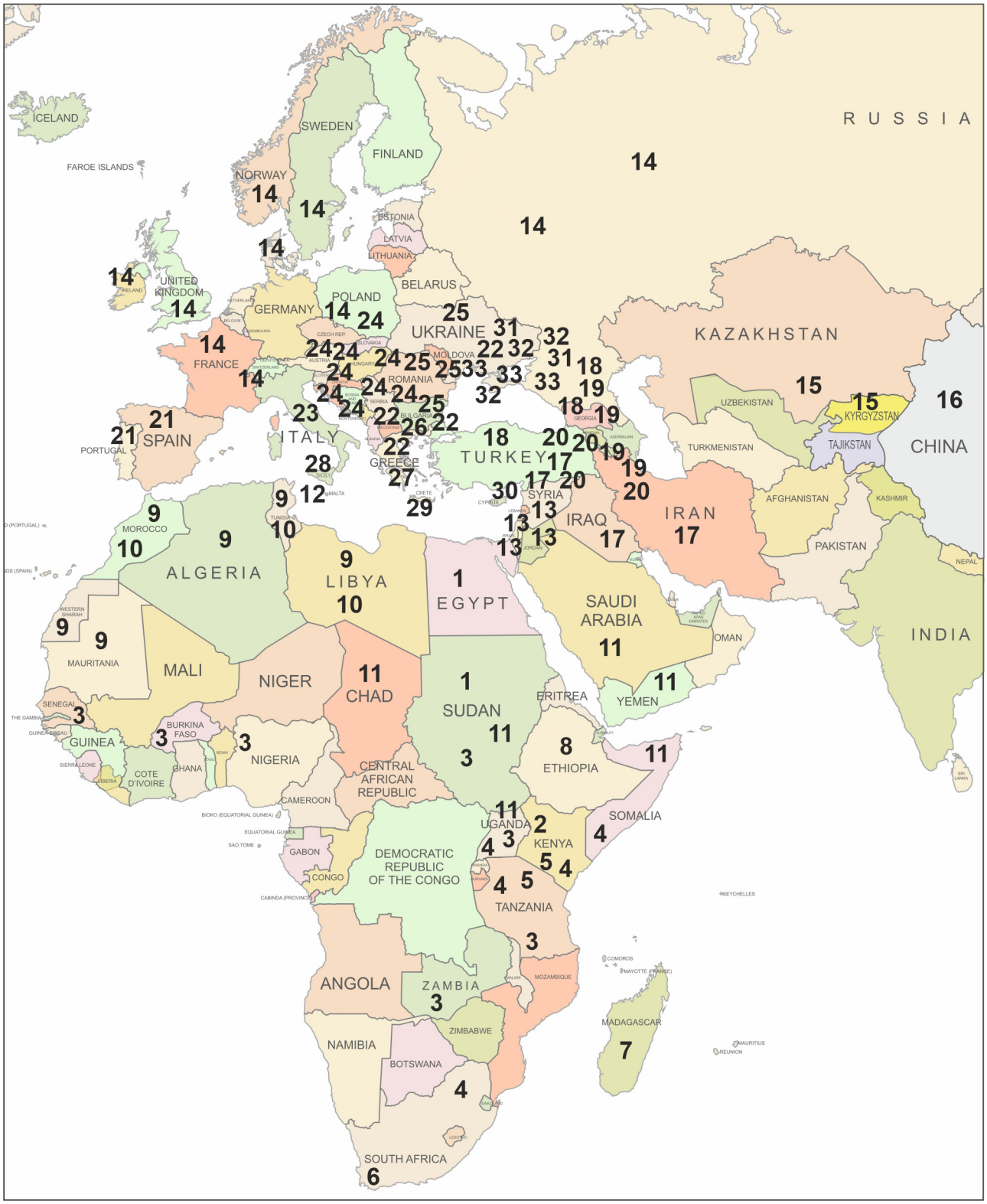

Fig. 1. The spatial distribution of 33 subspecies of honey bee *A. mellifera* on geographic map. The numbers correspond to numbers of subspecies in the table.

other morphometry (Ruttner, 1988), by allozyme (Meixner et al., 2000), by mtDNA (Franck et al., 2001; Kasangaki et al., 2017; Techer et al., 2017). The subspecies *A. m. jemenitica*, *A. m. adansonii* cannot be discriminated by morphometry (Radloff et al., 1998) but can be discriminated by other morphometry (Ruttner, 1988; Dukku, 2016), by mtDNA (Franck et al., 2001). The subspecies *A. m. carpathica*, *A. m. carnica*, *A. m. macedonica* cannot be discriminated by morphometry (Radloff et al., 1998) but can be discriminated by other morphometry (Foti et al., 1965; Engel, 1999; Cauia et al., 2008; Mărghitas et al., 2008; Teleky et al., 2009), by mtDNA (Mărghitas et al., 2009; Bouga et al., 2011; Coroian et al., 2014; Syromyatnikov et al., 2018; Ilyasov et al., 2018). The subspecies *A. m. rodopica*, *A. m. macedonica* cannot to be discriminated by morphometry (Engel, 1999), by allozyme (Bouga et al., 2005; Kandemir et al., 2005; Ivanova et al., 2010), but can be discriminated by other morphometry (Foti et al., 1965; Engel, 1999; Cauia et al., 2008; Mărghitas et al., 2008; Teleky et al., 2009), by mtDNA (Lazarov, 1936; Tzonev, 1960; Velichkov, 1970; Bouga et al., 2011), by microsatellites (Nikolova, 2011; Uzunov et al., 2014), by mtDNA (Bouga et al., 2005; Martimianakis et al., 2011; Meixner et al., 2013; Radoslavov et al., 2017).

The honey bee subspecies can be variously assigned to the evolutionary lineages by different methods. The subspecies *A. m. syriaca*, *A. m. anatoliaca, A. m. meda* assigned to the O lineage by morphometry (Ruttner, 1988), by mtDNA (Arias and Sheppard, 1996), but assigned to the A lineage (Z sublineage) by mtDNA (Arias and Sheppard, 1996; Franck et al., 2000; Bouga et al., 2005; Alburaki et al., 2011, 2013). The subspecies *A. m. caucasia* assigned to the O lineage by morphometry (Ruttner, 1988; Adl et al., 2007; Meixner et al., 2007; Kandemir et al., 2011), but assigned to the C lineage by mtDNA (Franck et al., 2000; Alburaki et al., 2011, 2013), by allozyme (Smith, 1991; Garnery et al., 1992; Kandemir and Kence, 1995; Ivanova et al., 2011), by mtDNA (Cornuet and Garnery 1991; Koulianos and Crozier, 1997; Smith et al., 1997; Garnery et al., 1998; Palmer et al., 2000; Franck et al., 2000; Smith, 2002; Özdil et al., 2009; Mărghitas et al., 2009; Ilyasov et al., 2018). The subspecies *A. m. cypria*, *A. m. adami* assigned to the O lineage by morphometry (Ruttner, 1988) but assigned to the C lineage by mtDNA and allozyme (Bouga et al., 2005). The subspecies *A. m. lamarckii* assigned to the A lineage by morphometry (Ruttner, 1988) but assigned to the O lineage by mtDNA (Arias and Sheppard, 1996). The subspecies *A. m. jemenitica* assigned to the A lineage by morphometry (Ruttner, 1988) but assigned to the Y lineage by mtDNA (El-Niweiri and Moritz, 2008; Alburaki et al., 2011, 2013; Coulibaly et al., 2019).

In the current review of all available literature, the existence of 33 subspecies of honey bee *A. mellifera* is stated. These 33 subspecies subdivided into five evolutionary lineages: lineage A – 10 subspecies, lineage A (sublineage Z) – 3 subspecies, lineage M – 3 subspecies, lineage C – 10 subspecies, lineage O – 3 subspecies, lineage Y – 1 subspecies, undefined lineage C or O – 3 subspecies. Geographically these subspecies distributed in three regions: Africa inhabited by 11 subspecies, Western Asia and the Middle East inhabited by 9 subspecies, Europe inhabited by 13 subspecies (Table 1). The spatial distribution of 33 subspecies of honey bee *A. mellifera* was shown on geographic map (Fig. 1).

4. Conclusions

The current taxonomic pattern of the honey bee *A. mellifera* is described. Thirty-three distinct honey bee subspecies are presented in Africa (11 subspecies), Western Asia and the Middle East (9 subspecies), Europe (13 subspecies), which subdivided into 5 evolutionary lineages: lineage A (10 subspecies), sublineage Z of the lineage A (3 subspecies), lineage M (3 subspecies), lineage C (10 subspecies), lineage O (3 subspecies), lineage Y (1 subspecies), lineage C or O (3 subspecies). The taxonomy of honey bee *A. mellifera* has a lot of issues due to the specificity of population structure and resolution of honey bee subspecies discrimination methods. Transition zones between ranges of honey bee subspecies led to the gradual changes of all characteristics between neighbors. There is constant gene flow between most of the subspecies due to the lack of natural isolation mechanisms. Some isolated populations remained on mountains and islands, like populations of the dark European honey bees on the Ural Mountains (Russia), Ireland (Republic of Ireland and Northern Ireland), and Læsø Island (Denmark). Leading by professor Nikolenko A.G. under the Grant RFBR No. 19-54-70002 e-Asia_t we are studying the taxonomy of the sisterly honey bee species Apis cerana based on molecular tools, and our further paper could be "A revision of subspecies structure of eastern honey bee Apis cerana".

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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