# Introduction

## 1. Enthralling Colour Patterns

The diverse patterns of colours and shapes that decorate the body or wings of the living organisms are known for playing tremendous number of ecological roles that involve interspecific visual communication, such as crypsis, aposematism and mimicry (Endler, 1984; Vane-Wright & Boppré, 1993; Mallet & Joron, 1999; Bond & Kamil, 2002), intraspecific interactions, such as sexual selection (Cook *et al.*,1994; Lederhouse & Scriber, 1996; Knutte & Fiedler, 2001), mate localization and reproductive isolation (Jiggins *et al.*, 2001), and thermoregulation (Veron , 1974; Holloway *et al.*, 1997; Van Dyck *et al.*, 1997; Gunn, 1998; Thorpe, 2002; Thorpe & Stenson, 2003). Although the diverse array of functions of animal colouration has been extensively studied and captivated biologists as well as amateurs for years (e.g. Nijhout, 1980, French & Brakefield, 1995; Brakefield, 1996; Brunetti, 2001; Monteiro *et al.*, 1994, 1997; Koch *et al*., 1998; Carroll *et al.*, 1994; 1991; Jiggins *et al.*, 2001; Beldade & Brakefield, 2002; Beldade & Brakefield, 2002), our knowledge of how animal colouration is used in communication and recognition is still limited.

There are numerous methods being developed to analyse the colour patterns that are exhibited in complex format (Nijhout, 1980, 1991; French & Brakefield, 1995; Brakefield, 1996; Brunetti, 2001; Monteiro *et al.*, 1994, 1997; Koch *et al*., 1998; Carroll *et al.*, 1994; Beldade *et al*., 2002). The model being developed for analysing wing patterns of

butterflies (Schwanwitsch, 1924; Süffert, 1927; Nijhout, 1991) represents one of most classical examples. Nijhout developed a popular and idealised "groundplan", which comprises all the wing pattern elements that were identified from the Nymphalidae species examined. This "nymphalid groundplan plan" has been providing a descriptive basis for the great variety of lepidopteran colouration. However, homology of the wing pattern elements that are considered playing an important role in sexual selection, aposematism (e.g. eye spots and hindwing lunule patches) and phylogenetic inference was not re-assessed until molecular evolutionary and evo-devo tools were introduced to the research area (French & Brakefield, 1995; Brakefield, 1996; Beldade & Brakefield, 2002; Monteiro *et al.*, 1994, 1997; Monteiro, 2006).

## 2. Using colour pattern characters in phylogenetic analysis

Homology is "the relation that systematists and comparative anatomists use in generating hypotheses of relationship" and synapomorphy identified by a cladistic analysis (Patterson, 1982). Therefore when inferring evolution a group of organisms, assessing homology of the characters being introduced in the analysis becomes a compulsory task (Hennig, 1966), even though we should not judge the homology of a character before the tree established (Patterson, 1982). Ideally and theoretically assessment of character homology does not only apply the phenotypic correlation, but also the genetic and developmental bases behind the phenotype (Abouheif, 1997; Gilbert & Bolker, 2001). Although the characters obtained from body colours and patterns are

visually much easier to recognize than those of internal structures, they are seldom included in most morphology-based phylogenetic analyses due to the variability with environmental, ethological, ontogenetic and dietary changes (Wiley, 1981; Quicke, 1993; McMillan *et al.*, 1999; Winston, 1999), adaptation to microhabitats (Hofmann *et al.*, 2006) and fade or attacked by pests in museum specimens (Carter, 2001; Areekul & Quicke, 2006). In addition, including character of colour patterns in a phylogenetic analysis may cause circularity if the characters being included are directly related to the character evolution to be addressed by the phylogeny (Zrzavý & Nedvěd, 1999; Yen *et al.*, 2005) The other reason that the character involving colour and patterns are often excluded from phylogenetic studies is that these character are considered to be more phylogenetically constrained due to their direct relationship with the whole colour pattern which may show strongly structured evolution possibly causing phylogenetic opinions in conflict with the signal of other morphological characters (Quicke, 1992; Areekul & Quicke, 2006). In other words, the biological phenomena which colour/pattern characters involved in are conventionally considered to be convergent. Therefore there is a tendency that some phylogenetists who study the organisms with aposematic or mimetic coloration do not intend including colour characters or avoid adopting adult wing pattern characters into the data matrices (Penz, 1999; Kitching ,2002; DaCosta *et al.*, 2006; Willmott & Freitas, 2006) as they may have assumed that colour characters may result in homoplasy and mislead phylogenetic reconstruction.

A recent study by Areekul & Quicke (2006) first investigated the effects

of colour characters in inferring phylogenies using an "up-weighting" strategy, which give differential weights to colour characters to observe the variation in trees reconstruction, and compare those experimental result tree populations by agreement subtree method. They suggested that colour characters involving aposematism and mimicry (termed A/M) were more phylogenetically constrained and unnecessarily good indicators in phylogenetic reconstruction. They also cautioned against including colour character from aposematic or mimicry pattern while reconstructing a phylogeny. However, aposematism involving visual cues does not necessarily incorporate with mimicry (Speed & Ruxton, 2005, 2007) if the features involving aposematism of one taxon are not shared by another taxon which is phylogenetically distant (or related) and sympatric in distribution. Different models of mimicry may also involve different phylogenetic predictions of character distribution (Simmons & Weller, 2002). Simmons & Weller (2002) show that the phylogenetic distribution of the mimetic characters involving Müllerian mimicry are phylogenetically conserved, that is, these characters may still provide phylogenetic signal rather mislead phylogenetic reconstruction.

## 3. The questions to be addressed

In Simmons & Weller's (2002) study, three types of character distribution were predicted to accommodate the three mimicry scenarios involving visual signals in a phylogenetic context. In the Müllerian mimicry scheme (Müller, 1879), the species participating in the same mimicry complex and included in the same phylogeny are suspected to be monomorphic, as

stated by Willmott & Mallet (2004), and to form a monophyletic clade (Fig.1E) that is, the characters involving this kind of mimicry are phylogenetically concentrated and potential synapomorphic of a clade. By contrast, the Batesian (Bates, 1862) and quasi-Batesian mimicry schemes (Pough *et al*., 1973; Huheey, 1988; Speed, 1993), the character distribution is suspected to be randomly distributed among different lineages and thus the characters involving mimicry are more likely to be convergent. However, as already stated by Yen *et al.* (2005), the example given by Simmons & Weller (2002) does not include the mimicry occurring among the species included in the same phylogeny and the characters that were considered to be mimetic were not included in the data matrices which were used to generate the trees. Therefore the effect of colour pattern characters on phylogenetic reconstruction could not be detected under this circumstance, but my study was still inspired by their concept of phylogenetic predictions based on different mimicry models.

In the present study, I would apply Simmons & Weller's (2002) concept and Areekul & Quicke's (2006) strategy to re-address the following two questions: (1) if colour/pattern characters involving different models of aposematism or mimicry effect differently on phylogenetic reconstruction? (2) if the colour/pattern characters not involving aposematism or mimicry (e.g. crypsis) are less phylogenetically constrained? I wish this study would provide a practical thinking of adopting colour/pattern characters in morphology-based phylogenetic studies.