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A review of *Apis mellifera caucasica* (Hym., Apidae): History, taxonomy and distribution

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ABSTRACT. The taxonomic status and placement of the Caucasian honey bee (*Apis mellifera caucasica* Gorbachev, 1916) (Hymenoptera: Apidae) remains puzzling, largely based on outdated investigations. After reviewing available scientific sources, we conclude that initially there was a confusing mismatch between the traditional geographical understanding of the Caucasus and the actual distribution of *A. m. caucasica*. Insufficient geographic sampling of honeybees across the Caucasus, a statistically inadequate number of studied samples, and incomplete research methodology are major drawbacks of previous studies. Morphometric reference data derived from an extremely limited number of samples still is in use as a standard for the identification of *A. m. caucasica*. It is highly probable, that this standard does not reflect true morphometric diversity, covering natural geographical variations, which most importantly hinder preservation or breeding efforts. To resolve these deficits, honeybees of the Caucasus and adjacent regions need to be studied in more detail with greater depth of sampling. A thorough study, using modern morphometric approaches and molecular genetic methods, is needed to characterize *A. m. caucasica* and produce a statistically robust dataset for due reconsideration of its taxonomic status and placement.

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INTRODUCTION

Native honeybee populations are invaluable resources for sustainable beekeeping, demonstrating greater resilience within their natural habitats compared to introduced subspecies (Meixner et al., 2014). This has spurred significant conservation efforts in Western Europe (De La Rua et al., 2009), where native populations have often been replaced by commercially attractive subspecies (vanEngelsdorp & Meixner, 2010; Requier et al., 2019). Among these subspecies, *Apis mellifera caucasica* is globally renowned for its gentleness, rapid spring colony buildup, high nectar collection efficiency during moderate honey flows, and pronounced propensity for propolis collection (Bilash & Krivtsov, 1991). These traits often make it the species of choice even outside its natural distribution range, contributing to its commercial popularity (Farshineh Adl et al., 2007).

However, the genetic purity of *A. m. caucasica* faces significant risks due to migratory beekeeping practices and the introduction of non-native subspecies diluting the genetic traits unique to specific

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environments. Despite these threats, conservation initiatives for *A. m. caucasica* remain limited and poorly assessed. This delay arises in part from insufficient data on the natural distribution range and the ecotypes of the subspecies, complicating the development of effective conservation strategies. Moreover, the taxonomic status and placement of *A. m. caucasica* have been a subject of debate since its initial, controversial description by Pallas (Koschevnikov, 1900). Morphometric studies by Koschevnikov (1900), and Gorbachev (1916) highlighted unique morphological traits such as longer proboscis lengths and specific colouration patterns. However, these and subsequent studies, including those employing molecular biology tools, have been limited in scope, leaving critical gaps in understanding the subspecies' taxonomy, distribution, and biological variation.

This paper aims to address these gaps by revising and summarizing existing knowledge on the taxonomic placement, current distribution, biological characteristics, and conservation status of *A. m. caucasica*. Building upon Ruttner's (1988) summary, we incorporate additional insights from Georgian, Russian and English literature, offering a more comprehensive and updated perspective. By redefining terms such as "Caucasian honeybee" and *A. m. caucasica* within the context of the Caucasus as a distinct geographic zone, this study provides a multifaceted understanding of the subspecies and its conservation needs.

MATERIAL AND METHODS

This study is based on a comprehensive literature review covering historical and contemporary sources on *Apis mellifera caucasica*. The literature examined spans from the earliest references in the 1880s to the most recent studies published in 2024. The selection of sources prioritized available articles, monographs, and expert contributions discussing the taxonomy, biogeography, and conservation status of *A. m. caucasica*. The review mostly excluded fragmented and inconclusive DNA-based studies, as they do not provide a complete taxonomic picture. The natural distribution range of *A. m. caucasica* was delineated based on data from key sources, including Gorbachev (1916), Alpatov (1948), Ruttner (1988), Kandemir et al. (2005) and Çakmak et al. (2014). These references were supplemented with historical records and regional studies on honeybee populations in the Caucasus.

To define the borders of *A. m. caucasica*'s natural habitat, we used ecological and topographical data from WWf-Caucasus GRID-Arendal (http://www.grida.no/resources/7894) designed by Manana Kurtubadze (2016) alongside climatic and vegetation zone classifications by Zazanashvili et al. (1999, 2004). The mapping approach incorporated biogeographical and ecological barriers such as mountain ranges, semi-deserts, and glacial regions, which influence honeybee distribution. The subspecies distribution map (Fig. 1) we propose illustrates the six main types of landscapes that do not support honeybee habitation or provide habitats for sparse honeybee populations. Discrepancies between different naming conventions were addressed by referring to the International Code of Zoological Nomenclature (ICZN, 1999). Specimens of *A. m. caucasica* used for Figure 3 were collected from an apiary in Senaki, Samegrelo, Georgia, and photographed by the first author. This region is historically recognized as the genetic center of *A. m. caucasica*.

RESULTS

The Caucasus – A. mellifera biogeography. To understand the natural distribution of *A. m. caucasica*, it is essential to examine its habitats within the Caucasus and describe the natural barriers that isolate honeybee populations and subspecies. The Caucasus is a region of exceptional biodiversity, encompassing diverse climatic and geographic conditions within a relatively small area (Tarkhnishvili, 2014). The topographic heterogeneity has presumably impacted the evolution of local honeybee populations, enabling *A. m. caucasica* to thrive in contrasting environments, from humid subtropical zones with year-round brood rearing to alpine regions with short summers and prolonged broodless periods even within Georgia only (Irakli Janashia's (I.J.) observation).

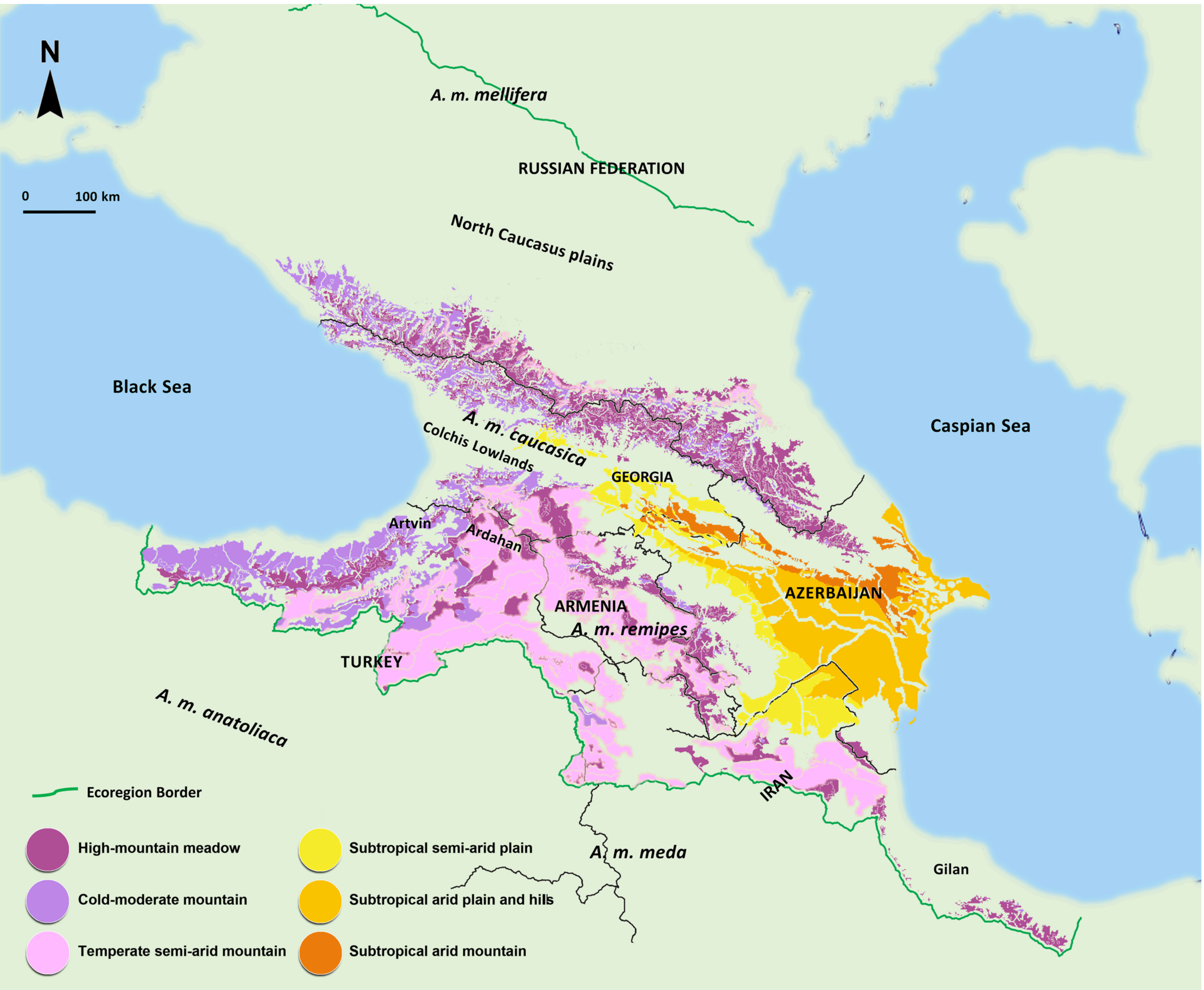

Figure 1. Map of the Caucasus ecoregion suggesting honeybee subspecies isolation areas.

The Caucasus composite ecoregion spans approximately 580,000 square kilometers, encompassing Armenia, Azerbaijan, Georgia, the North Caucasus region of the Russian Federation, northeastern Türkiye, and a small portion of northwestern Iran (Zazanashvili et al., 1999, 2004). Situated between the Black and Caspian Seas, the Caucasus acts as both a biodiversity hotspot and a glacial refugium. During the last glaciation, it most likely provided stable habitats that supported species survival and post-glacial recolonization (Japoshvili et al., 2016; Tarkhnishvili, 2014), presumably contributing also to the distinct genetic and adaptive diversity of *A. m. caucasica*.

Given that the high mountain meadow landscapes of the Greater Caucasus are unsuitable for sustaining honeybee populations year-round, it seemingly serves as a northern barrier almost impermeable to honeybees (Fig. 1). It offers passages for potential external gene flow primarily at the eastern and western edges where the mountain chain transitions to lowlands. However, it remains unclear to what extent the 'Caucasica gene center' extends along the eastern reaches of the Greater Caucasus mountain chain, and even more uncertain is the distribution of *A. m. caucasica* along the northern slopes and adjacent lowlands of the Greater Caucasus. The Lesser Caucasus, by contrast, is lower in altitude, less consistent and dense with high montane peaks and chains offers relatively favourable climatic conditions for honeybees compared to the high mountains of the Greater Caucasus. The unique landscape of the Lesser Caucasus suggests more direct and diverse possibilities for bilateral gene exchange among *A. m. caucasica*, *A. m. meda*, *A. m. remipes* and *A. m. anatoliaca*. These highlands of the Lesser Caucasus may act as a setting for soft gene flow in the context of interspecific interactions among the listed subspecies.

We hypothesize that the highlands of the Lesser Caucasus, particularly the cold-moderate and temperate semi-arid mountain landscapes, are less densely populated by honeybees compared to the Colchis lowlands and adjacent mountainous areas, which we propose as the 'Caucasica gene center'. These highlands are fragmented by high mountain meadow landscapes creating multiple relatively isolated zones for honeybee populations.

Taxonomic history. To avoid further confusion, we clarify that the term 'Caucasian honeybee' in this publication refers exclusively to *Apis mellifera caucasica* Gorbachev 1916, which is also recognized as *Apis mellifera caucasia* Pollmann 1889, following a proposition by Engel (1999). However, we could not find a detailed justification for this suggestion or any source linking Pollmann to the Caucasian bee. Pollmann (1889) mentioned *A. mellifida var. caucasia*, based on the description done by Butlerow (1880) where he describes it as a gentle and morphologically distinguished variation. This name is *nomen nudum* (lapsus). Engel (1999) states that Gorbachev (1916) made an unjustified emendation and made *A. m. caucasia* Pollman as a valid name, later this proposal was supported by Momeni et al. (2021), however, Kaskinova et al. (2024) revives name *A. m. caucasica* Gorbachev, 1916, without explanation and detail discussion. Based on ICZN (1999) article 50.1 the name must be *A. mellifera caucasica* Gorbachev, 1916, as it is in GBIF (2025) and *A. mellifera caucasia* Pollmann, 1889, must be considered as a junior synonym of *A. m. caucasica* Gorbachev, 1916.

The history of the Caucasian honeybee's first discovery is somewhat unclear (Ruttner, 1988). Pallas, a German zoologist and botanist who led an expedition (1768–1774) across various regions of Russia, was the first to mention the Caucasian honeybee (Koschevnikov, 1900). He collected and published extensive data on agriculture, botany, entomology, and mineralogy in 'Reise durch verschiedene Provinzen des Russischen Reichs' (1771–1776). In his work, Pallas states, that beekeeping is a significant agricultural activity in the Ufa Governorate (Khazuev & Baimatov, 1996). However, Pallas has never documented the discovery of the Caucasian honeybee, explicitly. In 1862, Gerstäcker reclassified a honeybee sample exhibited by Pallas at the Zoological Museum of the University of Berlin as *Apis remipes* Pallas (Ruttner, 1988). This sample, originally labelled as collected from the Caucasus, was actually sourced from Hyrcania (modern Northern Iran). Alpatov (1948) suggests that, during Pallas's time, parts of Iran and Turkmenistan were considered within the Caucasus region. Even today, a small portion of historic Hyrcania's area remains part of the Caucasus ecoregion.

In 1877, the renowned chemist Butlerov visited the Northern Caucasus where he identified gentle local honey bees and imported eight honey bee queens into Russia (Andguladze & Prangulashvili, 1982). Two years later, in 1879, he travelled to Sokhumi in the Southwestern Caucasus, exporting honey bees to Russia once again. During this visit, Butlerov observed that the honey bees in the Southern Caucasus were darker than those from the Northern Caucasus, leading him to propose the existence of two subspecies: yellow and grey, inhabiting opposite slopes of the Greater Caucasus (Alpatov, 1948; Andguladze & Prangulashvili, 1982) The same observation has been made by Shavrov in 1893 (Koschevnikov, 1900). However, while attempting to advance studies with a bit more complex morphometric characterization of honeybee workers, measuring proboscis length and tergites width in addition to colouration pattern assessment Koschevnikov in 1900 has come to the conclusion that previous studies were too simplistic to assume their conclusions as a determining and so were his own attempts (Koschevnikov, 1900).

In spite of Koschevnikov's (self) criticism regarding methods used for discrimination of Caucasian honeybees, a simplistic approach has continued to be employed by Chochlov and Gorbachev to describe Caucasian honeybee (Gorbachev, 1916). By measuring proboscis length both Chochlkov and Gorbachev came to the conclusion that Caucasian honeybees from western Georgia possessed the longest proboscis. By 1916, Chochlov measured the proboscis length of 1,899 worker bees collected in Georgia, Armenia, Azerbaijan, Iran and Russia. Samples of the worker bees from Western Georgia (Apkhazeti-Abkhazia) had the longest proboscis among all tested groups (Gorbachev, 1916). Additionally, Chochlov calculated the percentage of bees with yellowish abdomen segments in each geographic group. The workers from Apkhazeti samples were mainly grey, with 1% yellow and 28% dark yellowish (rusty) abdomens (most likely tergites) (Gorbachev, 1916). Gorbachev, spent much of his career in Tbilisi (Sakartvelo-Georgia) and named the local honey bee *Apis mellifera var. caucasica* (Alpatov, 1948). Gorbachev, without giving convincing arguments or presenting analysed data, claimed that the Caucasus was populated by two different honey bee subspecies (breeds):

1. Mountain Grey – preserved in mountainous regions of Georgia (Svaneti, Apkhazeti) and in Dagestan (Northern Caucasus, Russia).

2. Yellow honey bee (Persian honey bee described by Pallas- *A. m. remipes*) which is spread at the border between Azerbaijan and Iran (Lenkoran), Kars (North East Türkiye) and Erevan Governorate (Armenia). According to Gorbachev (1916) the homeland of those honey bees is Iran and interbreeds of those two are honey bees with rusty appearing dorsal parts of tergites, which in respect of appearance and biological traits were closer to Grey Caucasian honey bees.

Gorbachev (1916), in final conclusion, has limited natural distribution of the Grey Caucasian honey bees to Transcaucasia's (Southern Caucasus) - specific mountainous areas, identifying only Georgian regions without mentioning the country itself. But in the very same book, he mentioned that those honey bees exist also in Dagestan, which is located in the North-Eastern Caucasus. Gorbachev accepted the main characteristics for discriminating Caucasian honey bees previously proposed by other authors during that period, which included proboscis length, abdomen colouration, cover hair, worker honey bee size, and behavioural traits (Gorbachev, 1916). However, information regarding the sampling procedure and the morphometric study methodology applied by Gorbachev is lacking. Since then the question referred to which populations have to be classified as *A. m. caucasica* subspecies was argued by many authors. Scoricov thought that Persian honey bees were different from other Caucasian subspecies; this hypothesis was objected to by Alpatov (Alpatov, 1948).

In 1927, the Pallas's honeybee exhibit was observed by Alpatov. In spite of the indicted origin of the exhibit and the already existing conclusion of Gorbachev, Alpatov has interpreted that Pallas used the title *A. m. remipes* for Transcaucasian and Caucasian yellow (origin not specified) honey bees (Alpatov, 1948). Bilash shared a similar opinion placing Caucasian Mountain Grey (*A. m. caucasica.*) and Caucasian Yellow (*A. m. remipes* Gerst) (Bilash & Krivtsov, 1991) among Eastern subspecies of honey bee samples. Thus, Caucasian honeybees with rusty tergites and Persian honeybees have been wrongly considered as the same bees. Later, during 1924–1930, Alpatov performed more complex biometrical measurements of Caucasian bees (Alpatov, 1929). Working in the laboratory at Cornell University, Alpatov used European dark, Italian and Caucasian honey bees collected in the Northern Caucasus (Stavropol and Maykop) and Southern Caucasus (Apkhazeti, Svaneti, Kutaisi, Tbilisi). He performed much more complex morphometric data analysis but, at the same time, he admitted the drawbacks of using sample preservation (treatment) methods, which did not allow him to use all samples for all measurements. Considerable work was done by Skorikov in 1928, studying local honey bee populations in the Caucasus (Alpatov, 1948). He introduced the measurement of the first tarsal segment index and confirmed Chochlov's and Gorbachev's earlier findings that bees near the Enguri River (Samegrelo-Svaneti, Georgia – Colcheti lowlands) had the longest proboscis (7.21 mm) among the subspecies studied (Alpatov, 1948).

There were some unsuccessful attempts by Georgian scientists during the Soviet era to study various ecotypes of *A. m. caucasica* which we do not discuss here (Mumladze, 1971). As methodology used has not been professional and focused exclusively on the comprehensive morphometric study. Nowadays, when communicating with queen breeders all over the world on the matter of *A. m. caucasica* breeding, they refer to various sources providing the morphometric standard libraries. Some reference the Oberursel Morphometric Bee Data Bank, a professionally curated database that we could not find published online but is cited in various studies (Sheppard & Meixner, 2003; Pourelmi & Fuchs, 2017; Puškadija et al., 2020).

Behaviour. Different specific behavioural characteristics of Caucasian honey bees have made them the subject of various studies. In 1908, Klingen studied Caucasian honey bees (originating from Apkhazeti-Abkhazia, Georgia) for four years to assess their effectiveness in red clover pollination. He observed that due to their longer proboscis, Caucasian bees were more effective at pollinating red clover than other honey bee subspecies (Andguladze & Prangulashvili, 1982). According to Bilash and Krivtsov (1991), Caucasian honey bees show specific preferences for some melliferous plants, favouring legumes while avoiding buckwheat.

Taranov (1951) conducted a comparative study by testing "Georgian mountain bees" (a beekeeper-friendly term for the *A. m. cauc*asica Taranov introduced in 1949) in trials assessing features important for industrial beekeeping. He distributed 207 Georgian-Caucasian honey bee colonies in 17 beekeeping units across the middle zone of Russia. The behaviour of these introduced "Georgian mountain bees" was compared to that of local bees. Beekeepers involved in the trial noted that the Georgian-Caucasian honey bees began flights earlier and ceased later than local populations. They were also able to fly in light rain. Additionally, the Georgian-Caucasian bees took more frequent cleansing flights in late fall and early spring compared to local bees. The trials also confirmed the gentleness of the Georgian-Caucasian honey bees, and it was observed that Georgian queens continued laying eggs even when a comb was removed from the hive for observation. Earlier Glushkov in 1947 made similar observations (Taranov, 1951). He also noted the ability of Georgian bees to quickly switch from one nectar source to another, which Taranov linked to their tendency towards robbing. Taranov viewed this behaviour as an advantage, as it allowed honeybees to locate new food sources more rapidly. As evidence, he described an experiment in which Georgian mountain bees, compared to Russian bees, more quickly found hidden feeders of flavourless sugar syrup and emptied them much faster.

Wet capping of honeycomb is another characteristic of Georgian-Caucasian honeybees (Gorbachev, 1916; Taranov, 1951). When handling nectar, they tend to store newly collected nectar close to the brood nest, even in cells from which young bees have just emerged. Later, the nectar is transferred above the brood area to storage space. This behaviour restricts egg laying and allows the colony to focus on storing honey even during weak nectar flows, ensuring vital reserves. In contrast, Italian bees expand the brood area under similar conditions (Alpatov, 1948; Taranov, 1951). The building of a few queen cells by Georgian-Caucasian bees during swarming was noted by Gorbachev (1916), suggesting a low swarming propensity in *A. m. caucasica*. However, based on the author's (I.J.) 30 years of experience with Georgian *A. m. caucasica* populations, no notably low swarming tendency has been observed.

The hygienic behaviour of Caucasian honey bees (Woźnica line) was studied in four breeding lines in Poland, where the Caucasian line displayed lower cleaning behaviour compared to Carniolan (Kortówka) and *Apis m. mellifera* (Augustowska) lines (Bąk et al., 2010). However, the greater tendency to collect and use propolis to seal cracks, close hive entrances (Fig. 2), and fill holes (Bilash & Krivtsov, 1991) may serve as a compensating factor, as propolis collection plays a significant role in the social immunity of honeybees as discussed by Simone-Finstrom and Spivak, (2010). At the same time, Georgian beekeepers, including the author of this publication (I.J.), frequently observe the vivid behaviour of Georgian populations of Caucasian honey bees, which often bridge combs with wax deposits and seal hive entrances after mid-summer, leaving only small openings. Sealing hive entrances in this manner, particularly after mid-summer, is common for Georgian populations of *Apis mellifera caucasica*.

Current distribution. The isolation of *A. m. caucasica* populations differs from island-type confinement. Semi-deserts, glaciers, mountain chains, and seas act as natural barriers in the Caucasus, but the permeability of these barriers varies. The mountainous landscape and climatic gradients within the region contribute to the diversification of evolutionary lineages in general. In addition, incomplete isolation likely plays a role in the evolutionary divergence of Caucasian honeybees, driven by gene flow and selection.

Figure 2. The hive entrance that is extensively sealed with propolis. [photograph courtesy of Vakhtang Kakhniashvili]

In **Georgia**, *A. m. caucasica* remains the sole honeybee subspecies used in beekeeping. While non-native *A. mellifera* subspecies have rarely been imported, large-scale introductions were minimal due to Georgia's self-recognition as the homeland and source of *A. m. caucasica*. However, migratory beekeeping within the country may have altered specific characteristics of local sub-populations (ecotypes), distorting previously noted differences in regions such as Apkhazeti, Samegrelo, Guria, Imereti, and Kartli (Mumladze, 1971).

The northeastern part of **Türkiye** represents another significant area of *A. m. caucasica*'s native range. Kandemir et al. (2005) identified *A. m. caucasica* colonies in Artvin, Ardahan, Kars, and Iğdır. According to a later study *A. m. caucasica* is mostly prevalent in some Eastern Black Sea locations, while *A. m. anatoliaca* seems to be a widely spread subspecies in the northern part of Türkiye (Çakmak et al., 2014).

In **Russia**, *A. m. caucasica* is still widely used, more commonly named the "Caucasian Grey Mountain bees" (Krivtsov et al., 2011). According to Liubimov (2010), a pure genetic pool (Apkhazeti, Samegrelo, and Kartli lines) is maintained at the Krasnaya Polyana Apiculture Experiment Station. However, in Dagestan (Northern Caucasus), cross-breeding with *A. m. carpatica* has affected the genetic purity of local populations (Krikorova, 2001). The parallel use of several honeybee subspecies in the northern Caucasus (Dolgieva et al., 2021), complicates efforts to maintain pure *A. m. caucasica* populations.

In **Azerbaijan**, *A. m. caucasica* historically dominated apiaries, valued for its industrious nature and high honey production. However, in the 1980s, a parasitic infestation severely impacted the state's apiaries, leading to the introduction of a different honeybee subspecies from the southern regions. This new subspecies was more reproductive but weaker in honey production. Over time, hybridization between the native *A. m. caucasica* and the newly introduced bees led to a mixed-race population, which was less efficient in honey production than the original Caucasian bees (FAO, 2015) plausibly suggesting the loss of local adaptations due to hybridization.

In **Armenia**, despite bordering *A. m. caucasica*'s natural range, this subspecies may have been overlooked in studies. Ruttner (1988) suggests that *A. m. remipes* formerly referred as *A. m. armeniaca*, which inhabits Armenia, has been provisionally classified due to its unique traits, including a shorter proboscis, yellow pigmentation, and aggressive behaviour—features that clearly distinguish it from the gentler *A. m. caucasica*. These observations suggest a stronger connection between *A. m. meda* and *A. m. anatoliaca* rather than *A. m. caucasica*.

Breeding and Conservation. The following chapter presents an overview of breeding and conservation efforts for *A. m. caucasica* within its natural distribution range and elsewhere.

During the Soviet Union period, the main breeding station for *A. m. caucasica* in Georgia was located in Mukhuri village (Taranov, 1951), where only local Georgian lines were used for breeding. The Mukhuri breeding station distributed honey bee queens, known internationally as Caucasian Mountain Grey honeybees. However, mass queen production ceased following the collapse of the Soviet Union. The station was reestablished in 2017, but as of 2024, the team has yet to publish any scientific findings on conservation or breeding progress. Beekeeping in Georgia today is primarily a small-scale activity, with most beekeepers rearing queens from local colonies for their own use. Nonetheless, there remains a lingering preference for queens from the Mukhuri area among some Georgian beekeepers.

Türkiye has undertaken conservation efforts for *A. m. caucasica* since 2000, focusing on the Artvin and Ardahan provinces, which were designated as isolated conservation zones. These efforts aimed to counteract the effects of introgression caused by intensified migratory beekeeping practices. However, a recent study within the protected zone revealed low genetic diversity, based on an analysis of 30 microsatellite loci, which was attributed to ongoing inbreeding (Yıldız et al., 2023). Krasnaya Polyana Apiculture Experiment Station is now one of the few remaining centers maintaining lines of Caucasian bees. It has also developed a novel breeding line known as "Gray Mountain Caucasian — Krasnaya Polyana' (patent no. 4111, June 23, 2008)" (Liubimov, 2010; Krivtsov et al., 2011). Outside its native range, *A. m. caucasica* breeding lines are maintained in Poland and Norway (Bouga et al., 2011). In the USA, semen collected from *A. m. caucasica* in Georgia By 2011, was cryopreserved, allowing future use in breeding programs and part of it was used to inseminate Carniolan virgin queens under the Managed Pollinator Coordinated Agricultural Project, which aimed to increase genetic diversity within US honey bee populations (Sheppard, 2012).

DISCUSSION

The Caucasus serves as a biogeographic crossroads, facilitating genetic exchange between European and Asian species. The geographic features such as the Greater and Lesser Caucasus ranges, the Black and Caspian Seas, and the Armenian Highlands likely act as ecological boundaries, both in terms of climate and terrain, shaping the genetic center of *A. m. caucasica*. While these barriers do not entirely restrict interaction with other honeybee subspecies, they appear to influence patterns of gene flow, fostering differentiation and promoting the evolutionary development of the subspecies. It is particularly important to note that during the ice ages, two warm and humid refugia—Colchic and Hyrcanian—were established (Zazanashvili et al., 2020). Considering the current distribution of *A. m. caucasica*, the subspecies might qualify both as a relict and an endemic taxon to the Caucasus region. Certain regions, such as the Kura-Araks Lowlands and Armenian highlands, may function as corridors for honeybee movement, enabling introgression with neighbouring subspecies like *A. m. anatoliaca*, *A. m. meda* and *A. m. remipes.* A similar process may occur at both ends of the Northern Caucasian mountain chains, where interactions with *A. m. mellifera* populations are expected. While natural soft introgression can enhance genetic diversity (Randi, 2008), anthropogenic factors like intensified migratory beekeeping could amplify these effects, potentially eroding the distinctiveness of *A. m. caucasica* and its specialized traits. Landscape genetics, which links population genetics with environmental and geographic factors, offers valuable tools to delineate the boundaries of *A. m. caucasica*. Applying this approach may help clarify gene flow patterns and local adaptations, providing a foundation for managing the genetic diversity of the subspecies under increasing ecological pressures (Manel et al., 2003).

The taxonomy of *A. m. caucasica* has been shaped by various historical and morphometric studies. Gorbachev (1916), whose name is somehow associated with the subspecies, described it as comprising two distinct populations: Mountain Grey bees, found in regions such as Svaneti, Apkhazeti, and Dagestan, and yellow honey bees, associated with areas bordering Iran (Lenkoran), Kars, and the Erevan Governorate. However, Gorbachev's classification overlooked much of the Caucasus, including large portions of

Georgia. Alpatov (1948) later reviewed available data, concluding that the classification of Caucasian bees primarily relied on abdomen colouration. Notably, there has been no study to date exploring the differences between Northern and Southern Caucasian honeybee populations.

The variation in tergite colouration among honeybees in Georgia has fueled the belief in the coexistence of distinct subspecies and hybrids (Fig. 3). However, this assumption is likely unfounded, as sustained hybridization would eventually result in hybrid dominance. Even the earliest studies reveal that Georgian honeybee colonies consistently include workers with entirely grey colouration alongside individuals with rusty-coloured tergites, primarily on the second tergite (Koschevnikov, 1900; Gorbachev, 1916; Mumladze, 1971) which is the case today as well (I.J. observation). Phenotypic divergence in *A. m. caucasica* resulting from local adaptation is an overlooked topic.

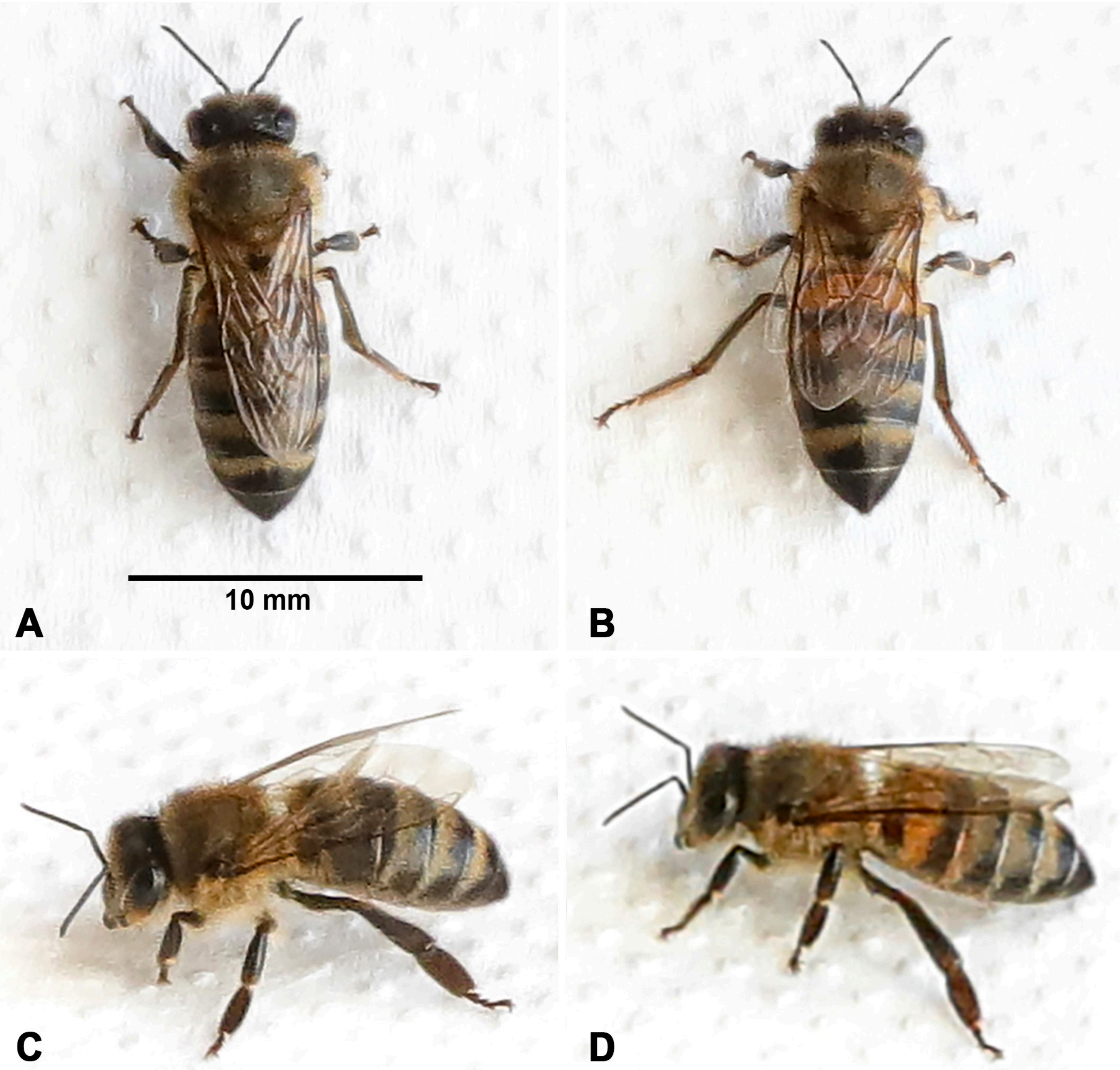

Figure 3. The typical appearance of Georgian *A. m. caucasica* worker bees. **A–B.** Dorsal, and **C–D.** Lateral views of worker bees with the completely grey abdomen and grey abdomen with rusty second tergite respectively.

This phenomenon has been studied in a topographically heterogeneous region in Kenya, where the morphological divergence of local honeybees (*A. mellifera*) in neighbouring forests raised questions about whether they belong to different subspecies. Mitochondrial sequencing has not supported this hypothesis but instead confirmed the phenomenon of phenotypic plasticity (Gruber et al., 2013). The notion of a "pure grey race" may have been also influenced by selective breeding efforts aimed at producing uniformly grey worker bees. Misunderstanding the natural variation within *A. m. caucasica* could lead to unsafe preservation strategies, such as irrational selection from a limited number of "selected grey" colonies. The practice of centralized queen breeding and distribution in commercial beekeeping has been shown to reduce genetic diversity in honeybees (Meixner et al., 2010). A recent study *of A. m. carnica* in Croatia and Slovenia has shown that, despite historically being under more detailed scientific attention, current findings of a wide variety of ecotypes data do not fully correspond to the existing morphometric reference material database, highlighting the importance of further studies (Puškadija et al., 2020).

Historically, evaluations of honeybee subspecies have prioritized commercially desirable traits, such as honey production, gentleness, and reduced swarming tendencies, often neglecting long-term ecological fitness and survivability. For example, a longer proboscis may not necessarily provide an advantage in all environments. Recent research has challenged this narrow perspective, demonstrating, that bees evolved in specific ecological contexts exhibit higher survival rates, better disease resistance, and greater overall fitness than those selected primarily for commercial traits when placed in non-native environments (Meixner et al., 2015). These findings emphasize the importance of genetic diversity and local adaptation over the exclusive selection of commercially attractive traits, promoting a shift toward more sustainable and ecologically informed honeybee management practices. Even within Georgia only, native honeybees demonstrate remarkable versatility in adapting to highly varied environments—from warm, humid subtropical zones, which allow near year-round brood rearing, to dry continental climates and alpine conditions with short summers and prolonged broodless periods of up to six months.

Georgia may offer the most viable mainland strategy for conserving pure *A. m. caucasica* populations, as large-scale introductions of non-native subspecies have been minimal. Hypothetically, the exclusive use of native honeybees by Georgian beekeepers supports the expectation that the country still harbours *A. m.caucasica* populations in their purest form. However, the natural distribution of *A. m. caucasica* remains poorly defined due to insufficient data from key regions, including Georgia, Türkiye, Armenia, Azerbaijan, and Russia (Northern Caucasus).

Understanding the Caucasus' biogeographic context is crucial for the effective conservation of *A. m. caucasica*. Conservation efforts should prioritize the protection of isolated populations, minimize introgression in areas where natural barriers are more permeable, and expand research to address gaps in our understanding of this subspecies. Future research should: **1.** Conduct extensive sampling across the whole Caucasus region to refine the understanding of the natural distribution of *A. m. caucasica*; **2.** Integrate advanced morphometric and genetic analyses to assess population structure, evaluate genetic diversity, and trace evolutionary history.

AUTHOR'S CONTRIBUTION

The authors confirm their contribution to the paper as follows: I. Janashia and G. Japoshvili: conceptualized, planned and wrote the paper; L. Westover: made important suggestions and corrected the text. All authors read and approved the final version of the manuscript.

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AVAILABILITY OF DATA AND MATERIAL

The voucher specimens examined in this study are deposited in the Institute of Entomology, Agricultural University of Georgia, Tbilisi, Georgia, and are available from the curator, upon request.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This study only included literature and few arthropod materials, particularly honey bees and all required ethical guidelines for the treatment and use of animals were strictly adhered to in accordance with international, national, and institutional regulations. No human participants were involved in any studies conducted by the authors for this article.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this paper.

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مروری بر زنبور عسل قفقازی، *Apis mellifera caucasica* (Hym., Apidae) تاریخچه، طبقه‌بندی و انتشار

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چکیــده: وضعیت و جایگاه طبقه‌بندی زنبور عسل قفقازی (*Apis mellifera caucasica* Gorbachev, 1916) (Hymenoptera: Apidae) همچنان مبهم و عمدتاً بر اساس تحقیقات قدیمی می‌باشد. پس از بررسی منابع علمی موجود، مشخص شد که از همان ابتدا یک نوع عدم‌تطابق و سردرگمی بین درک جغرافیای سنتی قفقاز و انتشار واقعی *A. m. caucasica* وجود دارد. نمونه‌برداری جغرافیایی ناکافی از زنبورهای عسل در سراسر قفقاز، تعداد ناکافی نمونه‌های مطالعه شده به روش‌های آماری و روش‌شناسی ناقص تحقیق از جمله معایب عمده مطالعات قبلی هستند. داده‌های مورفومتریک مرجع که از تعداد بسیار محدودی از نمونه‌ها استخراج شده‌اند هنوز به عنوان استاندارد برای شناسایی *A. m. caucasica* استفاده می‌شود. به احتمال زیاد، این استاندارد، تنوع مورفومتریک واقعی را که شامل تغییرات جغرافیایی طبیعی است را منعکس نمی‌کند و به‌همین لحاظ به عنوان عامل بازدارنده انجام فعالیت‌های خاص برای حفاظت یا پرورش آن شده است. برای حل این نواقص، نیاز است که زنبورهای عسل قفقاز و مناطق مجاور با جزئیات و عمق نمونه‌برداری بیشتر مطالعه شوند. یک مطالعه جامع با استفاده از روش‌های مدرن مورفومتریک و روش‌های ژنتیک مولکولی برای شناسایی *A. m. caucasica* و تولید یک مجموعه داده آماری قوی برای تجدید نظر در وضعیت و جایگاه طبقه‌بندی آن ضروری است.

واژگـان کلیدی: زنبور عسل خاکستری قفقازی، زنبور عسل گرجستانی، خاکستری کوهستانی، ساکارتولو