

that emerges is whether there are several kinds of boundaries. For instance, a kind of boundary may mark start or end of the heterochromatin stretch in a directional fashion while other kind may include weaker boundaries within an active or inactive stretch which may respond to more subtle regulatory mechanisms. With the availability of an *in vitro* boundary assay system and several mutations related to such boundaries<sup>16</sup>, it may not be too distant a future when such questions will be answered.

Inactivating and or maintaining regions of genome by means of methylation (in mammals) by a set of chromosomal proteins (in fruit fly) or by elimination of stretches of DNA itself (in *ascaris*) shows that organization of the genome (including repetitive DNA) has evolved in parallel with the corresponding mechanisms to meet the complex genetic obligations of somatic differentiation and germ line totipo-

teny. It is notable that during evolution as the species have digressed they have built upon one mechanism or the other leading to a common goal, viz. to have genetic information for a mechanism to unfurl the developmental programme in the majority of cells which may or may not be reversible, while maintaining the blue-print in the germ line for the progeny.

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Rakesh K. Mishra is in Laboratoire de Biophysique Moleculaire, Universite de Bordeaux II, 146, Rue Leo Saignat, 330076 Bordeaux Cedex, France.

## Rabid roles in vesicle fusion

Mani Ramaswami

Rab proteins are members of the ras superfamily of family of GTP-binding, peripheral membrane proteins; rab proteins regulate the fusion of intracellular transport vesicles. Bowser *et al.* report<sup>1</sup> the sequence of a protein likely to associate with a member of the rab protein family during vesicle fusion. In addition, it adds to the growing number of identified cytosolic proteins involved in fusion of intracellular transport vesicles.

Studies on various membrane traffic pathways have revealed that rab proteins are required for the fusion of a wide range of transport vesicles. Each vesicle type is believed to be associated with a specific rab protein; molecules governing this specific association are unknown. As target specificity and vectoriality are salient features of vesicle fusion<sup>2</sup>, considerable effort has been focused on identifying proteins that interact with rabs; such associated proteins are candidates for specific markers of donor or

target membranes, potentially involved in bio-genesis and function of transport vesicles. It is fitting that the first rab-associated protein involved in vesicle fusion may have been identified for the *sec4* protein of *S. cerevisiae*, the first member of the rab family to be described<sup>3</sup>. The rab-associated protein is *sec8p*, a protein also required for fusion of secretory vesicles with plasma membrane. Its association with *sec4p* is argued from genetic interactions, *sec4-8*, *sec8-9* double mutants show synthetic lethality, and a duplication of *sec4* partially suppresses a temperature sensitive (*ts*) mutation in *sec8*; from biochemical association studies, a portion of intracellular *sec4p* is found in a protein complex that contains *sec8p* and *sec15p* (yet another late-acting *sec* protein); and from sequence analysis of *sec8* that shows weak but recognizable similarity to a non-catalytic domain of adenylate cyclase required for responsiveness to ras regulation.

*Sec8p* is hydrophilic and only peripherally associated with plasma membrane. Thus, the identification of *sec8p* as a potential *sec4p*-binding protein, does not constitute a major advance in the question of target recognition by secretory vesicles. It remains unclear how *sec4p* associates specifically with secretory vesicles and *sec8p* with plasma membrane. It is yet unproven that the binding of vesicular *sec4p* with membrane *sec8p* is a primary event in target recognition; also unresolved is whether this binding stimulates a GTPase activity of *sec4p* that has been postulated to accompany vesicle fusion. However, since rab proteins are key components for function of transport vesicles, the identification of proteins that interact directly with *sec4p* constitutes a significant advance. It is possible that new families of *sec8p* and *sec15p* homologs that interact with different rab proteins may be involved in the function of varied transport vesicles.

The accumulated findings from many laboratories (ref. 4 and references therein) that fusion of intracellular vesicles requires several cytosolic proteins brings yet another question into focus. Are there different mechanisms used during fusion of biological membranes? It appears that there must be at least two classes of fusion events; extracellular fusion such as cell-cell or cell-virus fusion, and intracellular fusion events of the kind discussed in Bowser *et al.*<sup>1</sup>. Due to the constraints of topology, cytosolic factors involved in intracellular fusion cannot conceivably play similar roles during extracellular fusion. Significantly, while integral membrane proteins involved in the physical act of membrane fusion have been identified for extracellular fusion events<sup>5</sup>, none have yet been identified for intracellular fusion. It appears that drawing close parallels between studies on extra-

cellular and intracellular fusion events must be done with caution.

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*Mani Ramaswami is in the Department of Biochemistry and Biophysics, University of California, San Francisco, CA 94143-0534, USA, and Molecular Biology Unit, Tata Institute of Fundamental Research, Homi Bhabha Road, Bombay 400 005, India*

(For general information about thrips and their galls, see refs. 12, 13). The thrips Crespi describes seem tailor-made for the evolution of eusociality. Galls (the equivalent of single foundress nests in eusocial Hymenoptera) are initiated by single inseminated macropterous (fully winged) females in spring. After fighting off other similar females over possession of a presumably valuable young growing phyllode tissue of *Acacia oswaldii* and *A. melvillei* respectively, the foundress oviposits inside the gall. Her offspring hatch, feed, develop and eclose inside this gall. She produces four kinds of offspring: macropterous females (like her), macropterous males, micropterous (short-winged) females as well as micropterous males. The term micropterous is somewhat distracting for, the important feature of micropterous adults is their enlarged and armed forelegs specialized for fighting. Sure enough micropterous adults (both females and males) eclose earlier than macropterous females and males. Notice the analogy with the first batch of brood becoming workers and subsequent batches becoming future reproductives in social Hymenoptera.

Crespi has convincingly demonstrated that in both species, micropterous adults attack and attempt to kill *Koptothrips* spp. (inquiline thrips that invade galls of other species, kill the gall formers, and breed inside), lepidopteran larvae and *Iridomyrmex humilis* ants and do so more often than foundresses (the macropterous offspring of the foundress had not yet eclosed at the time of the experiment). He has also provided evidence that *Koptothrips* spp. form a real threat to the *Oncothrips* and that the micropterous offspring provide a substantial benefit of protection to the foundresses. The micropterous adults are therefore termed 'soldiers'. Dissection of foundresses and micropterous adults show that although many soldiers had developing oocytes, their ovarian development was clearly inferior to that of the foundresses. Besides, Crespi points out that "there is simply insufficient space in the gall for micropterous females to produce as many adult offspring as do foundresses". Thus *O. tepperi* and *O. habrus* appear to satisfy all the three criteria required to label them as eusocial. There is overlap of generations, the morphological specialization and defensive behaviour of the

## And now... eusocial thrips!

Raghavendra Gadagkar

Eusocial insects (the only truly social insects, by definition) are defined as those that possess all of the three fundamental traits of eusociality namely, (a) cooperative brood care, (b) differentiation of colony members into fertile reproductive castes (queens or kings as the case may be) and sterile non reproductive castes (workers) and (c) an overlap of generations such that offspring assist their parents in brood care and other tasks involved in colony maintenance<sup>1,2</sup>. When this definition was formulated, eusociality was known to be restricted to the class Insecta and even there to just two orders namely Isoptera (termites) and Hymenoptera (ants, bees and wasps). While all known termites are eusocial, the distribution of eusociality in the Hymenoptera is curious. The suborder Symphyta, consisting of several families of free-living phytophagous species is devoid of eusociality. In the other suborder Apocrita, the subgroup Terebrantia consisting of several families of parasitoid species is also completely devoid of eusociality. It is

only in the subgroup Aculeata that eusociality is seen. But even here, while all ants are eusocial, most bees and wasps are not eusocial. Nevertheless eusociality is believed to have originated at least eleven times independently within the Aculeata<sup>2</sup>.

In recent times, eusociality has been demonstrated in another order of insects namely Homoptera (in the aphids)<sup>3-5</sup>. There is also an unsubstantiated claim of a eusocial spider<sup>6</sup> and a clear demonstration of eusociality in a mammal, the naked mole rat<sup>7,8</sup>. The discovery of eusociality in any species of animal outside the Isoptera and Hymenoptera has come to be regarded as sensational, usually warranting a report in *Nature* or *Science*<sup>7,9</sup> but claims and counter-claims about whether something should be classified as eusocial continue<sup>5,10</sup>.

And now Bernard J. Crespi<sup>11</sup> of the Simon Fraser University in Canada has demonstrated eusociality in two species of Australian gall thrips *Oncothrips tepperi* Karny and *O. habrus* Mound.