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A butterfly's chemical key to various ant forts: intersection-odour or aggregate-odour multi-host mimicry?

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Abstract Deception is a crucial yet incompletely understood strategy of social parasites. In central Europe, the Mountain Alcon Blue, *Maculinea rebeli*, a highly endangered butterfly, parasitises several *Myrmica* ant species. Caterpillars gain access to host nests probably by faking the ants' odour. We analysed gas chromatography–mass spectrometry data of body surface hydrocarbons of pre-adoption and hibernated larvae of *Maculinea rebeli* and of their host species *Myrmica sabuleti* and *M. schencki*. Data were ordinated by different methods, based on similarities in the relative quantities of compounds between chromatograms. The two *Myrmica* species exhibit species-specific profiles. The *Maculinea rebeli* pre-adoption larva has a complex profile that simultaneously contains species-specific substances of the two investigated host species. This evidence leads to the interpretation that, in central Europe, *Maculinea rebeli* is predisposed for multi-host use by the chemical signature of its pre-adoption larva. The *Maculinea rebeli* larva clearly does not rely on an “intersection-odour” of compounds common to all host

ant species, but synthesises an “aggregate-odour” containing specific compounds of each of the investigated hosts. We term this previously unknown chemical strategy “aggregate-odour multi-host mimicry”.

Introduction

An estimated 10,000 insect species are obligately associated with ants (Schönrogge et al. 2000). Many of these are social parasites and live inside the fortresses of ant colonies, at least temporarily (Hölldobler and Wilson 1990). Because ants possess a complex system of communication that allows discrimination between nestmates and foreigners, alien guests had to develop integration strategies (Dettner and Liepert 1994). In the butterfly family Lycaenidae, larvae of most of the estimated 6,000 species associate with ants. Associations range from facultative to obligate and from mutualistic to parasitic (Pierce et al. 2002). The Mountain Alcon Blue, *Maculinea rebeli*, an obligate parasite, is among Europe's most endangered butterflies (van Swaay and Warren 1999), not least because of its demanding life cycle (Pierce et al. 2002; Fig. 1). After feeding on a gentian, the young larva must be adopted by a *Myrmica* host for further development in the ant nest (Akino et al. 1999). There, the larva is fed and cared for by its host. It hibernates, sometimes even twice, and, having gained 98% of its final biomass, it pupates in the host nest (Elmes et al. 2001). One month later, the adult butterfly emerges (Thomas et al. 1998).

A crucial moment in the life of *Maculinea rebeli* is the first contact with the potential host. During this encounter, signals such as size, touch, behaviour and sound are apparently important (summarised by Elmes et al. 2002). Chemical communication, however, probably plays the key role (see Hölldobler and Wilson 1990) because ants are known to distinguish between friend and foe according to a bouquet of semiochemical surface hydrocarbons (Singer 1998; Lenoir et al. 2001). As the butterfly larva has never been in contact with its host ants before, the pre-adoption larva probably achieves olfactory similarity

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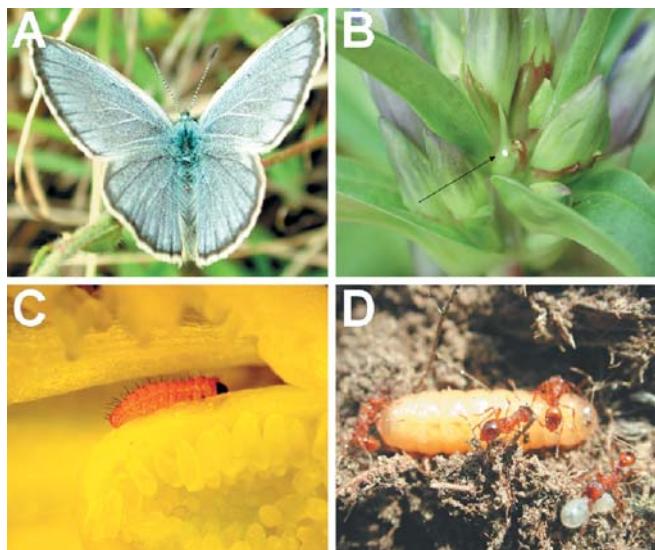


Fig. 1A–D Life cycle of the Mountain Alcon Blue, *Maculinea rebeli*. **A** male adult; **B** egg on the host plant, the cross gentian *Gentiana cruciata*; **C** pre-adoption larva (3 mm) feeding inside a blossom of its host plant, **D** *Myrmica sabuleti* host ants tend to a *M. rebeli* larva after hibernation (15 mm)

by chemical mimicry, i.e. the biosynthesis of host-ant odour cues (see Elmes et al. 1991). Chemical mimicry has commonly been assumed to be involved in insect–insect interactions (Dettner and Liepert 1994), but experimental proof through the use of radio-labelling is rare (e.g. Howard et al. 1980, 1982). Nevertheless, Akino et al. (1999) presented the first evidence for chemical mimicry by *Maculinea rebeli* larvae, with samples from western Europe, where *Myrmica schencki* is the almost exclusive host (Elmes et al. 1998). Using glass dummies with extracts of the cuticular chemicals of pre-adoption *Maculinea rebeli* larvae, they demonstrated that *Myrmica schencki* workers carry the dummies into their nest just as they do with live pre-adoption *M. rebeli* larvae. Gas chromatography–mass spectrometry analyses showed that the bouquet of *M. rebeli* larvae was quite simple and more similar to the bouquet of *Myrmica schencki* than to that of other *Myrmica* species. Elmes et al. (2002) considered the chemical signatures of various *Myrmica* species to be sufficiently different to explain the host-specificity patterns of European *Maculinea* butterflies by chemical mimicry. However, they also observed that the simple profiles of *M. rebeli* larvae contain substances that are present not only in *M. schencki* but in the profiles of most other *Myrmica* species as well.

Only recently has it been shown that the host use of *Maculinea rebeli* in central Europe differs from the situation in western Europe. In central Europe, *Myrmica sabuleti* is the main host ant, whereas *M. scabrinodis*, *M. sulcinodis*, *M. speciosoides* and *M. schencki* are less frequently used (Steiner et al. 2003). The successful use of different *Myrmica* hosts by individuals even of the same *Maculinea rebeli* population was established. However, while multi-host use in the related *Maculinea alcon*

has been described (Elmes et al. 1994) and studied in detail (e.g. Als et al. 2001, 2002), we still know little about host-use patterns in central European *Maculinea rebeli*. The mechanism and the chemistry behind multi-host use in *M. rebeli* are completely unknown.

In this study we investigated for the first time the surface hydrocarbons of *Maculinea rebeli* from populations with multi-host use, and for the first time examined the hydrocarbons of *M. rebeli* larvae that hibernated in nature. We posed two competing hypotheses concerning the chemical signature of the pre-adoption larvae of *Maculinea rebeli*: (1) the pre-adoption larva produces only key compounds which all of the host ant species have in common (“intersection-odour”; simple bouquet); (2) the pre-adoption larva produces a spectrum of hydrocarbons that includes species-specific compounds of every single host species (“aggregate-odour”; complex bouquet). We used GC–MS data to assess whether one of these hypotheses would be supported based on similarities in the relative quantities of compounds.

Materials and methods

Maculinea rebeli pre-adoption larvae, larvae after hibernation, and host ant workers from parasitised nests (from one *Myrmica schencki* and three *M. sabuleti* nests) were sampled at six sites of five *M. rebeli* populations in eastern Austria (summer 2001; for details see Schlick-Steiner et al. 2002; Steiner et al. 2003):

- Nördliches Weinviertel (sites 1 and 2, 250 m asl): *M. rebeli* pre-adoption larvae and hibernated larvae with *M. sabuleti* and *M. schencki*
- Steinfeld (site 3, 330 m asl): *M. rebeli* pre-adoption larvae
- Rosaliengebirge (site 4, 300 m asl): *M. rebeli* pre-adoption larvae
- Günser Gebirge (site 5, 420 m asl): hibernated *M. rebeli* larvae with *M. sabuleti*
- Rothwald (site 6, 720 m asl): *M. rebeli* pre-adoption larvae and hibernated larvae with *M. sabuleti*.

At site 1, *Myrmica sabuleti* and *M. schencki* were used simultaneously as hosts, at sites 5 and 6 (both 150 km away from the first site and from each other) only *M. sabuleti* was found as a host.

Caterpillars and ants were anaesthetised at -21°C and hydrocarbons were extracted with *n*-hexane. From the ant material we used exclusively workers, because Elmes et al. (2002) have shown that the cuticular hydrocarbon profiles of adult ant workers fall within the range of variation exhibited by ant larvae. Individuals were pooled (five pre-adoption larvae, three ant workers), except for hibernated larvae. A total of 20 samples were extracted (*M. rebeli* pre-adoption larvae: seven samples from five sites; *M. rebeli* larvae after hibernation with *M. sabuleti*: seven samples from three nests and three sites; *M. rebeli* larvae after hibernation with *M. schencki*: two samples from one nest; *M. sabuleti* workers: three samples from three sites; *M. schencki* workers: one sample). In addition, one sample of *Myrmica speciosoides* workers from the Steinfeld population was extracted (three workers). Extracts were analysed by gas chromatography–mass spectrometry (GC–MS) (HP 6180C GCD Systems; EID; HP-5 column diameter 0.25 mm, length 30 m; carrier gas helium; 1- μl samples injected in splitless mode; column oven set at 50°C for 5 min, programmed from 50°C to 200°C at $20^{\circ}\text{C}/\text{min}$, then from 200°C to 300°C at $5^{\circ}\text{C}/\text{min}$ and maintained at the final temperature for 10 min). Chromatograms were profiled as described by Steiner et al. (2002), using a single profile of 107 selected components (master GC). MS data were

used only to ensure that corresponding peaks indicated the same compound.

Based on the relative quantities of the compounds, profiled chromatograms were ordinated by principal components analysis (PCA).

Similarity in the hydrocarbon peaks was estimated between each of the 190 possible pairs of samples using the Bray-Curtis similarity index S_{ij} as described by Elmes et al. (2002). For any two samples i and j :

$$S_{ij} = 1 - \frac{\sum_k |X_{ik} - X_{jk}|}{\sum_k |X_{ik} + X_{jk}|} \quad (1)$$

where X_{ik} = relative intensity of peaks k in sample i . S_{ij} varies between 0 (when two samples have no peaks in common) and 1 (when the composition in two samples is identical). The Bray-Curtis similarity values were calculated using X_{ik} equal to the fourth root of the relative intensity of each peak (see Clarke 1993; Elmes et al. 2002).

Non-parametric one-way analysis of ranked similarities randomisation (ANOSIM; Clarke 1993; Clarke and Green 1988) was used to test the probability that the pairwise similarities within and between groups of samples were the same. We defined five groups: pre-adoption *M. rebelei* larvae; hibernated *M. rebelei* larvae with *M. sabuleti* and *M. schencki*, respectively; *M. sabuleti* workers; *M. schencki* workers.

Non-metric multidimensional scaling ordination plots (MDS) were used to visualise the Bray-Curtis pairwise dissimilarities. The extent of any final lack of agreement is measured by a statistic called the STRESS (standardised residual sum of squares), defined in non-metric MDS as:

$$\text{STRESS} = \sqrt{\left[\frac{\sum_{i < j} (\text{rank}(D_{ij}) - \text{rank}(A_{ij}))^2}{\sum_{i < j} \text{rank}(D_{ij})^2} \right]} \quad (2)$$

The lower the STRESS, the better the MDS plot represents the original Bray-Curtis dissimilarities (Krzyszowski 1988).

Calculation of Bray-Curtis similarity values, ANOSIM tests, MDS-plotting and calculation of STRESS values were accomplished using Primer 5.2.9 (Clarke and Gorley 2001).

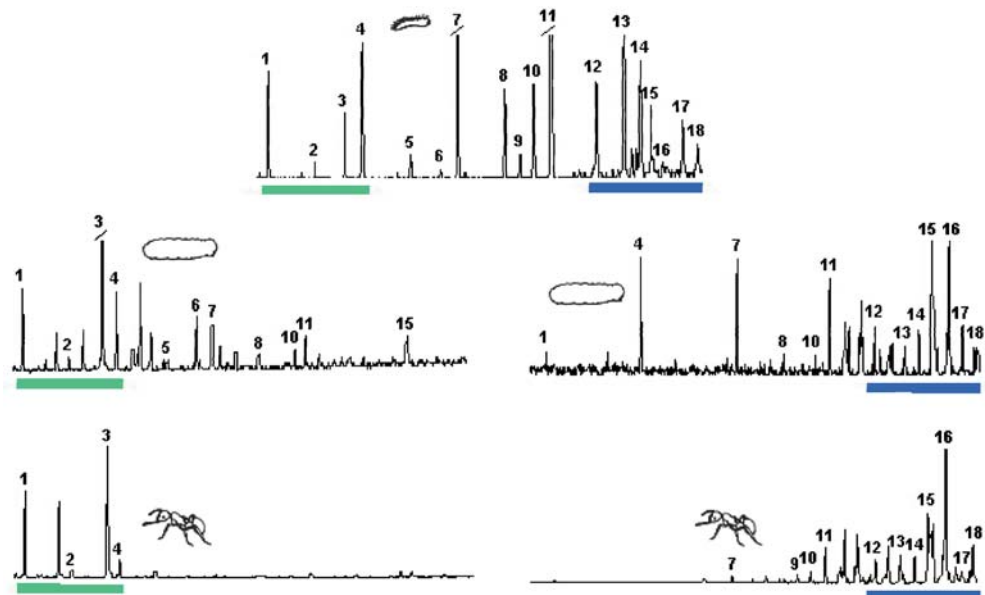
Self-organising maps (SOM; Kohonen 2001) were used for ordination of the same data as subjected to PCA. SOM represent a neural network algorithm based on unsupervised training. Their advantage over supervised algorithms such as the multilayer perceptron is that the final target values of any vectors do not

need to be known. While some linear methods such as PCA are unsupervised too, SOM is known to perform better than linear methods in visualising patterns behind complex data sets, as it separates the data in a multidimensional space. PCA uses a simple projection of data points on a plane defined mostly by the first and second eigenvectors, whereas SOM uses so-called weight vectors that are placed within and near the data vectors after the training epochs. The nearby locations in the input space correspond to the neighbouring neurons. In the final state, the weight vectors are laid down like a flexible net over the hypersurface built by the data vectors. Hence, SOM reveals more information on the structure of the data than PCA. SOM have become an important tool in data mining, knowledge discovery in databases, and especially in assessing classifications. They have already been successfully used in the classification of GC-MS data (Steiner et al. 2002). SOM visualisation was based on a hexagonal output grid (where each hexagon represents a neuron) of 6x6 neurons. Samples located in the same neuron or in a neighbouring neuron are more similar than samples ordinated in neurons distant from one another.

Results

The chromatograms of *Maculinea rebelei* pre-adoption larvae, of hibernated larvae and of the two investigated *Myrmica* host ants differ from each other (see Fig. 2). *Myrmica schencki* workers and *M. sabuleti* workers are completely different and have no high-intensity peaks in common. The profiles of the *Maculinea rebelei* pre-adoption larvae are rather complex. We define 18 high intensity peaks in these profiles. The pre-adoption larvae share four of these peaks (peaks 1–4) with *Myrmica sabuleti*, and ten peaks (peaks 7 and 9–18) with *M. schencki*. Out of the peaks shared with *M. schencki*, however, only peaks 12–18 are defined as typical for *M. schencki*. Preliminary GC-MS analyses of *Myrmica speciooides*, used as another host ant in the region (Steiner et al. 2003), showed that peaks 7 and 9–11 also occur in *M. speciooides*. The *Maculinea rebelei* pre-adoption larvae, however, do not contain all substances of the two

Fig. 2 Typical partial chromatograms of *Maculinea rebelei* pre-adoption larvae (upper row), of their host ants (lower row) *Myrmica sabuleti* (left) and *M. schencki* (right), and of the *Maculinea rebelei* larvae that hibernated with the respective host ant (middle row). High-intensity peaks of *M. rebelei* pre-adoption larvae and their equivalents in the other profiles are numbered consecutively. Colour bars indicate the ranges of specific peaks of *Myrmica sabuleti* (green) and *M. schencki* (blue)



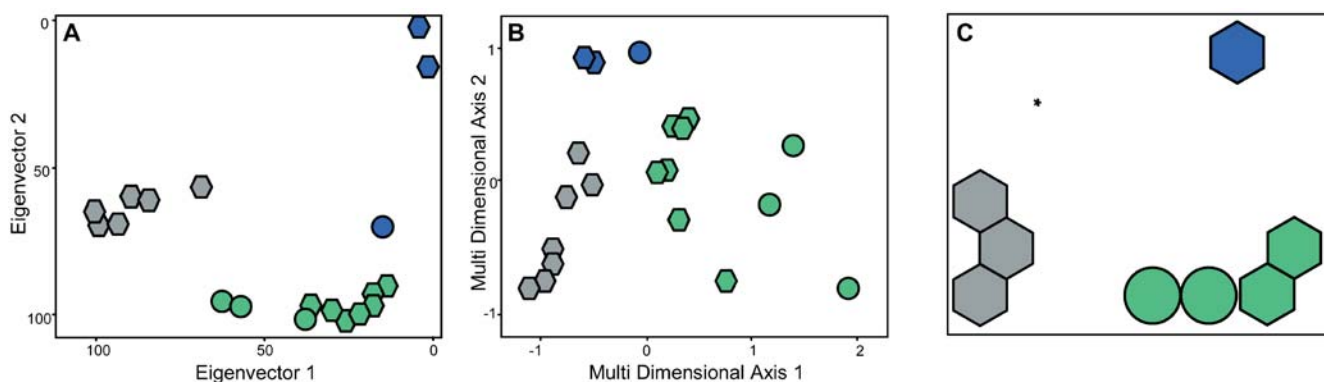


Fig. 3A–C Ordination of the 20 samples of *Maculinea rebeli* larvae and of their *Myrmica* host ants, based on the intensity peaks of 107 compounds. **A** Principal components analysis (PCA) of the profiled chromatograms, based on the relative quantities of compounds. **B** Two-dimensional non-metric multidimensional scaling (MDS) ordination of the Bray-Curtis similarity values for the relative peak intensities, based upon fourth-root transformations. **C** Results of a self-organising maps (SOM) analysis mapped on a

hexagonal output grid (6x6 neurons, represented by one hexagon each). Samples located in the same or in a neighbouring hexagon are more similar than samples ordinated in distant hexagons. *Circles* host ants, *blue* *M. schencki*, *green* *M. sabuleti*. *Hexagons* *M. rebeli*, *grey* pre-adoption (including the sample marked with an asterisk), *blue* after hibernation with *M. schencki*, *green* after hibernation with *M. sabuleti*

Myrmica species. For example, one peak before peak 2 in *M. sabuleti* is absent in the *Maculinea rebeli* pre-adoption larva. The same holds true for two peaks between peaks 11 and 12 in *M. schencki*. Hibernated *M. rebeli* larvae have profiles that differ from the pre-adoption larvae's and are more similar to their respective host ant's profile. They are less complex than those of the pre-adoption larvae. Peaks which pre-adoption larvae share with the future host ant persist without exception, the other high-intensity peaks of the pre-adoption larvae may lose intensity or vanish completely. In *Maculinea rebeli* larvae that hibernated with *Myrmica sabuleti*, several substances were found which occurred neither in the pre-adoption larvae nor in the host ant workers (e.g. a peak after peak 2, three peaks between peaks 4 and 5).

The three applied ordination methods arrive at similar results. PCA reveals that the pre-adoption larvae, the larvae that hibernated with *Myrmica sabuleti* and *M. schencki*, respectively, as well as *M. sabuleti* and *M. schencki* workers, each form a group separated from the others (Fig. 3A). Only one *M. sabuleti* sample is closer to the *Maculinea rebeli* larvae hibernated with *M. sabuleti* than to the other *M. sabuleti* samples. The *M. schencki* sample is closer to the hibernated larvae from *M. sabuleti* nests than to the *M. rebeli* larvae hibernated in the *M. schencki* nest.

The MDS ordination based on the Bray-Curtis dissimilarity values after fourth-root transformation (Fig. 3B) gives a good representation of all the measured dissimilarities (STRESS = 0.09). It resembles the PCA of the raw data, but the samples of the groups cluster less closely within the group, with the exception of larvae hibernated with *M. schencki*. The larvae hibernated with *M. schencki* and the *M. schencki* workers are very closely ordinated. An ANOSIM test of the Bray-Curtis values after fourth-root transformation showed that a grouping within the set of data as a whole exists (global R value = 0.984) and that

the groups are well separated from each other (pairwise R values = 0.942–1.000).

SOM classifies all the samples of each group containing more than one sample into the same or into neighbouring neurons (Fig. 3C), except one pre-adoption larva sample (Nördliches Weinviertel, site 1). The groups are separated by one or more neurons between them except for the *M. sabuleti* workers and the *M. rebeli* larvae that hibernated with *M. sabuleti*.

Discussion

Our finding of species-specific patterns of cuticular hydrocarbons in the two investigated *Myrmica* host ants – as revealed by the existence of exclusive peaks not shared by the other species (Fig. 2) and confirmed by all three ordination methods – is in agreement with earlier reports (Akino et al. 1999; Elmes et al. 2002). There is some variation within *M. sabuleti*, as suggested in the MDS ordination of the Bray-Curtis values, but this agrees with the variation found by Elmes et al. (2002). At this point, our data set does not allow us to put forward an explanation based on geographical variation (distance of about 150 km between each of the sites) because at each of the three sites only one *M. sabuleti* nest parasitised by *Maculinea rebeli* was found.

The seven samples of pre-adoption larvae are quite similar to each other. Again, slight variations cannot be attributed to geographical distance due to the small number of samples.

For the first time, data on laboratory adoptions (based on a short-term period between pre- and post-adoption sampling; Akino et al. 1999) are confirmed based on adoption and hibernation in nature. Accordingly, the profiles of *Maculinea rebeli* change between the pre-adoption and post-adoption stage. Those authors, howev-

er, did not report any loss of peaks. The present results indicate that the profiles lose certain peaks, depending on the host ant species, and thus become less complex after adoption. As a consequence of this reduction, the profile of the hibernated larva is more similar to the respective host ant than the pre-adoption larva is. This effect is increased by the occurrence of additional substances, which the hibernated larva shares with the host ant species. This was likewise observed by Akino et al. (1999), who assumed that chemical camouflage, i.e. the passive adsorption of ant surface hydrocarbons (Dettner and Liepert 1994), was involved in acquiring the full colony odour after adoption. In a re-interpretation of this data set, Elmes et al. (2002) identified substances in the post-adoption larvae which were absent in both the pre-adoption larvae and the host ants, a phenomenon that also occurs in our material. They argued that the post-adoption larva, being capable of synthesising substances that are absent in the host ants, might synthesise all the substances of the host ant. Elmes et al. (2002) interpreted this as post-adoption mimicry in addition to the pre-adoption mimicry. By assuming that the larvae can mimic only the western European main host *Myrmica schencki*, the authors explain the higher mortality rate of larvae adopted by ants other than *M. schencki*. This line of argument does not apply to the populations in central Europe, where a successful multi-host use was found, with *M. schencki* being only a secondary host. It remains open to debate whether central European post-adoption larvae can synthesise certain substances of the bouquet of different host ants, or whether they acquire these substances by passive adsorption.

The novel finding of the current study is that the signatures of the pre-adoption *Maculinea rebeli* larvae from central Europe partly match two different host ants. Thus, the caterpillars appear to be disposed for multi-host use. The occurrence of different species-specific (and not overlapping!) odour compounds of two resident host ant species in the bouquet of the pre-adoption larva, the general complexity of the signature, and the similar results of quantity-based ordination by different methods, support the “aggregate-odour” hypothesis over the “intersection-odour” hypothesis. We term this chemical strategy “aggregate-odour multi-host mimicry” because, along with a high flexibility in the post-adoption development of the chemical signature, it facilitates the use of several host species. This interpretation partly matches the observation by Elmes et al. (2002) that the profile of the pre-adoption larva is dominated by substances also present in profiles of most other *Myrmica* species. The main difference between their and our observations is that they found a simple profile of the pre-adoption larva, whereas in our material the pre-adoption larva exhibited the most complex profile. This difference is probably due to the different geographical origin of the samples and to the different host-uses and host-specificities in the two regions. The chemistry behind the butterfly–ant relationship clearly differs between western and central Europe. The Mountain Alcon Blue promises to yield deeper

insights into the host–parasite interaction, provided that our protection effort succeeds.

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