



Hazy days. Humbert is on the right, Dolores the left. As Christer discovered many years ago, Dolores is good at saying “yes” but not saying “no”, relying on Humbert to do the decent thing when she is not interested. (Wiklund, C. (1977). Courtship behaviour in relation to female monogamy in *Leptidea sinapis* (Lepidoptera). *Oikos* 29: 275-283.) [Courting wood whites, *Leptidea sinapis*, photographed in Surrey by Adrian Hoskins, FRES. Reproduced here with permission.]  
See <http://www.learnaboutbutterflies.com/Lifecycle%20-%20mate%20location%20courtship.htm>

# Thoughts on the Biology of Butterflies – Turku 2014

*Prediction is very difficult, especially about the future.*  
[Often attributed, incorrectly it seems, to Niels Bohr]

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*Leptidea*. Lep-tid-ee-ah (apologies to VN). And rather like Humbert Humbert’s muse, small, delicate, beautiful, captivating.

Since attending the 7th International Conference on the Biology of Butterflies, which took place in Turku, Finland, 11-14 August, I had the further pleasure to spend a short vacation in Parga. September 2014 saw a great deal of rain in this NW corner of Greece and, to my innocent mind at least, I was surprised to see a good number of butterflies, many very fresh.

The various species and genera set me thinking about where we have got to with an understanding of the biology of butterflies . . . beautiful creatures, sources of perennial fascination . . .

Many *Leptidea* were flying in olive groves and on verdant sea cliffs. The modern biology of wood whites is forever in my mind linked to the work of Professor Christer Wiklund. *Kris-ter Vik-lund*. So it was great to find that one of the main sessions on the very first day of the Turku conference, on the Evolutionary Ecology of Butterflies,

was dedicated in Christer's honour. Ten papers covered a wide range of topics, launched by a keynote from Jeremy Thomas (Oxford) on that remarkable tri-trophic system – *Maculinea* butterflies, their hymenopteran parasitoids, and *Myrmica* ants. This is another great success story of butterfly biology, stretching back to Frederick William Frohawk and other pioneers, but year on year now brought to modern sophistication through many contributions – often spearheaded by Jeremy himself. As would seem appropriate, given Christer's Stockholm base, all the papers in this session involved work on north temperate species, including various *Euphydryas*, *Pieris*, *Maniola*, *Speyeria*, *Colias* and *Araschnia* – but not *Leptidea*! Instead, we had to wait for a catch-all session two days later, on general butterfly biology, to hear Vlad Dincă (Guelph) give a paper, on behalf of 10 co-authors including Christer, “*Leptidea* wood white butterflies as an emerging model to study speciation”. The wood whites in question consist of three highly cryptic species (*L. sinapis*, *L. reali* and *L. juvernica*), with *L. sinapis* itself the metazoan with the greatest known intraspecific variation in chromosome number ( $n = 28-53$ ). However, even this now seems to be an underestimate. Moreover, this karyotypic variation is expressed clinally, making it a superb model for speciation studies. *Lep-tid-ee-ah* will soon ‘benefit’ from genomic studies – even Nabokov would surely never have dreamt of that.

A single male *Argynnis paphia* was encountered at the supposed source of the Acheron River, gateway to Hades. Only relatively recently has the relationship of *Argynnis* to the equally but differently fabled *Heliconius* butterflies of South America been confirmed to the point where these fritillaries (with *Boloria*, *Issoria*, etc.) are now firmly placed together with *Heliconius* in the monophyletic nymphalid subfamily Heliconiinae (Wahlberg et al., 2009). Paul Brakefield (Cambridge) noted in his talk during the Ecology and Evolution session, how studies on butterfly biology have contributed a great deal to biosciences in general, with the suggestion that, amongst the butterflies, the leading model system today is probably *Heliconius*. At least eight papers were given largely or entirely based on *Heliconius* species, including two remarkable presentations in the Genomics of Adaptations session



*Argynnis paphia* drinking at the source of the Acheron River, NW Greece, 16.ix.2014. Part of the androconial field of the forewing upperside is clearly visible – but, despite the early work of Rudolf Barth (1944), how these male scent organs really work is still largely unknown. [Photograph: R.I. Vane-Wright; Barth, R. (1944) Die männlichen Duftorganen einiger *Argynnis*-Arten. *Zoologischer Jahrbucher (Anatomie)* 68: 331-362.]

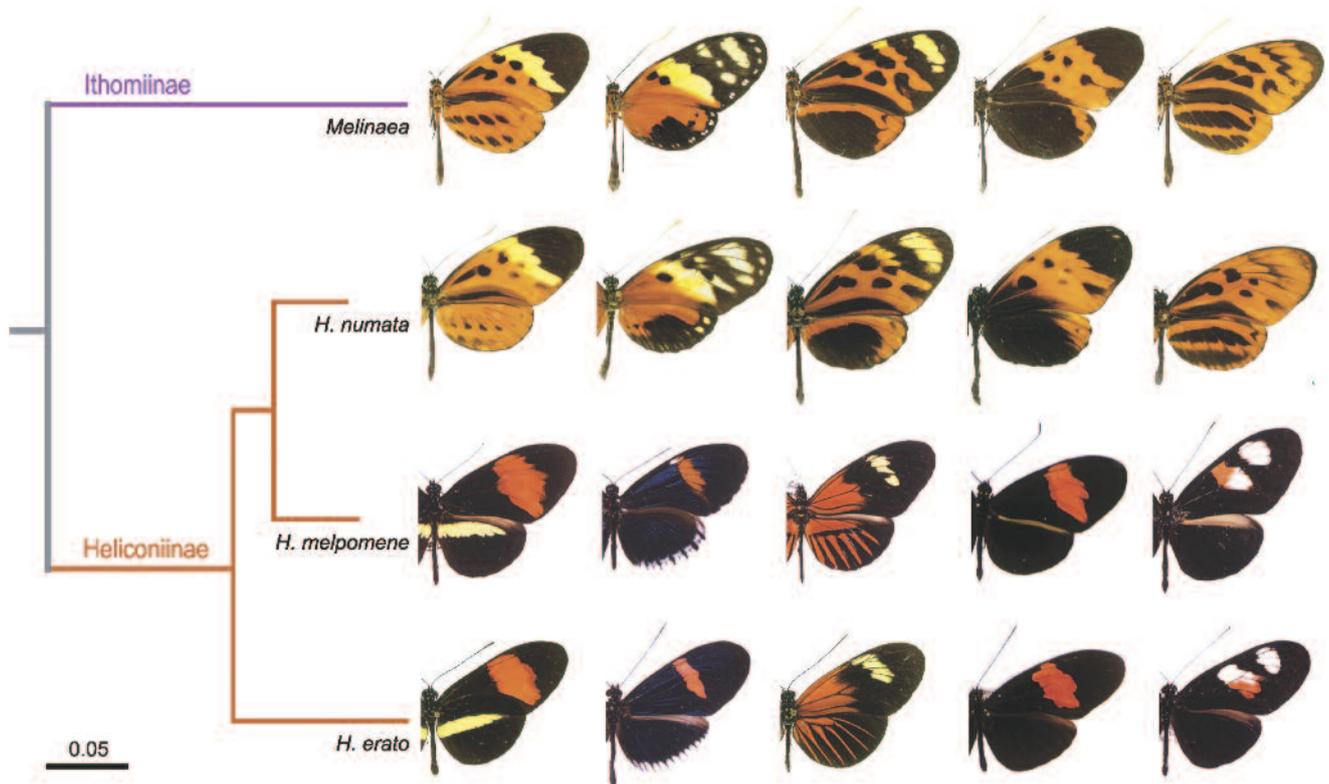
by Mathieu Joron's team (based at the Muséum National d'Histoire Naturelle, Paris), concerning pattern polymorphism in *H. numata*. These papers gave very up-to-date accounts of fundamental issues in evolutionary genetics (e.g. frequency enhanced and frequency attenuated selection, evolution of dominance) going right back to Ronald Fisher's classic work.

Around Parga, Lasiommata megera were numerous. As a child growing up in outer London, the Wall Brown was a common and lovely sight, even in suburban gardens. I have not seen one in Kent now for many years, although they still occur sparsely. Why would a grass-feeding species become so diminished? Perhaps it is like the Comma, *Polygonia c-album*, always considered a butterfly that cycled from common to infrequent and back – and there is some evidence for this in *L. megera*. However, for such organisms, not tied to very specific localities or ecosystems, untangling ‘natural’ trends and cycles from the effects of human ‘enterprise’ is a key challenge for conservation biology. Thus it was good to see two of the five papers presented in the ‘Population Biology and Conservation’ section address general habitat issues, both within the framework of climate change. Rob Wilson (Exeter) presented a co-authored summary of work on population persistence in relation to topography and microclimate, featuring another grass-feeder, *Hesperia comma*,

with the conclusion that in the north-temperate at least, with respect to offsetting climate change effects, conservation efforts should best be focused on topographically varied landscapes. In some contrast, Jenny Hodgson (Liverpool), in a presentation also featuring work on the Silver-spotted Skipper, argued for a focus on habitat quality and availability, with the need at continental level to link isolated landscapes on a much larger scale than current approaches to fostering “ecological networks”.

The debate will surely continue – as it did on day two in the Butterfly Movement session, notably in a paper from Elizabeth Crone (Tufts) and colleagues on habitat use and habitat quality in *Plebejus*, *Euphydryas* and *Satyrodes* butterflies. Yet our concerns for so many species are tempered by the conviction that action is essential now. If hasty action is misinformed, will the opportunity to make a difference be lost forever? But if we wait for better understanding, will it be too late anyway? The application of our increasing knowledge of butterfly population biology to conservation faces this seemingly perpetual difficulty – when do we have enough information to act wisely? The skill of a good professional conservationist still lies to some considerable extent in the realm of intuition.

*Neptis sappho* was seen on several occasions. Although one might consider



A hint of why *Heliconius* is probably “the leading model system”. Five sympatric forms of *H. numata* from northern Peru are shown on the second row, with corresponding separate species of danaine co-mimics above. Below, part of the classic *erato/melpomene* parallel mimicry system. Figure 1 from Joron et al. (2006). (Joron, M., Papa, R., Beltrán, M., Chamberlain, N., Mavárez, J., 10 others & Jiggins, C.D. (2006). A conserved supergene locus controls colour pattern diversity in *Heliconius* butterflies. *PLoS Biology* 4(10): e303. doi: 10.1371/journal.pbio.0040303. Open access.)

the ‘white admiral’ wing patterns of *Neptis* to be disruptive, I always feel that, being so striking, they may (also) offer species or species-group recognition characters – what Alfred Wallace might have included in his category of ‘normal colours’. Generally among the numerous Asian and African species of *Neptis* there are subtle differences in wing pattern between species, but within each species the sexes are visually almost indistinguishable. Wallace also recognised ‘sexual colours’ – which he thought of as originally gaudy in both sexes. Where sexual dimorphism occurs, he considered this to be a result of natural selection favouring more cryptic or mimetic female patterns, for better protection against predators.

Wallace, as is well known, disagreed with Darwin’s sexual selection hypothesis, which proposed that the more gaudy male colours of many species are driven by female preference. This debate is still very much alive in butterfly biology, and was evident in several of the 10 papers presented in the sexual selection session. Following a masterly overview by Ron Rutowski (Arizona State) of Darwinian sexual selection as applied to butterflies, a wide variety of related topics were covered – including mate preference learning, species recognition within Müllerian mimics, the possibility of sexual conflict driving pattern diversification in Müllerian mimics,

interactions between olfactory and wing-pattern diversity in a radiation of Satyrinae, and an attempt to explore the possibility of cryptic female choice in the Monarch. This last paper reminded Michael Boppré of the need to determine what really passes for ‘normal’ courtship in *Danaus plexippus* – is it just the widely reported ‘brutal’, coercive strategy now widely considered ‘normal’ for this species, or perhaps one of the other known courtship sequences that would seem to allow greater possibilities for female (and male) choice in this species – as long ago described by Tom Pliske (1975). Presentations involving questions about sexual selection were also given in other sessions, including a paper by Krushnamegh Kunte and Deepa Agashe (Bangalore) in Ecology and Evolution on drivers of sexual dimorphism and polymorphism in mimetic butterflies – in which they concluded that, contra views expressed in the past, neither sexual selection nor physiological tradeoffs were involved in female-limited polymorphisms.

*The dazzling blue coloration of Polyommatus butterflies in the Greek autumn sunshine led to thoughts of the remarkable co-adaptations between butterflies (Lycaenidae, Riodinidae) and ants.* Queen of lycaenid butterfly biology, ever since the London meeting, has been Naomi Pierce (Harvard). In her plenary lecture opening the Ecology and Evolution session on day 3, Naomi

cast her net wide to look at major diversification patterns across the whole of the Lycaenidae. She identified two major rapid radiations. Diversification of the Polyommata (approaching 500 known species) appears to relate to, among other factors, ant associations, wide thermal tolerances and, perhaps in particular, karyotype instability. The Eumaeini, with over 1200 species and more than 80 recognised genera, are the most speciose tribal level grouping in all the butterflies. As long ago suggested by John Eliot, in this group speciation seems associated with hyper-diversity of male secondary sexual characters – including remarkable black wing pads now demonstrated to be capable of broadband infrared absorption and emission.

Across the Lycaenidae as a whole, ant associations seem important in diversification. However, when this leads on to carnivory (succumbing in an evolutionary sense to “the temptation to cheat”, as Naomi put it), the phylogenetic patterns suggest this is usually an “evolutionary dead end”. My only unfulfilled wish from this lycaenid extravaganza was some discussion of the exclusively African Lipteninae – with well over 600 species, apparently all linked to a larval feeding shift to exploit terrestrial algae (including algae within lichens). Judging by the phylograms presented, this is an older group, so arguably the diversification rate is not above average. Even so, the



Day one (left). An apparently tense and apprehensive organizer-in-chief gets the conference under way. [Niklas Wahlberg, photographed by R.I.Vane-Wright.]; Day two (right). Antónia Monteiro delivering her plenary lecture on nymphalid border ocelli, Tuesday 12th August 2014. [Photograph by R.I.Vane-Wright.]



Day 3. A now happy and relaxed Niklas Wahlberg charms and amuses his flock at the Conference Banquet, Pikku-Pukki Island, 13.ix.2014. One of the most popular banqueting locations in Turku, the island is 30 min by boat from the centre of town, along the Aura River. [Photograph: R.I. Vane-Wright.]



*Ethope himachala* has one of the most even and complete sets of border ocelli in all the Nymphalidae. But why the blue eyes? Butterflies pose so many interesting questions! [Photographed near Sessa, Arunachal Pradesh, NE India, v.2013, by Ray Cannon; reproduced here with permission. <http://rcannon992.com/2014/11/23/old-blue-eyes/>]

existence of this group is without parallel in the rest of the butterflies.

Five species of *Maniola* occur in Greece, but only the most familiar, the Meadow Brown, is found on the mainland – and was common around Parga. *Maniola jurtina* holds a special place in the history of biology, being a key study organism for E.B. Ford and his collaborators in establishing the field of ecological genetics. With his remarkable ability to breed successive generations of this species, Paul Brakefield engaged in the meadow brown world after leaving Oxford to become a University of Liverpool PhD student in the late 1970s, creating new insights into the genetics and ecology of seasonal changes affecting the border ocelli of *M. jurtina*. Encountering the remarkable Torben Larsen at the London meeting, Paul started to explore the greater phenotypic seasonal plasticity exhibited by tropical Satyrinae – notably *Melanitis*, and then *Bicyclus*.

Paul's ability to culture *B. anynana* has led to this species become something akin to the 'Drosophila' of butterfly biology – most notably perhaps with respect to 'evo-devo'. In a tour de force, Antónia Monteiro (Singapore) introduced the Genomics and Development section with her plenary lecture on "The origin and evolution of novel gene regulatory networks". The substance of her presentation was based on an analysis of development of the border ocelli (Nijhout, 1991: 26) across the whole of the Nymphalidae. According to Monteiro, eyespots, and four out of five genes expressed in eyespots, have the same single origin near the base of the nymphalid tree [the two basal groups

excluded being the Danainae and Libytheinae], leading to the conclusion that this system originated through the co-option of pre-existing, modular gene regulatory networks, and these were subsequently modified in increasingly sophisticated ways.

In all of this, *B. anynana* held centre stage as a key 'lab rat'. Based on the observation that there is considerable variation in the plasticity of expression of particular eyespots in this species, one can ask the question not only how, but also where and when in the phylogenesis of the Nymphalidae this plasticity originated. It seems the molecular tools and model systems are now available that should enable these questions to be answered.

Another fascinating paper in this session, by Marcus Kronforst (Chicago) and co-authors, described how a single gene, doublesex, is now known to be responsible for the control of female-limited polymorphism in *Papilio polytes*. This work has recently been written up in *Nature* (Kunte et al., 2014). Thanks to genomics, our understanding of the intricate mechanisms underpinning continuous and discontinuous variation in butterfly colour patterns is now advancing at a remarkable pace.

On the edge of the wetlands at the mouth of the Acheron river I saw two *Danaus chrysippus*. The milkweed butterflies exemplify many key aspects of butterfly biology, perhaps most notably chemical ecology and the many issues surrounding larval food preferences and specialisations. Somewhat to my surprise, relatively few papers given at Turku addressed larval food, and these were scattered

across several sessions. This could reflect the growing emphasis of *in vitro*, laboratory-based molecular methods that give more predictable results for the now all-important student theses. If so, butterfly biology must be mindful of its roots in basic natural history – something Robert Ricklefs (2012) has recently emphasised for the whole of ecology and evolutionary biology. Notable contributions on larval food relationships were given, at species level, by the irrepressibly entertaining Mike Singer ("One butterfly, six host shifts"), and in a multidisciplinary presentation at family level by Niklas Janz, regarding questions of host range and diversification.

Another favourite childhood butterfly was also flying at my Greek resort – *Vanessa atalanta*. The Red Admiral is unusual, although not unique, in being partial to both rotting fruit and nectar as sources of 'refreshment'. The dramatic differences between larval and adult feeding can be highly significant for butterfly biology, but this thread was not strongly represented at Turku. No paper was given on pharmacophagy, or comparing fruit and nectar feeding, while just two touched on polyandry as a source of female material 'income' affecting fecundity – which can be influenced by the feeding activities of adult males as well as the females themselves. Three papers explored diversity patterns and population dynamics in fruit-feeding butterfly assemblages, but not the energetics involved. Perhaps this aspect of butterfly biology should be the subject of a dedicated session at a future meeting.

Plenty of clouded yellows were in evidence at Parga. I find a certain irony that, in the early days of 20th century butterfly genetics, some of it – such as the work of H.C. Gerould on *Colias* polymorphism – became associated with the now widely (but not entirely) discredited eugenics movement. This was based on genetic determinism – in the sense that 'good' and 'bad' genes of themselves controlled what an organism (specifically you!) would become, and what its (your) descendants would become also. In other words, genetics was seen as highly predictive. To some extent, even if state-controlled eugenics movements have largely been abandoned, the idea of genetic determinism is still with us. "Gene for" talk in vernacular parlance is still widely heard regarding various



Day 3. Discovering the waitresses thought we were very friendly people! Author with (left to right) Michael Boppré, Nils Ryrholm, Niklas Wahlberg and Krusnamegh Kunte, at conference banquet, Piku-Pukki Island. [Photograph courtesy of K. Kunte.]



Day 4. The group photo! Conspicuous at the front, far right, is André Freitas. [Photograph: K. Kunte.]



Left: Deepa Agashe nectaring at Turku. One of the rising stars based at NCBS, Bangalore, where 'BoB 8' is due to take place in 2018, Deepa has a special interest in bacterial evolution – a subject area of ever increasing importance for butterfly biology. [Photograph: R.I. Vane-Wright.]; Right: Ilkka Hanski, “legendary Finnish metapopulation biologist”, at the conference banquet. [Photograph: R.I. Vane-Wright.]

genetic diseases, and even psychological traits. But the idea of ‘bean-bag’ genetics has largely been abandoned (Rao & Nanjundiah, 2011), with the realisation of the highly interactive nature of the whole genome, and its dynamic relationship with cellular metabolic processes (e.g. Shapiro, 2011).

Following publication of Willi Hennig’s *Phylogenetic Systematics* in 1966, many biologists protested that his methods could not reliably infer phyletic relationships – and even if they did, cladograms were an insufficient or inappropriate basis for ‘good’ systematics. For a time three approaches – evolutionary, phenetic and cladistic – vied for supremacy. Some 50 years on, cladistics has largely prevailed, and genetics is no longer the science of powerful predictions, but increasingly of retrodictions. Based on the amazing advances in molecular methodology, genetics (and proteomics and genomics) has become the dominant data source with respect to Hennig’s aims – extending right up to exploration of the ancient diversification of life (at the level of domains) and right down to within-species studies, as in phylogeography. This change in perspective, from London 1981 to Turku 2014, was very evident. At the London meeting no papers were presented on systematics (Phillip Ackery’s well known paper was written after the event, especially for the symposium volume). In Turku cladograms were abundant, in both talks and posters – with Paul Brakefield going so far as to say “systematics and

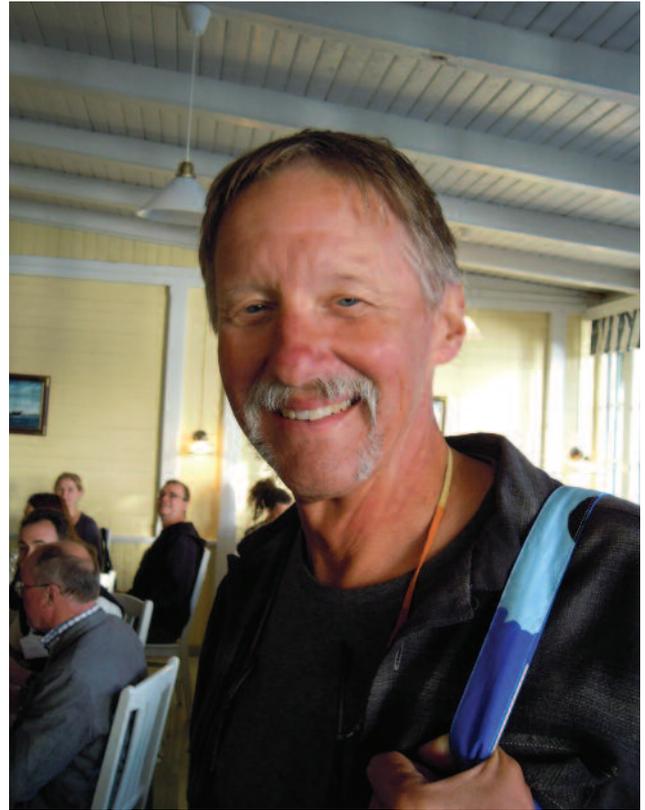
phylogenetic reconstruction remains the foundation of ‘all good things’.”

There were other striking differences between Turku 2014 and the RES meeting held 33 years earlier. Thirty-three papers were presented in London with a total of 43 authors; in Turku there were almost 100 talks with an average of 3.75 authors per paper. Turku also featured over 120 posters – far, far more than the handful exhibited in London. These ‘statistical’ differences reflect the great increase in multidisciplinary scientific work over the intervening decades. This can also be appreciated from the structure of the meeting. The London event had six basic and one applied themes: populations and communities; food; predation, parasitisation and defence; genetic variation and speciation; sex and communication; migration and seasonal variation; and conservation. The studies presented within this structure were largely grounded in one or other of the primary disciplines of 20th century biological sciences, notably genetics, ecology, ethology and evolution. In some (but not total) contrast, the eleven main themes at Turku were more overtly interdisciplinary: population biology and conservation; evolutionary ecology; genomic basis of adaptations; genomics and development; butterfly movement; sexual selection; ecology and evolution; butterflies as hosts; systematics and diversity; evolutionary phylogenetics; and behavioural ecology. Papers on closely-related subjects were often placed in different sessions.

Highlights of Turku? Inevitably any such list is very personal – especially as

it was not possible to hear all talks. I felt the ‘Paris’ presentations from Mathieu Joron’s group on *Heliconius numata* polymorphism were exceptional. Then there were the bravura performances of Naomi Pierce and Antónia Monteiro. A paper by Jaap de Roode (Emory) on the neogregarine parasite *Ophryocystis elektroscirrha* and ‘self-medication’ in Monarch butterflies was fascinating, although it seemed to raise as many questions as answers. But perhaps for me the most exciting moment came in the very first talk, by legendary Finnish metapopulation biologist Ilkka Hanski (Helsinki) concerning an effect of flight muscle activity.

In Glanville Fritillary (*Melitaea cinxia*) butterflies from fragmented versus non-fragmented landscapes, recent work in ‘ecological genomics’ strongly suggests that “differences in gene expression between the landscape types reflect genomic adaptations to landscape fragmentation” (Somervuo et al., 2014). Hanski reported how his extensive team of researchers had investigated over 1800 genes differentially expressed between the two landscape types. Genes significantly more strongly expressed following just 15 minutes of flight activity also had higher basal levels of activity in butterflies from the fragmented landscapes – from which it appears that butterflies from dissected landscapes, where there is a selective premium on movement, “are genetically primed for frequent flight”. In the words of one of Hanski’s students, “these studies have revealed that metapopulation dynamics and habitat fragmentation causes selection



Left: Felix Sperling (Alberta), lead organiser of BoB 6, gave an outstanding day-4 plenary on the species problem, as applied to butterflies. [Photograph: R.I. Vane-Wright.]; Right: Ron Rutowski, master of butterfly semiotics. [Photograph: R.I. Vane-Wright.]



Pierce lab reunion, Turku 2014. From left to right: David Lohman, Naomi Pierce, Gerard Talavera (front), Sami Schar (back), Marianne Espeland, Roger Vila. [Photograph courtesy of Naomi Pierce.]

pressure on an intricately connected set of genes and pathways. At the organismal level these genes translate to phenotypic traits which are also connected in multiple ways and make up the so called “life history syndrome” (Kvist, 2014: 29).

Such complex links between behaviour (flight activity), selection (move/not move), metabolism (muscle anoxia in present case) and gene expression reflect one of the major strands in the emergent discussion regarding physiology and evolution (Shapiro, 2011; Noble, 2013; Noble et al. 2014). They also reflect a contemporary ‘systems view’ of the processes of life (Capra & Luisi, 2014). And yet, how does spatial metapopulation biology differ from phenotypic plasticity induced by temporal change? – as in the remarkable phenomenon of seasonal polyphenism so familiar to butterfly workers.

Perhaps another message is that, as long suspected (consider the hypothetical diagram of Hennig, 1966: 57), so much more is going on at the cryptomorphic level as opposed to the literally obvious phaneromorphic level (to use the distinction of Huxley, 1955) – despite the latter being the level of variation that inspired so much of the early interest in butterfly biology (wing pattern polymorphism, crypsis, mimicry, colouration etc.). Following the work of early specialists like Gerould and Hovanitz, it was discovered that ‘alba’ versus ‘male-like’ females of *Colias* butterflies have many associated but cryptic physiological

differences. For sure it is not an accident that another key person in this recent step in unfolding the *Melitaea cinxia* story is Chris Wheat (Stockholm) – a former student and collaborator of Ward Watt, one of the greats of *Colias* physiology. Following in Ward’s footsteps, Chris is now addressing the issue of the “central metabolism” of butterflies, using a genomics approach.

All those attending Turku 2014 have a huge debt to lead organiser and Professor of Genetics, Dr Niklas Wahlberg (Department of Biology, University of Turku), his co-organiser Dr Marjo Saastamoinen (Department of Biosciences, University of Helsinki), and their extensive band of symposium leaders and logistical and technical helpers (<http://nymphalidae.utu.fi/icbb2014/organization.html>). Turku itself proved a happy location, including a very warm welcome reception at the City Town Hall, and providing a venue for the most delightful symposium dinner, held at the banqueting pavilion on Pikku-Pukki island – a 30 minute ferry boat ride along the Aura River.

It would not be an exaggeration to say that the organisation was faultless. High standards, intensity and good fellowship characterized Turku 2014. With 230 delegates representing 28 countries – including the remarkable statistic that almost 10% came half way across the world from Brazil (for sure largely inspired by the irrepressible André Freitas, Campinas) – this was the largest BoB meeting yet.

At least one of the primary organisers of each of the six previous ‘BoB’ symposia was present in Turku. Following the original London event, run through the RES, special credit is due to Sören Nylin and Bengt Karlsson (both present in Turku) for organising the 1994 meeting at Stockholm University (Wahlberg et al., 2013). This was the key step in making BoB the regular event it is now. Since then, all meetings have not only been organised by university workers, they have also been run independently. This may be part of the reason why these meetings always evoke a wonderful spirit of cooperation and friendship – something even the waitresses noticed during the Pikku-Pukki dinner! I feel confident this great tradition will be maintained at the National Center for Biological Sciences, Bangalore, where Krushnamegh Kunte will be organiser-in-chief for BoB 8, in 2018. NCBS is a postgraduate research centre, part of the great Tata Institute of Fundamental Research. Over the past 10 years, NCBS has developed a highly significant Ecology and Evolution programme (<https://www.ncbs.res.in/node/152#evolutionary>). This will be the first time for BoB outside Europe or North America. The future for the Biology of Butterflies is bright.

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