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Western Honey Bee (*Apis mellifera*)

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Synonyms

Hive bee

> The bee's life is like a magic well: the more you draw from it, the more it fills with water. (Karl von Frisch)

Definition

Honey bees (genus *Apis*) are a distinct group of 9–12 species of highly social bees. One of these, *A. mellifera*, has been of intense interest to humans since antiquity and has long been the most thoroughly studied of all invertebrate animals. In fact, until two centuries ago, the study of social insects could be characterized as the study of this one species with comments on our sparse knowledge of social wasps, ants, (later) termites, and other bees noted for comparison. In contrast to other honey bee species, which are almost entirely confined to South and East Asia, the native range of *A. mellifera* can be summarized as most of Africa and Western and Central Europe.

Introduction

Our relationship with honey bees dates back to prehistoric times and likely began with the search for honey. A cave painting in Spain (circa 10,000–8,000 BC) shows hunter gatherers in pursuit of the sugar-rich food. To harvest honey, hunter gathers destroyed the whole hive and, to avoid stings, collected the product as quickly as possible [5]. The San people of South Africa advanced honey harvesting by taking ownership of feral colonies, marking them with rocks or sticks outside the entrance. This primitive form of beekeeping advanced to man-made hives, apiaries, and the agricultural system we have today.

The transition from hunting bees to keeping them (▶ Beekeeping or Apiculture) required substantial care and control, starting with providing the colony with a suitable home. The first man-made hive was likely a hollow log, which would have been possible to produce with Stone Age tools [5]. Beyond the hollowed-out log, early hive designs considered both bees and the beekeeper. For the bees, the hive had to be safe, dry, insulated, well-ventilated, and spacious. For the beekeeper, the hive had to be easy to build with low-cost, abundant materials. For this reason, early hives varied greatly in design. Evidence of apiaries dates to as early as 2400 BC in Egypt and

C. Starr (ed.), *Encyclopedia of Social Insects*,
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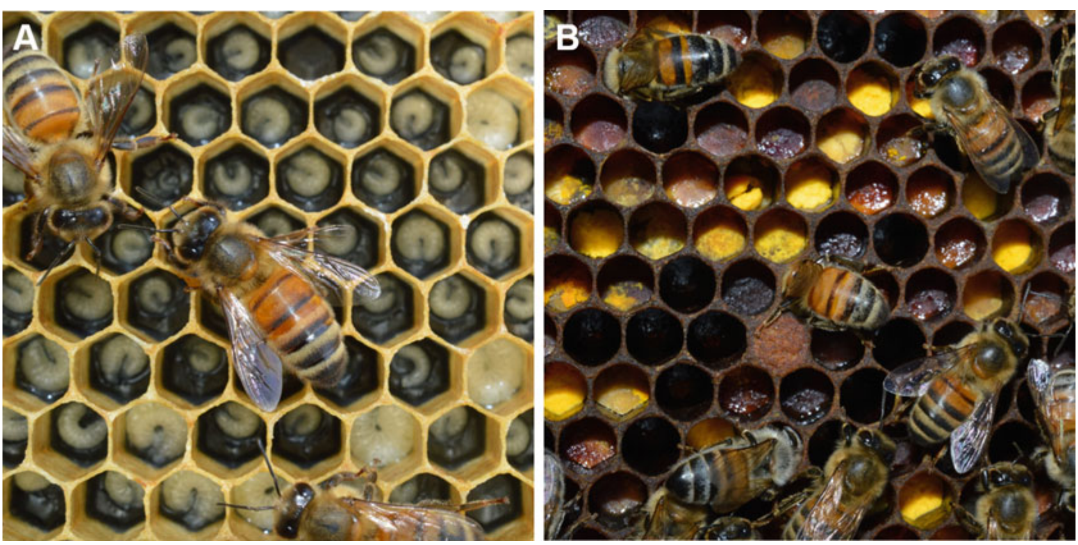
970 BC in Greece. Despite the early origins of beekeeping, there is no evidence of protective beekeeping gear until the fifteenth century. Thus, harvesting honey often required killing the bees via drowning or sulfur smoke [5]. During the sixteenth century, however, beekeepers decided they wanted permanent stock, so they started paying close attention to honey bee biology and social behavior.

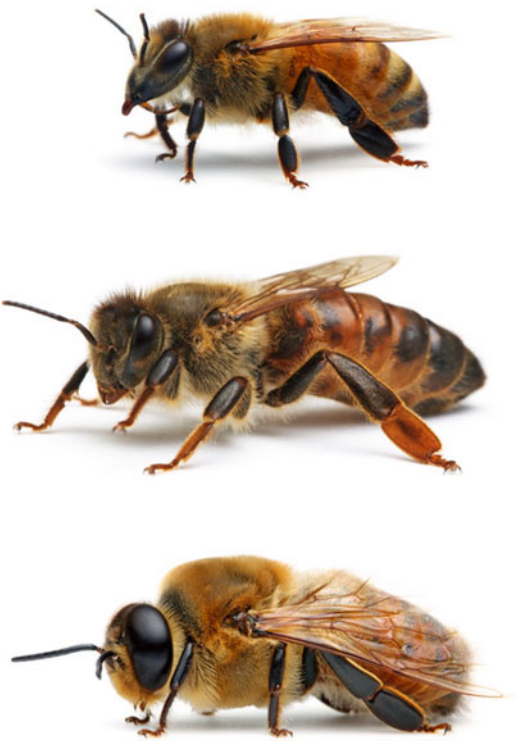
Life Inside the Hive

A. mellifera are cavity nesters. Inside the cavity, sterile females (workers) build vertical wax combs of hexagonal cells for raising brood and storing food (Fig. 1). *A. mellifera* choose nesting sites based on cavity volume, and entrance height and size, with preference for those with combs from an earlier colony [7]. A “dream home” for *A. mellifera* is 40 L in volume with wax comb built by a preceding colony, a south-facing entrance 1–5 m off the ground, and an entrance hole 12.5 cm^2 in size. A carefully chosen nest affords protection from predators and the elements. The presence of wax comb from a previous colony saves the new colony time and energy.

Once the colony has found a home, colony growth depends on a single reproductive female, the queen. In the wax cells, she lays fertilized eggs, which develop into females, and unfertilized eggs, which develop into males (drones) (Fig. 2). Drones pass on the colony’s genes by leaving and mating with newly eclosed queens from other colonies. Any fertilized egg can become a worker or a queen, its fate being determined by larval nutrition. Nurse bees visit queen-destined larvae more often than worker-destined larva, however, it is unknown if queen-destined larvae receive larger quantities of food. We do know, however, that there are nutritonal and chemical differences in larval food. Nurses feed protein- and carbohydrate-rich royal jelly to queen-destined larvae throughout the entire larval period, while worker-destined larvae are only fed royal jelly for the first few days of development. At this point, worker-destined larvae are switched to brood food, or worker jelly, which tends to have lower macronutrient levels [see attached citation if needed]. The presence of queen and worker larvae is signaled by ▶ pheromones; both emit primer pheromones that elicit cooperative brood care and stimulate foraging, tasks performed by workers [5].



Western Honey Bee (*Apis mellifera*), Fig. 1 (**A**) Nurse bees taking care of brood. Each larva develops in its own wax cell. (**B**) Worker bees storing pollen (the main source of protein) in wax cells



Western Honey Bee (*Apis mellifera*), Fig. 2 *Apis mellifera* worker (top), queen (middle), and drone (bottom). (Photos © by Alex Wild)

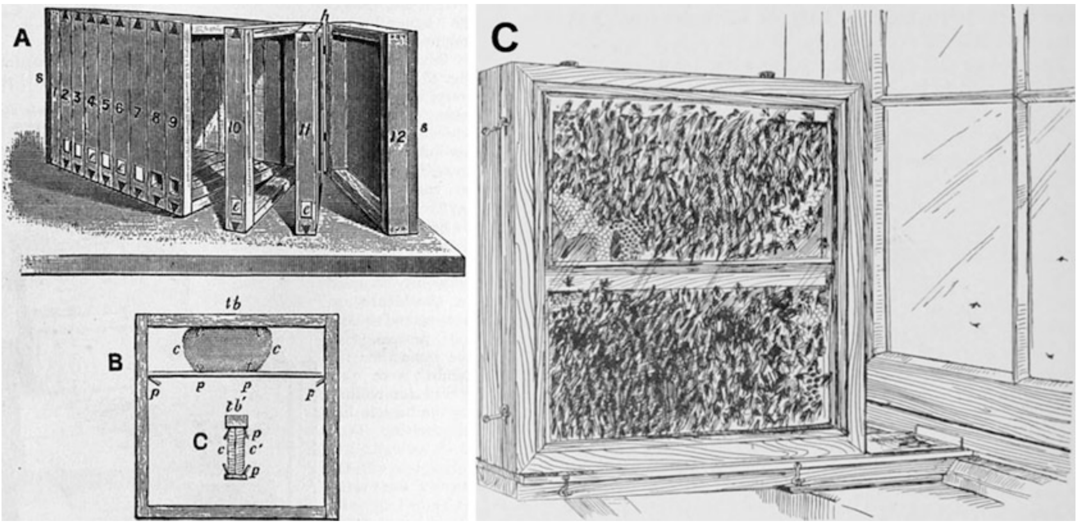
Workers make up the bulk of the colony and exhibit temporal ▶ polyethism; that is, they assume different tasks depending on their age. The youngest workers, nurse bees, clean cells and take care of brood. As workers develop, they exhibit a suite of behavioral tasks: food storing, heat shielding, undertaking, etc. The oldest workers are responsible for collecting food. Honey bees are mainly vegetarian: pollen, ▶ nectar, and water provide proteins, lipids, carbohydrates, vitamins, and minerals for an active colony. In 1 year, a typical hive will collect about 120 kg of nectar, 50 kg of which is made into honey and kept in reserve for the winter [5]. *A. mellifera* colonies are perennial; the queen and workers live on honey stores until early spring forage becomes available. That same year, a typical colony will collect only 15–30 kg of pollen, 1 kg of which is kept in reserve during the active brood-rearing season [5, 11].

Observation hives – smaller hives with clear windows to provide a way to observe the bees at home – were developed in the mid-1600s (Fig. 3a–c) [2]. While observation hives proved a useful tool for learning about honey bees, they were not ideal for management purposes. The small space was not in the range of a "dream home" and inhibited *A. mellifera* from storing food and producing honey, and often led to absconding and/or swarming. Long-term management and study of honey bees became possible with Lorenzo Langstroth's discovery of the "bee space" (~3/8 inches or 9.5 mm) in 1851 and his development of the moveable frame hive (Fig. 4a–c).

Advances in Agriculture: Migratory Beekeeping and Pollination Services

Like our relationship with honey bees, migratory beekeeping, or pastoral beekeeping, began with the hunt for honey. To increase honey production, beekeepers in temperate regions moved their hives with the bloom, similar to how livestock were moved for grazing. The earliest reference to migratory beekeeping dates back to 250 BC in Egypt [2]. Hives were often moved at night and either carried by their keepers or pack animals. In later years, hives were moved by boat, cart, and finally, mechanized rail (steam engines in the 1800s) and road (cars in the 1900s) transport. Railways and roadways revolutionized migratory beekeeping and led to the widespread use of *A. mellifera* for agriculture.

Although honey bees have a long history of providing honey and other hive products to humans, their most valuable service is in ▶ crop pollination [2]. An understanding of pollination began to develop in the 1670s and continued into the late 1800s. In 1750, Arthur Dobbs described the role of honey bees in collecting pollen and moving it from plant to plant, thus affecting fertilization and fruiting success. In 1793, C.K. Sprengel built upon this idea and published a book on the importance of cross-pollination for hybrid vigor in plants and the role played by bees and other insect pollinators [8]. Almost 100 years



Western Honey Bee (*Apis mellifera*), Fig. 3 (**A**) François Huber's leaf observation hive with 12 leaves. (**B**) Side view of one leaf. (Source: Carpenter, G. H., & Carr, W. B. (1911). Bee. In *Encyclopedia britannica*. Austria). (**C**) Two-frame observation hive similar to a modern-day design (Source: Kellogg, V. L. (1908). Wasps, bees, and ants. In *American insects*. New York: H. Holt)

later, Charles Darwin published his own observations regarding the coevolution between insect pollinators and their plants and ran his own experiments on the importance of cross-pollination.

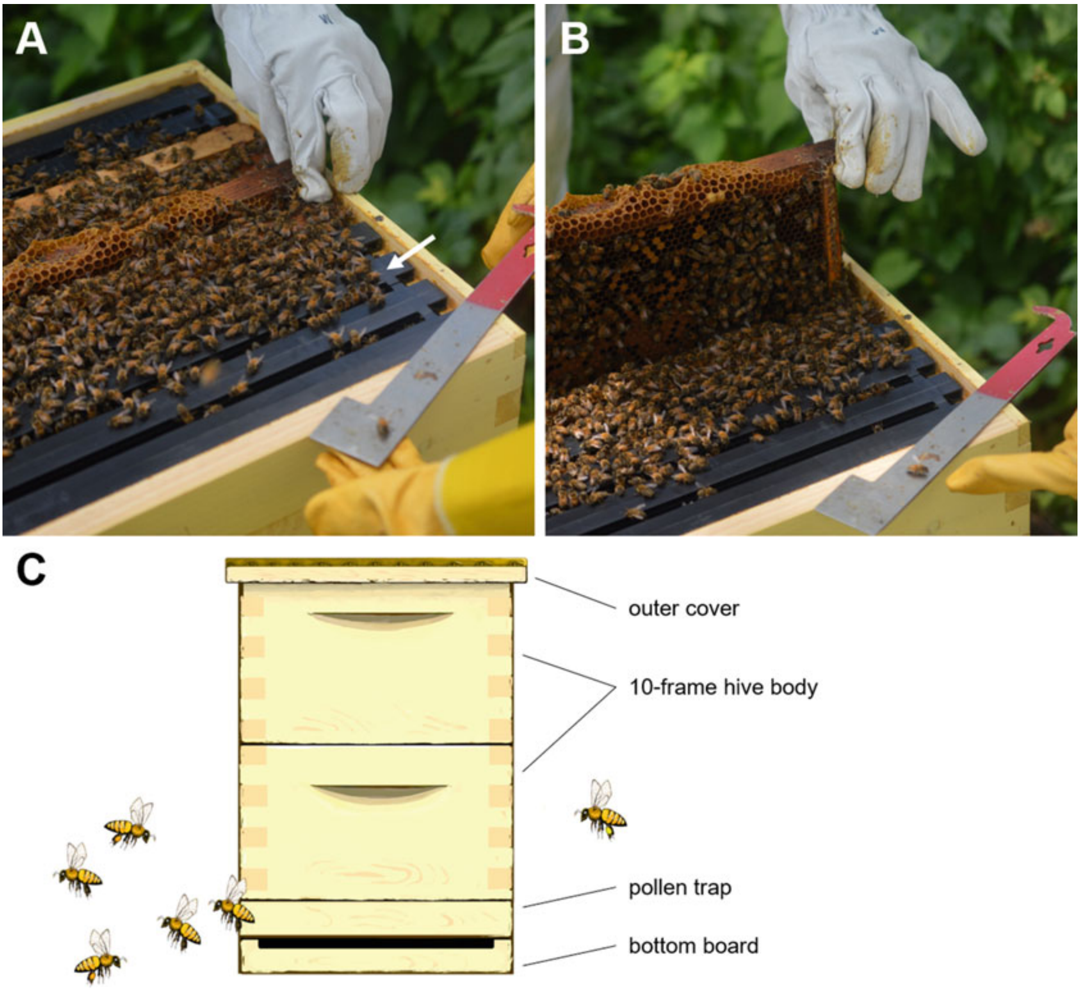
With the knowledge of cross-pollination came commercial beekeeping as a business beyond honey. At first, the beekeeper paid the grower for allowing the bees to forage on his/her land. In time, beekeepers realized that the grower benefitted even more than the beekeeper [2]. In the 1930s, Denmark beekeepers were the first to require payment for pollination services. By the 1940s, many other countries had followed suit and at this time, many countries were growing their crops in monoculture.

Advances in Applied Science: Disease Dynamics and Optimization Algorithms

While monocultures are an efficient way to provide food for the growing human population, recent honey bee research has shown that the lack of diet diversity a monoculture provides may be detrimental to pollinators. In this way, interest in honey bees has spurred research on how to continue current pollination practices in a more sustainable manner via restoring hedgerows, and/or maintaining forest edges. The epidemic of ► colony collapse disorder (CCD) in the mid-2000s also spurred public interest in honey bees and thus, insect pollinators and the environment. Today, ► ecosystem services provided by bees and their importance to our well-being are increasingly well understood by the general public.

Beyond agriculture and the environment, honey bees are a useful study system for understanding disease dynamics. ► *A. mellifera* diseases were recognized as early as 350 BC. Aristotle describes ailments such as starvation, dysentery, and failure to rear brood. Today, beekeepers, veterinarians, and scientists alike are interested in honey bee disease [10]. With advances in microbiology, genetic sequencing, and immunology came identification of the pests and pathogens responsible for the ailments Aristotle recognized and an understanding of honey bee immune pathways [3]. Furthermore, since honey bees live in societies of related individuals, they are a useful model organism for understanding disease spread in other social organisms, including ourselves.

One of the biggest pests to plaque *A. mellifera* is *Varroa destructor*, hereafter referred to as the



Western Honey Bee (*Apis mellifera*), Fig. 4 (**A**) Ten-frame Langstroth hive, frame indicated by white arrow. (**B**) One frame being removed for inspection. (**C**) Typical Langstroth hive setup with two hive bodies. As the colony grows, more hive bodies can be stacked on top. A pollen trap, a tool for both beekeepers and scientists, is included in this diagram. (Illustrations provided by Genevieve Pugesek)

varroa mite or mites [9]. The native host of the varroa mite is ► *A. cerana,* however, with transportation of bees, the mite has spread to a naive host, *A. mellifera*. Varroa mites feed on both larval and adult bee tissue, thereby spreading disease and weakening bees. What makes varroa mites difficult for both beekeepers and *A. mellifera* to manage is the mite's hidden reproduction. Female mites use chemical cues to find honey bee larvae that are near pupation. There, the mite hides in the wax cell (Fig. 1), in the brood food, and waits. Once the honey bee larva is old enough, worker bees cap the cell with wax. Safely under the wax capping, the female mite emerges from hiding and punctures a hole in the developing bee to make a feeding site for herself and her offspring. When she has gathered enough energy, the mother mite lays her first egg, a male, and glues it to the top of the capped cell. The mite then lays multiple female eggs, gluing them to the cell walls. While the honey bee is still capped, the mite eggs hatch, the mites develop, and the male mite mates with his sisters. When the host honey bee emerges from its cell as an adult, so do the mature female mites, ready to continue the cycle. In this way, the mite population grows exponentially and if left unchecked can overwhelm the bees. This exponential growth of pathogen populations and spread of disease within a society is of great interest in epidemiology.

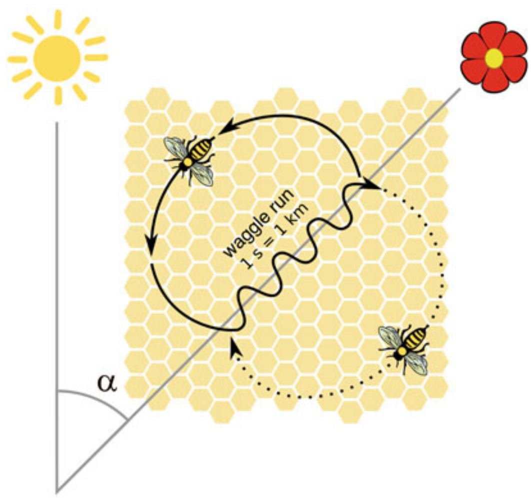
Beyond understanding disease spread, *A. mellifera* have helped inform optimization algorithms to make our internet servers faster. Using the way colonies allocate foragers to search for nectar [7], a decentralized algorithm is proposed to dynamically allocate internet servers. This algorithm uses the idea of scout bees to do a quick random search of internet sites to find good sites. The good sites, like a profitable patch of flowers, are then exploited repeatedly via a local search. This honey bee algorithm helps internet servers deal with spikes in demand and prevent long wait times.

Advances in Basic Science: Communication and Decision-Making

Despite humans having kept honey bees since prehistoric times, an in-depth understanding of what makes these creatures tick did not begin to build until the 1900s. New tools and lab-based techniques allowed for closer examination of honey bee communication and group-level decision making.

Sound and scent were the first two identified modes of honey bee communication. Even before the introduction of the term, the first honey bee ► pheromone was identified [1]: the queen mandibular pheromone (QMP), termed “queen substance” at the time. The term “pheromone” was introduced soon afterward. Since then, pheromone transfer is understood as an important mode of communication within the colony, as in a great many other social insects. QMP is especially important for proper functioning of a hive, as it regulates worker behavioral maturation/tasks, inhibits worker reproduction (though sterile, some workers can lay unfertilized eggs), and governs rearing of new queens for swarming (colony-level reproduction) or queen replacement (supercedure) [5]. QMP is made of over 100 chemical compounds. In *A. mellifera*, newly emerged virgin queens do not produce QMP compounds, but as they age, QMP components build up. Once they mate and are laying eggs, QMP components increase. In particular, homovanillyl alcohol (HVA) levels are strongly tied to queen laying behavior. A honey bee colony contains a complex blend of pheromones; workers and larvae also emit pheromones to regulate foraging, brood care, etc.

Another form of communication in the honey bee is ► dancing. Dancing was observed in *A. mellifera* as early as the 1650s; however, it was not systematically studied as a mode of communication until the 1920s [4]. Karl von Frisch showed that upon her return to the hive, a successful forager “shows” fellow nestmates where the food is via either the round dance (for nearby food sources) or the waggle dance (for faraway food). During the waggle dance, the forager gives out samples of the food. Coded in the dance is location information. The waggle dance is done in a figure-8 pattern (Fig. 5). As the bee passes through the center of the 8, it is called the waggle run. The angle of the waggle run in relation to the top of the hive is the angle of the food source in relation to the sun. The duration of the waggle run relates to



Western Honey Bee (*Apis mellifera*), Fig. 5 The waggle dance is done inside the hive, on the wax comb, usually near the entrance of the hive. Location information is coded in the angle and the duration of the waggle run. The angle (α) of the waggle run in relation to the top of the hive corresponds to the angle of the food source in relation to the sun. The duration of the waggle run encodes how far away the food source is, 1 s corresponds to about 1 km. (Image modified from Wikimedia Commons, https://commons.wikimedia.org/wiki/File:Bee_dance.svg) the distance of the food source; a longer waggle run represents a further food source. Honey bee dance language is the only known use of symbolic communication in invertebrates.

In addition to communication, *A. mellifera* stands out for their group decision-making, especially in finding a new home during swarming. When a honey bee colony outgrows its cavity, workers build new queen cells along the edge of the wax comb. When a new queen is about to emerge, the old queen leaves with about half of the workers, leaving the new queen and the rest of the workers to continue in the old hive. This division of the colony, similar to cellular division, is the hive's reproductive unit. Early beekeepers embraced the swarming process as a way to multiply their colonies [2]. When the swarm of bees is not caught by a beekeeper and placed in a new hive, however, the bees face the task of finding a new home. The swarm settles at an intermediate location in a cluster, the queen in the center, while scout bees fly out in search of a suitable nest cavity. To investigate the intricacies of group decision-making, Thomas D. Seeley and colleagues repeated a series of classic waggle dance experiments with modern video equipment. Taken together, their studies showed that honey bees use a combination of waggle dancing, quorum sensing, and sound to reach a consensus on choosing a new homesite [7].

The Future of Beekeeping and *A. mellifera*

Although it is getting harder to keep healthy bees in the current environment, the future of the honey bee looks bright. Since CCD, more people are interested in helping insect pollinators by planting more flowers and learning about beekeeping and bees in general. There has also been an increase in backyard (or rooftop) urban beekeeping. While most agricultural land (i.e., monocultures and grazed pastures) is likely an unhealthy environment for honey bees and other pollinators due to a lack of nutrients and a presence of pesticides, some cities may provide an unexpected haven. A study in Chicago, USA, showed that bee richness and abundance increased with human population density, likely as a result of greater floral diversity. ► Bumble bee colonies in the city produced more reproductives, reached a higher peak population density, had more food stores, and encountered fewer parasites than their rural counterparts [6]. Although the literature on "city bees" in comparison to "country bees" is still growing, our long-lasting relationship with charismatic *A. mellifera* bodes well for insect pollinator conservation.

Cross-References

► Beekeeping or Apiculture

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