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# VENTILATING HORNETS DISPLAY DIFFERENTIAL BODY TEMPERATURE

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**Abstract**—Our investigation entailed a thermal analysis of hornets engaging in ventilation activity at the nest entrance. In the hot summer months, between July–October, ventilating worker hornets are seen just outside the nest entrance, where they assume a typical stance, namely, with their feet erect and fastened to the substrate, their abdomen bent downward at a 90° angle to the thorax, their antennae vibrating, and their wings beating rapidly for minutes at a time. Eventually these hornets leave their position, either to retreat into the nest or else to fly off to the field, and are replaced by new hornets that assume the ventilation task. Infra-red (IR) photography reveals that in the course of the ventilation activity, the warmest region in the ventilating hornet body is the anterior upper part of the thorax, and the coolest regions are the wings, limbs, antennae and abdomen. This study involved precise and repeated measurements via IR photography of the temperature in the various body parts of the ventilating hornets, and it also offers a preliminary, tentative explanation for the observed differential body temperature. The communication value of the color of the hornet body when ventilating is discussed.

## 1. INTRODUCTION

The Oriental hornet *Vespa orientalis* (Hymenoptera, Vespinae) is a social insect. The queen waking from its hibernation founds an annual nest in the spring (April–May), in which the hornet population attains maximum in August–September, whereupon the sexual stages develop (drones and young queens). Subsequently the fertilized queens hibernate and the cycle repeats in the spring [1–3]. The temperature in the nest (as measured between the brood combs) is a stable 29±1°C [4]. In the summer, when the heat in the field rises and so also the temperature in the hornets' nest, which is usually constructed subterraneanly [1, 5], one can see worker hornets, and occasionally also young queens (Ishay, unpublished observations) beating their wings and arranging in circles (or in lines) around the nest entrance, with their heads directed outwards (see Fig. 1). The number of wing-beating hornets depends of course on the size of the nest population but per same nest and day it is in correlation with the time of day [6], considering that the warmest hours of the day in the summer are the afternoon hours. Thus we see the same picture repeating itself each day, to wit: few 'ventilating' workers (VW) in the morning hours, with their number increasing steadily toward the hottest time of day, usually about 3–4 in the afternoon. The vespan wing movement in the course of ventilating activity differs from that during flight, as is evident from the top pictures in Fig. 1. According to Sotavolta, 1947 [7], the frequency of wing movement in hornets is 117–247 beats/sec. Sade et al., 1977 [8], in very precise subsequent measurements, arrived at a rate of $f = 140$–$150$ beats/sec during ordinary ventilation, but in ventilating hornets warding off potential intruders the rate of ventilation rose to $f = 221$ Hz [9].

In a previous study [10] we reported that in flying hornets the temperature is not uniform throughout the body, but rather the head and thorax are warm, whereas the gaster and legs are several degrees colder than the thorax (which is the warmest) and the head. The present investigation focused on the temperature distribution along the ventilating hornet's body, and an attempt is also made to explain the observed thermal differences between various body parts.

## 2. MATERIALS AND METHODS

A hornet's nest is best found at the end of the active season, when the nest population is maximal (several hundred workers or more), and when the temperature outside the nest at noon or in the afternoon is at its highest, and therefore apparently requiring maximal ventilatory


**Figure 1A.** A worker hornet at the embryonal nest entrance engaged in ventilatory activity.


**Figure 1B.** A worker hornet flying out of the nest and carrying in its mandibles a grain of earth dug out to enlarge the volume of the nest. Note the manner of wing activation and the difference between Fig. 1B, where the wings are rather horizontal and Fig. 1A, where the wings are more vertical, and consequently the different positioning of the wings in each case.


**Figure 1C.** Ventilating worker hornets at the entrance of a subterranean nest at the end of the active season. There are hornets engaged in ventilation here. Note the spacing between them, which prevents interference and also enables free entry and egress of the other nest occupants.

activity [6]. Once a nest is detected, an infrared (IR) or ordinary camera is slowly and carefully moved close to the nest entrance, so as to photograph both the ventilatory hornets at the nest entrance as well as the traffic of hornets in and out of the nest. Hornet wings were prepared for sectioning, fixation and viewing through transmission electron microscope (TEM) as previously described [11, 12]. Use was also made of an infra-red digital video camera, model ThermaCam SC 500 (7.5–13 microns). Photos of live hornets were taken, using this camera, were viewed on a computer monitor using the PS Card interface Agewa THV 550, and were processed using commercial software ThermaCam Researcher Ver 2001. This camera directly detects energy flux $J_E$, which is translated into temperature readings by that software, which assumes a black-body spectrum and an emissivity value which must be provided by the user. We used an emissivity value of 0.97, which was determined in honeybees [13]. Since $J_E$ is proportional to $T^4$ ($T$ is the absolute or Kelvin temperature), even a 1% error in the emissivity will lead to a 0.8°C error in the measured temperature. However, over areas of uniform emissivity, the accuracy of *temperature differences* is 0.1°C, and depends only on the camera hardware properties. Control measurements of temperature distributions were made on dead hornets in thermal equilibrium with underlying comb or wooden substrates. These measurements showed that non-uniform emissivity can lead to a temperature difference of 0.9°C at most. Statistical analysis of rock particles was done on Origin version 6.1 software.

## 3. RESULTS

During the months marking the end of the active season, i.e., from September onwards, one frequently sees at the nest entrance a considerable number of worker hornets engaged in ventilatory activity. It is advisable to pick a nest located close to human buildings for this enables to photograph the ventilatory activity at all hours of the day (via electrical hookup). A typical view of a single hornet displaying ventilatory movements is given in Fig. 1A. One can see the worker standing "high" at the nest entrance and beating its wings at a rapid and steady rate. Such activity can continue, uninterrupted, for a few minutes at a time. Such workers are not aggressive, so that an observer can approach the nest without fear of being attacked. Note that the ventilating worker has a typical stance wherein the head always faces outwards and the abdomen is bent downward at a 90° angle to the thorax. In Fig. 1B is shown a 'digger' worker flying out to the field with a granule of earth dug out from the nest to enlarge its inner volume. Note that the wing posture of this hornet is different from that of the ventilating hornet, as it detaches from the nest floor and takes flight. Fig. 1C shows a full row of workers standing at the nest entrance and performing coordinated ventilatory activity; note that these workers stand apart from one another so as not to disrupt their wing movements, and at the same time other workers freely enter or leave the nest, or occasionally replace the ventilating hornets. One should also note that ventilating workers assume positions along the entire nest entrance, that is, laterally, dorsally and ventrally. Thus, the bottom-placed workers have their backs facing up while the ones standing at the top of the entrance have their backs facing down. A sample of the accomplishments of workers leaving the nest is shown in Fig. 2, where one can see a small pile of sand or stone grains removed form the nest by digger hornets enlarging the nest. We can reasonably assume that some of these particles were rather carried out and not flown out. Indeed, on the right side of the photograph a worker hornet can be seen in the process of dragging a small rock towards the pile on the left side. Upon weighing a handful of these rock diggings we find that the mean weight of such a particle is 0.53 grams, with a minimum of 0.2 g and a maximum of 1.5 g. The number of particles measured was 125 and the standard deviation was 0.22 g. This should be compared with the weight of an adult worker hornet, which is 0.3 g on average. On the right side of Fig. 2 one can see the left arch of the

**Figure 2.** Near the nest entrance (seen here on right of picture) and in proximity to a scaled ruler, one can see grains of limestone dug out of the nest by digger workers so as to enlarge its volume, then carried to a distance of tens of cm from the nest entrance. Some of the granules are a few cm in diameter and quite heavy.

nest entrance, which means that these particles were hauled out to a distance of several tens of centimeters.

We were greatly interested in ascertaining the body temperature of ventilating workers. Using IR photography, we first measured the body temperature of a hornet that was standing for a while outside the nest near to its entrance (Fig. 3A). Somewhat lower in the picture of this hornet, the light brown area denotes a temperature equivalent to 32.1°C at the nest entrance, whereas the gaster temperature of this resting hornet (viewed from the side) reads on the same scale as 32.2°C. Proceeding along the hornet's body towards the head and antennae, we record a somewhat higher temperature of 32.6°C, whereas the wings of the hornet are mostly colder 31.5°C. Above the hornet, that is, farther from the nest entrance, the temperature is higher (indicated by the yellow and white colors) — about 33.5°C. In the inset at the bottom right of Fig. 3, we see a smaller view of same hornet from its dorsal aspect and here, the gaster yields the same temperature value as when viewed laterally, but the two wings and the two hind legs are colder than the ambient temperature, showing a temperature of about 30.8°C.

Fig. 3B, C, D offers identical views of one typical hornet which have been processed differently (by the Researcher program) in order to provide a better visualization of temperatures in various body parts of

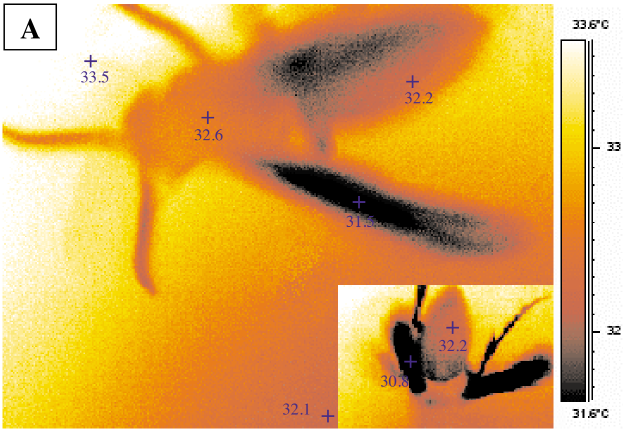


**Figure 3A.** Control (sentinel) hornet, i.e., a hornet standing outside the nest but near to the entrance. Gaster temperature is 32.2°C and thorax 32.6°C, while the ambient temperature at the nest entrance to the right of control hornet is 32.1°C and to its left, on the outside — 33.5°C. Temperature of the wings of the control hornet is 30.8–31.5°C, which is as much as 1.4°C lower than the temperature of its gaster. Note that this control hornet is not moving its wings although it might have done so previously, whether in ventilation or in flight.

the hornet. Thus, for instance, in Fig. 3B we can see that the vespan thorax is warmer than the head, and even more so than the gaster. The appendages like antennae, legs, and the single wing shown, as well as the dorsal and ventral surfaces of the gaster, are all cold by comparison. The difference between the highest temperature 35.3°C of the thorax and the lowest 33°C at the tip of the gaster — amounted to 2.3°C. Especially noteworthy is the fact that the temperature of the posterior part of the thorax 34°C is close to that of the anterior ventral part of the gaster 33.7°C. In the anterior region of the thorax, the temperature attains up to 35.3°C, that is on the dorsal aspect, where the aorta is situated. Fig. 3C displays the same hornet and in its thorax one notices two areas which are warmer than all the rest of the body. One of these thoracic areas is immediately behind the head, on the dorsal aspect, and has a temperature of 35.3°C, while the other, close to the legs and somewhat behind the first thoracic area on the ventral side, is smaller and shows a maximal temperature reading of 34.9°C. In other parts of the thorax, that is, the more posterior ones, the temperature drops as low as 33.8°C. In the remainder of the body, i.e., in the gaster, the temperature ranges between 33.5°C and 32.9°C.

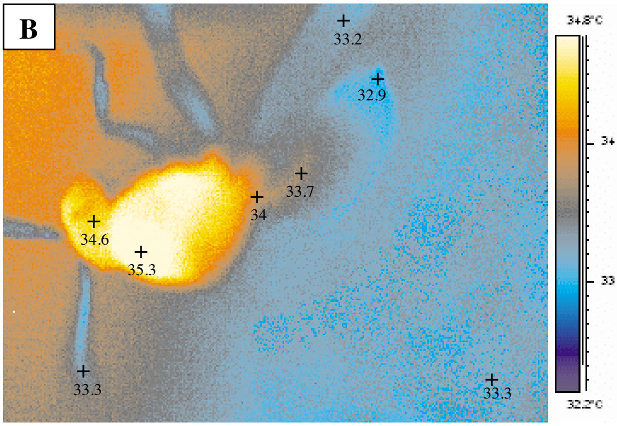


**Figure 3B.** Hornet engaged in ventilatory activity at the nest entrance. Note: the pictures 3B, C, D represent different color coding schemes of the same infra-red photo of ventilating hornet, in order to better exhibit the various local body temperatures. From these pictures it appears that the ambient temperature at the nest entrance (on the right) is 33.3°C. As for body temperature of the hornet, we have the following readings: anterior thorax 35.3 °C, posterior thorax 34°C, ventral gaster 33.7°C, head 34.6°C, antennae 33.3°C and gaster tip 32.9°C.

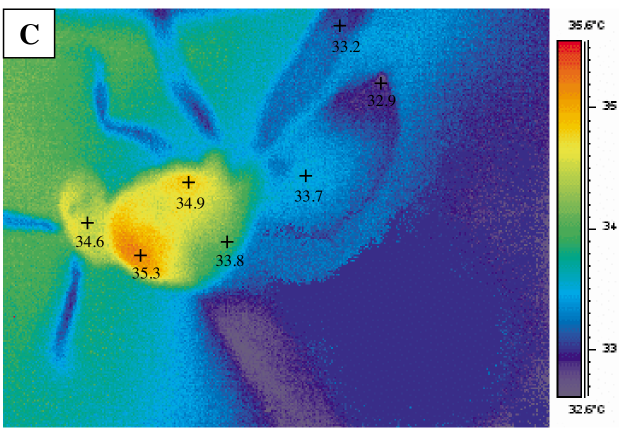


**Figure 3C.** Temperature readings: warmest part of thorax (the anterior most) 35.3°C, posterior part of thorax 34.9°C, head 34.6°C, anterior part of gaster 33.7°C, posterior part of gaster 32.9°C and wings 33.2°C.

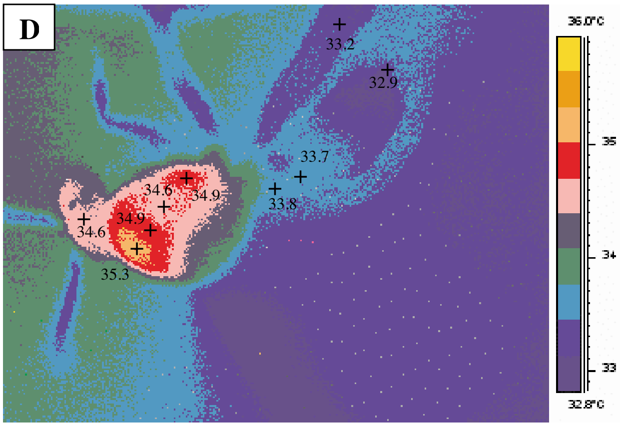


**Figure 3D.** Temperature readings here are: warmest part of thorax (the anterior most) 35.3°C, the area around it 34.9°C, and so also the warm area in the posterior thorax, head 34.6°C, area between the two warm spots in the thorax is about 34.6 °C, anterior gaster 33.7°C, posterior gaster 32.8°C and wings 33.2°C.

**Figure 3.** Body temperatures of ventilating hornets vs. sentinel hornets. Note that the temperatures quoted here may be off by a few degrees from the true values, due to insufficient information regarding emissivities. However, *temperature differences* are accurate to 0.1°C, assuming uniform emissivity. As explained in the main text, non-uniform emissivity could result in apparent temperature differences of up to 0.9°C. Such a large effect is only expected when comparing different types of surfaces, like cuticle vs. rock, not when comparing different parts of the hornet cuticle.

A similar temperature range is also found in the antennae and legs. Fig. 3D provides a clearer picture of the distribution of the isothermic regions in the thorax. Again we see, on the dorsal aspect in its anterior portion, a warm region (35.3°C) and around it, a greater area in which the mean temperature is marginally lower (34.9). A similar albeit smaller area occurs on the posterior part of the thorax, again with a mean temperature of 34.9°C. Between these two areas or spots and also on the head the prevailing temperature is about 34.6°C. In the juncture between the thorax and gaster, i.e., between the region of the aorta and that of the heart, the temperature drops to 33.8°C. On the gaster proper, in its anterior part, the temperature is about 33.7°C, and in the posterior part — about 32.9°C. In all the pictures shown in Fig. 3B,

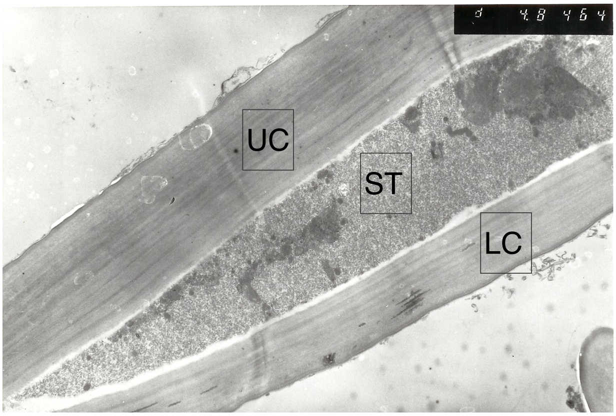


**Figure 4.** Cross-section through upper wing of freshly-ecloded hornet, seen via TEM. The wing is shown to be composed of two layers of cuticle, each, in turn, composed of numerous lamellae whose thickness diminishes as one proceeds from the outside inwards. Between the two layers there is soft tissue as well as tracheae. The fluids extant in the wing of this just ecloded hornet will be absorbed within a day so as not to hamper its flying ability (UC=upper cuticle; LC=lower cuticle; ST=soft tissue).

C, D the wing temperature is 33.2°C. In order to better understand the thermal differences between vespan body and wing (Fig. 3A), a wing was cross-sectioned so as to ascertain what was so special in its structure as to produce such rapid cooling as was observed. As can be seen from Fig. 4, the hornet wing is comprised of an upper half and a bottom half, each composed of numerous lamellae (just as the cuticle is) between which there is a soft tissue whose amount is high in newly ecloded hornets but diminishes rapidly within a few days, thereby lending the adult hornet wing greater lightness and strength.

## 4. DISCUSSION

Thermal measurements on the bodies of insects while they are engaged in various activities were previously carried out by many groups. It has long been reported that the temperature in the nest of social hornets is higher than the ambient temperature of the surrounding soil [14, 15] and is fairly constant in time, i.e., during the active season of hornets, which is in the summer months. In the case of the Oriental hornet *Vespa orientalis*, the temperature in-between the brood combs is quite constant at $29 \pm 1°C$. In fact, this temperature prevails in the nests of all species of social wasps thus far examined, provided there are enough worker hornets in the nest [16]. However, the body temperature of hornets leaving the nest for various tasks (e.g., foraging) changes, whether because the new ambient temperature exerts an effect on their own body temperature and/or because of the fact that in the course of these outside activities, part of their body (mainly the thorax) heats up while another part (mostly the gaster) cools down. We have recently reported [10] that the thorax of *V. orientalis* hornets flying out of the nest becomes warmer than the ambient temperature whereas the gaster gets colder, with the thermal difference between both ends of the body, in hornets returning to the nest after flight, amounting to about 7°C.

We assume that this temperature difference plays a very important role in communication between those members of the colony that stay at the nest entrance, always in light — as their different colors of their body is observed by the members arriving from outside of the nest; the colors displayed by these coming from the outside is different. The cuticle of the hornets is luminescent [17]. On examination of the luminescence phenomenon, carried out by laser pulse probing, it was found that in the yellow-colored cuticular areas there are at least two types of pigment which differ, by a 10-fold factor, in the luminescence lifetime, but only slightly in their emission wavelength. The duration of the luminescence in the brown region of the cuticle is less than one tenth that of the shortes yellow transient, while its luminescence intensity is two orders that of the yellow pigment [17]. The hypothesis of a natural sophisticated RADAR tracking system affecting hornet flight was described, analyzed and developed in previous papers [18–21]; similar observation have bee reported in moths [22, 23].

Kovac and Stabentheiner [24] have observed in the thorax of bees in the course of ventilatory activity an analogous gap of 31.7–42.1°C between its two ends, that is, a temperature difference amounting to 10.4°C, and this when the ambient temperature ranged between 26.1–30.4°C; the measurements here were made via infrared thermography in the course of the bees' collection of sugar solutions of various concentrations and interestingly the temperature differential was proportional to the sugar concentrations.

In the course of the bee's dance within the hive, and by the same methodology, the temperature differential across the thorax was 31.4–43°C, i.e., a gap of 11.6°C, in the dancing bees that had gathered nectar or pollen [25]. In another study [26] and by the same methodology, it was found that in the thorax of bees standing guard at the hive entrance, the temperature was lower by 2°C or more than that in the thorax of bees returning from the field; furthermore, there was a rise in the thoracic temperature of these returning bees as they were attempting to enter the nest, and this (probably) owing to their contact with the sentry bees and namely during their ensuing brief 'inspection'. Other investigators have assessed the influence exerted by the nature of the carried load (nectar or pollen) or the extent of reward on the foraging bee's level of metabolism [27, 28]. Interestingly, it was shown [29] that upon the gathering of water, the temperature readings from the bee's body were as follows: the thorax was the warmest, with a maximum of 44.5°C (and a mean of 36–38.8°C), while the head and gaster were colder, but invariably the body temperature of the foraging bee was higher than the ambient temperature. As for heat loss, it was found that "small" bees lose heat very quickly and large bees lose heat comparatively slowly, as would be expected from biophysical principles [30–32].

As well in swarming bees, that is, in bees that gather into a compact mass, the ones on the outside of the swarm show a thoracic temperature that starts rising before they commence flight in search of a protected and fixed site for settlement of the swarm [33]. The question arises as to what is the energy source that enables warming of the thorax in time of apian activity. Stabentheiner et al. [34] addressed this question by studying the oxygen consumption of bees.

These investigations found that the oxygen uptake of the bees was dependent on the ambient temperature, thus being low at low temperature of 11–21°C and increasing at higher temperatures of 30–40°C. It has been confirmed also in butterflies in flight that the thoracic temperature rises owing to activity of the flight muscles and is higher than that in resting butterflies [35]. Beetles, as well, get warmer during flight, so that the difference between the thoracic temperature of flying beetles and the ambient temperature can amount to 4.4–8.3°C [36]. Cicada, too, is a thermoregulatory insect [37–39], augmenting its body temperature by a combination of behavioral mechanisms and endogenous heat production.

From the above-cited studies, it seems clear that in the course of physical activity, especially flight, the body of winged insects, and primarily their thorax, heats up to above the ambient temperature. In the present study (see Fig. 3) we have ascertained via IR photography the differential temperature in various parts of the body of a hornet that beats its wings in the course of ventilatory activity. We were able to show that in the vespan thorax there are two heat centers, a large one possibly linked to and regulating the wing muscles and a smaller one possibly associated with the leg muscles. In our present and previous studies we also ascertained that the head was somewhat colder than the thorax, that the gaster in its anterior ventral part (but not in the region of the heart which is in the dorsal portion of the gaster) exhibits a temperature identical to or lower than the ambient temperature, and that the wings clearly show a temperature which is lower than the ambient temperature. As for the anatomy of the wing (see Fig. 4), it resembles that of the cuticle, with an upper part thicker than the bottom part and between the two — a soft tissue that nourishes the wing elements and is especially abundant in the young hornet. Again, like in the body cuticle, the two parts of the wing are composed of numerous lamellae whose thickness diminishes from the exterior to the interior [40, 41]. It should be mentioned that all the temperatures measured so far may differ from the true values by up to 0.9°C, as explained in the Materials and Methods section. Nevertheless, *temperature differences* among different parts of the hornet exterior are considerably more accurate, with accuracy that approaches 0.1°C, since the emissivity differences are then usually less than 1%.

We note that, not only does the temperature vary by up to 2.5°C over different parts of the hornet exterior, but that in some locations it is significantly lower than the ambient temperature of its near surroundings. As pointed out in Ref. [10], the fact that the temperature in some parts of the hornet body is sometimes lower than ambient requires the employment of some active cooling mechanism by the hornet. The mechanism suggested there, namely thermoelectric heat pump operating across the thickness of the cuticle, could explain the appearance of such cooling effects, if certain physical parameters of the cuticle have appropriate values. The values of these parameters are currently being studied — results of that study will be reported elsewhere.

The above-suggested cooling mechanism leads to a simpler explanation for our observation that the wings are sometimes the coolest objects in the hornet body (see Fig. 3A): The cooling power (per unit surface area) of the posited cuticular thermoelectric heat pump is presumably the same irrespective of the particular location of the cuticle. Thus, since the wings contain much less non-cuticular material than any other body parts, relatively speaking, the same cooling power will lead to a correspondingly greater lowering of temperature in the wings. Similar considerations apply to other appendages, such as legs and antennae.

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