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Pattern and process in the evolution of insect-plant associations: *Yponomeuta* as an example

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Abstract

Phylogenetic studies are increasing our understanding of the evolution of associations between phytophagous insects and their host plants. Sequential evolution, i.e. the shift of insect herbivores onto pre-existing plant species, appears to be much more common than coevolution, where reciprocal selection between interacting insects and plants is thought to induce chemical diversification and resistance in plants and food specialization in insects.

Extreme host specificity is common in phytophagous insects and future studies are likely to reveal even more specialization. Hypotheses that assume that food specialists have selective advantages over generalists do not seem to provide a general explanation for the ubiquity of specialist insect herbivores. Specialists are probably committed to remain so, because they have little evolutionary opportunity to reverse the process due to genetically determined constraints on the evolution of their physiology or nervous system. The same constraints might result in phylogenetic conservatism, i.e. the frequent association of related insect herbivores with related plants. Current phylogenetic evidence, however, indicates that there is no intrinsic direction to the evolution of specialization.

Historical aspects of insect-host plant associations will be illustrated with the small ermine moth genus *Yponomeuta*. Small ermine moths show an ancestral host association with the family Celastraceae. The genus seems to be committed to specialization per se rather than to a particular group of plants. Whatever host shift they have made in their evolutionary past (onto Rosaceae, Crassulaceae, and Salicaceae), they remain monophagous. The oligophagous *Y. padellus* is the only exception. This species might comprise a mosaic of genetically divergent host-associated populations.

Introduction

The remarkable diversity of associations between phytophagous insects and their host plants, with some feeding on a large number of plant species belonging to widely different plant families and others being restricted to one particular plant species, has prompted many biologists to investigate patterns and processes underlying such associations. In pattern analysis, one seeks to reconstruct ancestral food-plant associations and to understand how these have changed through evolutionary time; on the process side, the underlying mechanisms that govern the evolution of these associations are studied. Integration of macro- (phylogenetic and biogeographic) and microevolutionary (ecologi-

cal, behavioural and population genetical) studies is a prerequisite for a complete understanding of interactions between phytophages and plants. However, if microevolutionary investigations are limited to local associations, without considering geographic variation in interactions, only a fraction of the evolutionary process will be elucidated (Thompson, 1994).

Brooks & McLennan (1991) greatly stimulated research from a historical perspective as a means of gaining insight into the origin and evolution of, for instance, relationships between insect herbivores and their hosts. Progress in phylogenetic methodology (Hennig, 1966; Forey *et al.*, 1992) and molecular biology (Hillis & Moritz, 1990), allowing the reconstruction of phylogenetic relationships from molecular

data, has underscored the significance of a historical perspective in ecology. The evolution of present-day insect host-plant associations can be best understood by establishing phylogenetic relationships (from molecular, allozyme, morphological, and/or other data sets) among extant species and subsequently mapping their host plants onto the insect cladogram (Mitter & Brooks, 1983; Mitter *et al.*, 1991; Menken *et al.*, 1992).

Instead of evaluating these associations against existing cladograms, they can also be used as primary input for phylogeny reconstruction (Miller & Wenzel, 1995). It appears that, on average, ecological characters are no more homoplasious than are morphological traits (DeQueiroz & Wimberger, 1993). However, some ecological characters may be intrinsically labile (Ward, 1991), phytophage-host plant interactions being an example (e.g., related species feeding as oligophages on different, but partly overlapping combinations of food plants). In the following section I outline how phylogenetic studies are increasing our understanding of associations between phytophagous insects and their hosts.

Theories of insect – plant associations

Three major theories of insect-plant affiliations exist, viz., coevolution *sensu stricto*, diffuse coevolution, and sequential evolution.

Coevolution s.s. In their influential paper, Ehrlich & Raven (1964) assumed that reciprocal selection between insects and plants has induced both chemical diversification and resistance in plants and food specialization in insects. A plant species that has evolved a new chemical defence due to selection by a range of herbivores alleviates herbivory and therefore this species is able to diversify. A phytophagous insect species that evolves adaptation to these compounds can subsequently diversify. Ehrlich and Raven's hypothesis can be best called 'escape-and-radiation coevolution' (Thompson, 1994) and in fact they seem to have envisaged diffuse coevolution (see below) rather than coevolution *s.s.* 'Specific' coevolution results in a strict congruence between the cladograms of plants and insects (so-called phylogenetic tracking or cladogram congruence) in cases where a species has significant control over the reproductive success of its host, viz., pollinator-plant interactions and maternally inherited endosymbionts (see examples in Thompson, 1994). Coevolution is sometimes narrowed down to

cospeciation (Miller & Wenzel, 1995), in particular to dichopatric, i.e., vicariant, speciation (Bush, 1994); a physical barrier against gene flow can result in the acquisition of the species status for a plant and (some of) its specific phytophages. Such tandem speciation, however, is only one of the possible outcomes of evolving species interactions. Moreover, cospeciation can simply be the fortuitous outcome of an interaction and not necessarily the result of reciprocal evolutionary change. In phytophages, only two well-documented cases of cospeciation exist: chrysomelid beetles of the genera *Phyllobrotica* (Farrell & Mitter, 1990) and *Tetraopes* (Farrell & Mitter, 1993). Interestingly, in these two genera larvae and adults feed as monophages on different parts of the same food plant.

Studies of cospeciation are riddled with methodological and theoretical problems (summarized in Miller & Wenzel, 1995). Cladistic information on the plants is often lacking and there is confusion concerning how to deal with missing data. Furthermore, despite the fact that coevolution has occurred, there could be a poor fit of the cladograms due to asynchronous speciation or extinction. Finally, a strict concordance does not necessarily mean that a continual association has occurred between the two clades. This at least requires that the two clades be of similar age. It is, for example, possible that when host shifts were 'mediated by plant characters strictly concordant with plant phylogeny' (Mitter *et al.*, 1991) a recent diversification of an insect lineage has resulted in strictly congruent phylogenies. Suppose, for instance, that in general plant defences evolve towards increasingly toxic compounds. An insect taxon shifting to a new plant family might then first colonize the more primitive, less-defended plant species and after establishment sequentially attack more advanced and increasingly toxic hosts. In *Tetraopes*, it looks as if more derived species feed on rather advanced *Asclepias* hosts containing more complex, toxic cardenolides (Farrell & Mitter, 1993). In *Phyllobrotica*, however, the most toxic iridoids appear to be present in the most primitive plant species (Bowers, 1988).

Coevolution or not, phylogeny reconstructs the evolutionary history of characters themselves. For a complete understanding of the species interactions, it is necessary to identify some independent (most likely chemical) aspects of the host plants that provide an explanation for the observed pattern of associations.

Diffuse coevolution. Coevolution in this case is considered in a community context: species interactions

in communities are thought to be so tight that evolution of any member of the community will affect the evolution of the other members. It is extremely unlikely, however, that every species in a community will change in response to any change in every other species and patterns of diffuse coevolution appear to be much more specific at a local level (Thompson, 1994). Yet, an increasing number of interacting species goes hand in hand with an increasing difficulty to identify what constitutes reciprocal evolutionary change. The (degree of) complexity of picking out individual pairs of coevolving species certainly does not justify lumping such interactions into diffuse coevolution (also called guild evolution and multispecies coevolution) and does not relieve us of the task of investigating this important area of evolution.

Sequential evolution. It has been proposed that, instead of reciprocal evolutionary change, the evolution of insect herbivores follows that of their host plants without much affecting plant evolution (Jermy, 1976). Since plant chemistry is probably the most important source of information used by females to finally decide where to oviposit (Renwick & Chew, 1994), it is logical to assume that heritable changes in the insects' plant recognition mechanism are the primary event in the evolution of insect-plant relationships; this is particularly true of herbivorous insects with relatively immobile larval stages (like most Lepidoptera). Consequently, host-plant shifts are usually constrained in chemical channels and represent colonization of pre-existing plant species that are phytochemically similar, but not necessarily taxonomically related, to their extant hosts (Feeny, 1992). Sequential evolution results in cladograms of insects and hosts that are usually not congruent. There is now convincing evidence from cladistic analyses of insect-host associations in various orders of insects that colonization is the predominant mode for the evolution of insect herbivores (reviewed in Miller & Wenzel, 1995).

Diet breadth in insect herbivores: the predominance of specialists

In insect herbivores, three levels of diet breadth are commonly recognized, viz., monophagy, oligophagy, and polyphagy where insects feed on plant species that belong to one plant genus, one family, and more than one family, respectively. It appears that the majority of phytophagous insects are extreme specialists (Thomp-

son, 1994). However, this view is mainly based on studies in the temperate zones; our current understanding of host-plant associations in the tropics is still very fragmentary. In the only detailed, long-term study on feeding specialization in moths and butterflies in Costa Rica, Janzen (1988) estimated that over 50% of the caterpillars feed on only one plant species (strict monophagy) and that oligophagy predominates among the remainder. Whether future studies will reveal more or less specialization also depends on the amount of lumping and splitting.

As regards lumping, polyphagous species frequently consist of locally specialized populations, 'races' or even sibling species complexes (e.g., the *Yponomeuta padellus* complex, Menken *et al.*, 1992). Real polyphagy at the individual level is rare (Fox & Marrow, 1981). An extreme example of such hidden specialization is *Papilio glaucus*, the eastern tiger swallowtail. This species is known from over 500 different host plants belonging to 17 plant families (Scriber, 1988), yet local populations are sometimes restricted to one food plant (e.g., *Magnolia virginiana*) and northern populations of the assemblage comprise a different species, *P. canadensis* (Hagen *et al.*, 1991). Thompson (1993) has pointed out that in insect species in which ovipositing females determine the host-plant choice of their progeny two different mechanisms (one genetic and one ecological in origin) exist of how geographic specialization could develop. Either host use differs because populations evolve genetic differences in how females rank potential hosts, or – in the absence of genetic differentiation in host preference hierarchy – because top-ranked hosts are locally rare or absent. The actual host use will often be determined by a combination of the two. For example, *Papilio zelicaon* (Thompson, 1993) maintains its normal preference rank order irrespective of what plant species is present and thus the overall preference hierarchy appears to be evolutionary conservative. On the other hand, female *Euphydryas editha* exhibit appreciable differences in the way they rank host plants (Singer *et al.*, 1992). Furthermore, as Singer & Parmesan (1993) pointed out 'the diet is a property neither of the parasite nor of the host, but of the parasite host interaction'. Thompson (1994) has elegantly translated this geographic structure of specialization into the 'geographic mosaic theory of coevolution'.

With regard to splitting, many species of phytophagous insects have been described solely on the basis of their host-plant relationships. For instance, specimens of the monophagous nepticulid leafminer

species *Stigmella aurella* (feeding on *Rubus*), *S. gei* (on *Geum*), *S. fragariella* (on *Fragaria*), and *S. nitens* (on *Agrimonia*) all belong to one oligophagous species, *S. aurella* (Menken & Raijmann, 1996). A number of hypotheses, in which it is assumed that food specialization has selective advantages over generalist feeding habits, have been put forward to explain the observation that host-plant specificity is so common (for an overview see Jermy, 1993 and references therein).

Escape from interspecific competition

Until recently, competition has been dismissed, based on observations that under natural conditions defoliation is rare or lacking, so that food is rarely limiting for insect herbivores (Hairston *et al.*, 1960), and that empty niches exist (Lawton, 1982). In a recent review, however, Denno *et al.* (1995) conclude that interspecific competition is common among phytophages, though least likely in mandibulate folivores. Strict specialist herbivores might experience increased competition because they normally do not have the option of shifting host plants. Polyphagy, by contrast, might provide opportunities to diminish competitive interactions.

Escape from natural enemies (predators, parasites and pathogens; Strong et al., 1984)

Several authors have supported or refuted this hypothesis (Jermy, 1988; 1993 and references therein). It is clear that if predation on plant A is without exception higher than on plant B, this will lead to specialization on B, but enemy escape will often be the result and not the cause of the specialization (e.g., the mutualistic association between particular ant species and lycaenid butterflies; Pierce, 1984; but see Bernays & Graham, 1988).

Host-plant preference and performance

a. Increased efficiency of detoxification of plant allelochemicals should lead to more efficient food utilization in specialists. There is controversy over the magnitude of metabolic costs of detoxification and how well generalized enzyme systems can detoxify a chemically diverse array of secondary compounds (Jermy, 1988). Recently, Kawecki (1994) formulated a hypothesis on the costs of being a generalist (see also point d). The occurrence of much hidden specialization in generalists might be an important reason why consistent differences in efficiency of host utilization have not been revealed in comparisons between generalist and specialist

phytophages (Howard *et al.*, 1994 and references therein).

- b. Deterrent allelochemicals betoken toxicity of plants. Insects therefore evolved behavioural rejection (antixenosis) of toxic plant compounds, resulting in host specialization. Although some deterrents are indeed toxic to non-adapted insects if ingested (antibiosis), no general correlation between deterrence and toxicity has been found. Some authors (e.g., Chapman, 1980) believe that deterrence is the major cause of specialization; an insect must lose its sensitivity to the deterrents in a potential host before that plant becomes available as suitable host (e.g., insensitivity of *Yponomeuta rorelus* to salicin or insensitivity of *Y. malinellus* to phloridzin; Menken *et al.*, 1992).
- c. Limits to the rate at which plants suitable for oviposition can be found favours polyphagy (Jaenike, 1990). For instance, food abundance and predictability select for specialist behaviour. Host rarity, on the contrary, selects for risk spreading over a number of plant species.
- d. Host selection behaviour is expected to be correlated with offspring performance. Thus an evolutionary increase in offspring performance on one host concomitantly results in a reduction in adaptation to its former host. Such trade-offs in feeding efficiency stem from the premise that generalized detoxification systems are more costly than specialized ones (Levins, 1968), and that preference for a good host or avoidance of a poor host evolves at a greater speed than high feeding performance across hosts (Castillo-Chavez *et al.*, 1988). Although this is a potentially powerful explanation of host specialization (Jaenike, 1990), usually fitness trade-offs are not found (Futuyma *et al.*, 1994; Sheck & Gould, 1993). This result can be partly explained by the use of generalists as study objects in which physiological constraints are less likely to occur than in specialists.

Each of the above hypotheses probably holds for a certain number of insects, but it is difficult to champion one that provides a general explanation for the ubiquity of specialist insect herbivores. It is possible that the assumption that specialist feeding behaviour is selectively advantageous is in general erroneous and that the dearth of real generalists merely reflects higher relative speciation rates in specialists and directed evolution towards dietary specialism (Jermy, 1993). A new food plant usually means an extension of diet breadth

in a truly generalist species whereas in a specialist, specialization on patchy resources often leads to host race formation and speciation (Futuyma & Moreno, 1988; Menken *et al.*, 1992). Conversely, it is true that if a phytophage is fully dependent on one single plant species, it will become extinct when its host does so. Much depends on how common is total dependence on one food plant over the entire range of the specialist.

Specialists may be committed to remain so, not because of any selective advantage, but simply because they have little or no evolutionary opportunity to reverse the process due to constraints on the evolution of the insects' nervous system or physiology (e.g., to detoxify secondary plant compounds; Lindroth, 1989). However, phylogenetic analyses do not show a clear tendency towards increased specialization (Futuyma & Moreno, 1988; Feeny, 1991; Mitter & Farrell, 1991) and specialization does not appear to be a dead end of evolution (Thompson, 1994), but a comprehensive phylogenetic study is required before a more definite answer can be given. In addition, we hardly have any idea of how the overall neural perception in an insect must change in order to successfully shift to another host, let alone to become a specialist from a generalist or vice versa.

Phylogenetic conservatism

Besides host specialization, phylogenetic conservatism as displayed in the frequent association of related insect herbivores with related plants is a striking feature of phytophagous insects (but see Jermy, 1984). Host specialization and phylogenetic conservatism are supposed to result from genetically determined behavioural and physiological responses of insects to the secondary compounds of their host. Phylogenetic conservatism of diet presumably arises from the greater ease (chemosensory and physiological preadaptation) with which insects will successfully oviposit and feed on plants that are phytochemically similar (this can result in congruent as well as incongruent cladograms). What 'chemically similar' means to an insect is far less clear than what it means to a phytochemist. Insect herbivores are not only simultaneously exposed to a great variety of compounds, but are also able to recognize plants that differ only in one compound (a strong deterrent) as non-hosts and plants that differ much in secondary chemistry but have one particular compound in common (an attractant or phagostimulant) as hosts. An example of the former is the Colorado potato bee-

tle which does not accept *Solanum demissum* which is chemically similar to its major host *S. tuberosum*, but contains the alkaloid demissine, a strong deterrent (Schreiber, 1958). An example of the latter is the historical host shift in *Yponomeuta* from Celastraceae to phytochemically drastically different plants of the Rosaceae that contain dulcitol (see below).

Phylogenetic conservatism implicitly assumes that a specialist insect lacks adequate selectable variation to adapt to a greater range of host species and that the direction of host shifts is genetically constrained. Futuyma and co-workers (e.g., Futuyma *et al.*, 1994) explored the limits of evolution in various *Ophraella* leaf beetles by investigating the variation in features that have not evolved. Overall, *Ophraella* species seem to lack heritable variation for adaptation to other plants and, therefore, genetic constraints can account for the phylogenetic conservatism of host associations that is so widespread in many groups of insects. It is generally believed that behavioural rather than physiological constraints limit host-range expansion (Wiklund, 1974; Futuyma, 1983; Karowe, 1990).

Yponomeuta as a model

The genus *Yponomeuta* (Lepidoptera: Yponomeutidae) has been studied as a model system for the evolution of insect-plant associations and speciation in phytophagous insects (Menken *et al.*, 1992). The genus has a worldwide, but mainly palearctic, distribution and comprises about 75 species; food plant associations are known for about 25 species (S. A. Ulenberg & Z. Gershenson, unpubl.). With the exception of the oligophagous *Y. padellus*, all species are monophagous on trees or shrubs, the great majority of which belong to the genus *Euonymus* (Celastraceae). Some eighty percent of the species at all levels of relationships feed on *Euonymus*. Outside the genus *Yponomeuta* (but within the family Yponomeutidae), however, only three species (not closely related to *Yponomeuta*) of several hundreds use Celastraceae as food plants. Overall, *Euonymus* has a rather impoverished entomofauna: few phytophages are able to survive on these plants, most likely due to the presence of a great variety of toxic alkaloids and butenolides (Fung, 1986). Together, this information has led to the following working hypothesis: the present-day affiliations in the genus *Yponomeuta* evolved from an ancestral association with Celastraceae through speciation in allopatry, mostly on *Euonymus*, and through host shifts in

sympatry or allopatry to Rosaceae and two other plant families.

By mapping the host-plant associations as characters onto an independently derived estimate of the insect phylogeny, hypotheses can be generated on the evolution between *Yponomeuta* and its hosts. Several provisional phylogenies of a variable number of species are available, based on frequency data at some 50 allozyme and general protein loci (Menken *et al.*, 1992) and on DNA sequences of nuclear (ITS1 and 18S ribosomal RNA gene; J. Hermans, unpubl.) and mitochondrial genes (cytochrome b and 16S ribosomal RNA gene; N. Lieshout, unpubl.).

Figure 1 shows the phylogenetic relationships between 14 species based on allozymes and DNA sequence information. If Celastraceae indeed served as host plants of the common ancestor of *Yponomeuta*, then only a single shift from Celastraceae to Rosaceae has occurred in the evolution of the genus (in the phylogenetic tree entirely based on allozymes such a shift has occurred twice; Menken *et al.*, 1992). The alternative hypothesis of an ancestral association with Rosaceae requires at least six shifts to Celastraceae and is thus less likely. Minor shifts have occurred to Crassulaceae (*Y. vigintipunctatus*) and Salicaceae (*Y. rorellus* and *gigas*).

The genus *Yponomeuta* is made up of specialists, but there is no phylogenetic conservatism at the genus level. *Yponomeuta* species seem to be committed to specialization per se rather than to a particular plant group: whatever shift they have made in the evolutionary past, the descendant species remained monophagous. It is also conceivable that (some of the) specialists have originated from transient generalists (which are no longer around to document their existence). Populations of *Y. padellus*, comprising host races on a variety of Rosaceae plants (Menken *et al.*, 1992; Menken & Raijmann, 1996), could be a current example of such a bridging function for oligophages.

Yponomeuta is a good example of sequential evolution: the cladograms of insects and hosts are not congruent and the radiation of *Yponomeuta* postdated the divergence of their host plants. The hypothesis that *Yponomeuta* diversified in concert with its hosts would require that this moth genus be virtually as old as the angiosperms. The age of the genus, however (in the absence of fossils based on allozymes), is best estimated at between 10 and 20 million years (Menken, 1982; Menken & Ulenberg, 1987). As we have seen, this does not totally exclude the possibility of coevolution

sensu stricto during certain periods in the evolutionary past.

Mechanisms: did dulcitol facilitate the shift?

It can be assumed that the evolutionary changes in the perception and the behavioural responses required to realize a host shift might be minor if the new host plant shares major chemical properties with the original host plant. However, Celastraceae and Rosaceae are not only taxonomically totally unrelated but also differ phytochemically. Despite such differences some common features in their chemistry might have facilitated the host shift. A remarkable correspondence was found between chemosensitivity to and presence in the food plant of the primary sugar alcohol isomers sorbitol and dulcitol (Peterson *et al.*, 1990). Sorbitol is found exclusively in Rosaceae (and is a phagostimulant for Rosaceae feeders), whereas dulcitol (a phagostimulant for Celastraceae feeders) occurs only in Celastraceae. However, traces of dulcitol have also been found in various species of *Prunus* (Rosaceae), the very food plant genus to which the ancestral host shift (or shifts) occurred (Fung & Herrebout, 1988; Menken *et al.*, 1992).

A scenario is thus conceivable in which perception of dulcitol that is present in low quantities in some Rosaceae has been the basis for a shift from Celastraceae to the phytochemically radically different Rosaceae (Peterson *et al.*, 1990). Such a shift does not seem to require extensive modifications in the overall neural perception of the groups that switched. This scenario has been made plausible by experiments in which *Y. cagnagellus*, normally strictly monophagous on *Euonymus europaeus*, readily and successfully accepted *Prunus padus* (Rosaceae; the food plant of *Y. evonymellus*) that was impregnated with dulcitol (Kooi & van de Water, 1988). The natural levels of dulcitol in *P. padus* are, however, too low (0.0–0.3% of dry weight versus 2.7–4.7% in *E. europaeus*; Fung, 1986) to be perceived by today's *Y. cagnagellus*.

Of course we do not know what the dulcitol concentrations or the perception levels were at the time when the actual shift took place (higher concentration in some *Prunus* spp., lower threshold levels in the groups that shifted, a combination of these, etc.). Furthermore, analyses of dulcitol concentrations and perception levels were restricted to some populations of insects and plants (Fung, 1986). Possibly, geographic variation is such that perception levels and concentra-

Figure 1. Provisional cladogram of 14 species of *Yponomeuta* (with *Y. meguronis* as outgroup) based on allozymes and sequence data from ITS1 and the 16S ribosomal RNA gene. 'Shift' indicates the position at which the single ancestral host shift from Celastraceae to Rosaceae occurred. Host plant relations are indicated at the right hand side: C, Celastraceae; Cr, Crassulaceae; R, Rosaceae; S, Salicaceae.

tions somewhere in the distribution area match even nowadays.

The reverse is not true; Rosaceae-feeding *Yponomeuta* species did not retain the ability to respond to and develop on the ancestral host plant. *Y. evonymellus* hardly accepts *Euonymus*, and *Y. padellus* and *Y. malinellus* absolutely refuse *Euonymus* even after impregnation with sorbitol, possibly due to strong deterrent effects. Similar, but not so well-founded, scenarios for host shifts to the other plant families on which *Yponomeuta* species feed are available (Menken *et al.*, 1992).

A major shortcoming of the above formulated scenario is the fact that larval chemosensitivity to phagostimulants inside the leaf was analysed whereas the critical phase in the evolution of a host shift in Lepidoptera is the oviposition choice of a female, i.e., the behavioural response to compounds on the surface of the leaf. An electrophysiological study by Blaney & Simmonds (1988) revealed a good correlation between larval and adult chemosensory activities for *Spodoptera* and *Helicoverpa* species, and similar results were found in *Pieris* (van Loon, this volume). We therefore recently started a comparative study of both life stages in *Yponomeuta* to investigate whether the same compounds act as phagostimulants and oviposition stimulating factors: the fact that *Yponomeuta* larvae show qualitative differences in sensitivity of the peripheral chemosensory organs leads to the supposition that such

differences will also occur in the adult stage (P. Roessingh, unpubl.).

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