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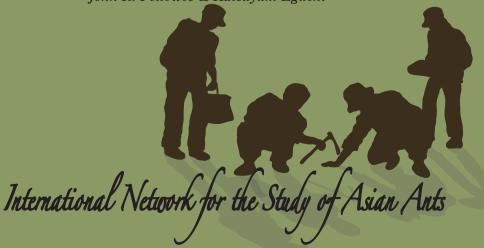
A new internet database on ant researchers comes with homepages for all ANeT members

Martin Pfeiffer & Hans Peter Katzmann

Ants and speciation patterns *Himender Bharti*

A record of the ANeT committee meeting held in India in October 2007

> Compiled by Bakhtiar Effendi Yahya, Himender Bharti, John R. Fellowes & Katsuyuki Eguchi



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ANTS AND SPECIATION PATTERNS

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The process of speciation has been a debated issue among evolutionary biologists for a long time now. How new species originate in nature and which selective agents force them to do so has been a puzzling question. Various models have been proposed theoretically, but the most accepted model to date is allopatric speciation, i.e. reproductive isolation attained by geographical separation. The late evolutionary biologist Ernst Mayr argued throughout his life in favour of allopatric speciation, but other models gained momentum as well. Guy Bush's findings in 1969 on fruitflies set the tone with the sympatric mode (in which reproductive isolation occurs without geographical separation). Subsequently there was recognition of other modes: peripatric (speciation by modification of peripherally isolated founder populations), parapatric (where populations have contiguous but not overlapping ranges) and stasipatric (speciation by chromosomal rearrangements giving homozygotes which are adaptively superior in part of the original range). Although it is hard to conceive of the forces that can prevent gene exchange in sympatry, scientific evidence has been pouring in consistently (Butlin & Tregenza, 1997; Dieckmann & Doebeli, 1999; Coyne & Orr, 2004; Feder *et al.*, 2005; Balakrishnan & Sorenson, 2006).

Ants could act as model organisms for the study of speciation patterns. Scattered evidence has trickled in from studies conducted on ants, but no serious effort has been made to investigate ants as model organisms. I wish to present here some plausible reasons to do so. They have been haunting my mind for a long time now; it seems timely to share them, as perhaps we will reach a pinnacle of myrmecological work in the coming years, given the efforts being put forth by ANeT and other myrmecologists around the globe.

1. The mode of reproduction in ants is based on the haplodiploidy phenomenon, the males being haploid and the workers and queens being diploid. Males receive only one genetic

complement (say either N_1 or N_2) whereas females receive two genetic complements (N_1 and N_2). Males with either the N_1 or N_2 genetic complement from the same mother queen may fertilize a female, depending upon their reproductive fitness. So either type of male can fertilize the egg, and consequently some future queens will be heterozygous, others homozygous. In the case that these different populations are subject to different selection pressures for a long time, they may end up as different species through the fixation of certain homozygous genes with favourable pleiotropic effects.

The increase in population variability associated with fixation of certain genes is also favoured by the fact that oogenesis in Hymenoptera is a continuous process (Buning, 1994). The more eggs are produced, the more cell divisions are required to produce each egg. If large number of eggs destined to be workers are produced before laying the eggs destined to be reproductives, then the overall number of cell divisions taken to produce sexual offspring will be much higher than in non-social species. The rate of DNA copy error mutations is higher in sexual offspring (Bromham & Leys, 2005). So, more mutations occur per generation and species with shorter generation turnover time are assumed to have more DNA replications.

Furthermore, the number of reproductive individuals which contribute alleles to the next generation is lower in the case of ants and other social insects. So, small populations of reproductives are subject to drift and selection as compared with large populations. In one instance Shoemaker & Ross (1996) examined variation in mitochondrial DNA and two unique nuclear genes in *Solenopsis invicta* demonstrating the potential for social selection to generate significant barriers to gene flow and to initiate reproductive isolation. Interestingly sympatric speciation has been predicted to be faster and involve fewer loci than allopatric (Via, 2001).

- 2. Another important aspect which can provide vital clues about sympatric speciation is social parasitism in ants. Buschinger (1990), a pioneer in the study of social parasites in ants, addressed the issue comprehensively. Even Ernst Mayr agreed that socially parasitic ants are the most convincing example for the existence of sympatric speciation (A. Buschinger, pers. comm., dated 29/4/2007, 12:12AM). Recently mitochondrial DNA studies conducted on social parasites by Savolainen & Vepsalainen (2003) provided some evidence for this mode of speciation. Bromham & Leys (2005) predicted that most social parasites should have faster rates of molecular evolution than their social relatives, which is consistent with an effect of reduced population size. In this pretext if more molecular studies were conducted on social parasites the results could be intriguing.
- 3. Since MacArthur and Wilson's (1963) theory of island biogeography many arguments had cropped up regarding its application, before Emerson & Kolm (2005) provided evidence based on their studies on the Canary and Hawaiian islands. The central tenet of their theory was that species diversity may itself promote speciation. They argued that the number of endemic species is expected to increase with an increase in species diversity. The applicability of the theory has proven equally good for mountain systems like the Himalaya. Studies conducted by the author reveal that about 45% of the Himalayan ant fauna (at more than 1000 metres above sea level) is endemic, though most of them have wide altitudinal ranges (Bharti, 2008). The only plausible reason for such a high level of

endemism is local speciation; under the alternative explanation, that these populations originated in adjoining regions and spread to the Himalaya, where they evolved into new species, we might expect to encounter the parent species throughout the adjoining regions and the Himalaya, which is not the case up to now. On the contrary allied ant species reported from high-altitude regions show pronounced differences among them – other interpretation of character displacement, as noted by Brown & Wilson (1956) – is possible through sympatric speciation.

4. Finally it's interesting to wonder why some ant genera, like *Pheidole, Camponotus, Polyrhachis* etc., are more diverse/hyperdiverse. What factors have driven speciation rates to be faster in these as compared to others (or else made extinction rates slower)? Which mode of speciation accounts for this radiation? Can allopatry drive speciation at such a high rate (keeping in mind the number of new genera and species reported in ants in recent years)?

Is this hyperdiversity general or patchy? Within the Himalayas, the genus *Myrmica* has the highest number of species (above 1000 m asl), more than *Pheidole* or any other genus, and the highest number of endemic species. Results in the coming years may reveal similar patterns in *Leptothorax* and *Lasius*. Probably species diversity leads to more diversity and endemism too in a region like the Himalaya; this does not seem conceivable under the banner of the allopatric mode. As put forth by Wilson (2003), "strong variation in species richness among genera, families and still higher taxa is a universal but still poorly understood biological phenomenon."

These are a few aspects which need some serious thinking on the part of evolutionary biologists/myrmecologists. I don't doubt the importance of the allopatric mode of speciation, but what has happened over the years is that when somebody has come up with evidence for sympatric or some other mode, it has been seen as a threat to the allopatric model and refuted immediately, seemingly with a closed mind.

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A RECORD OF THE ANET COMMITTEE MEETING HELD IN INDIA IN OCTOBER 2007

Compiled by

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The following agenda items were discussed in the committee meeting held as a part of the 6th ANeT workshop and meeting (Punjabi University, Punjab, India, 2007).

- 1. Venue of the 7th workshop and meeting
- 2. ANeT's Species-coding System

From Editors

We welcome research news, event information, self introductions, short essays, etc. Meeting records are also inserted. However, original papers including short communications should be submitted to our journal (Asian Myrmecology). Authors are encouraged to send their manuscripts as electronic versions attached to e-mail. Both text format (txt) and MS word format (doc) are accepted. Line drawings (jpg or tiff format, with a minimum of 400 pixels/inch) and grey-scaled and full-coloured illustrations (jpg or tiff format, with a minimum of 300 pixels/inch) are also accepted. The editors reserve the right to make minor textual corrections that do not alter the original meaning. Linguistic review will be done by a native speaker as the need arises. Proofs will be provided to authors as pdf files attached to e-mail. From No. 9 onward ANeT newsletter is available as pdf files on our website http://homepage.mac.com/dorylus/newsletter.html>. We plan to publish our newsletter at least twice a year. It depends on your contribution! All correspondence should be addressed to:

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Editing this issue took nearly six months, and we apologise that some articles, notably that of Dr. John Fellowes, may contain information that is now outdated. Fellowes san carefully reviewed all articles. Many thanks to Fellowes san!



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