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Meeting Review

"A Galling Uncertainty"

"Plant galls: organisms, interactions, populations", co-sponsored by the Systematics Association and the British Plant Gall Society, was held at the Royal Institute of Entomology, 15–17 July 1992.

Just over a hundred years ago *Nature* (1989; 1990) provided a forum for a cool exchange on a hot subject. The subject was the Darwinian theory of evolution; the issue was the doubt, expressed by St. George Mivart and George J. Romanes, that the formation of plant galls could be explained in terms of natural selection. The issue was unresolved. Soon after, the partitioning of biology into separate disciplines left galls in the "no man's land" between botany and zoology with predictable consequences: galls came to be regarded as minor biological curiosities, rather than a vital element in a general theory of evolution.

This recent symposium devoted to the biology of plant galls marked a long-overdue departure from this consensus. It brought together a multidisciplinary group of scientists sharing an interest in the biology of plant galls, and provided opportunity for re-appraisal of the evolutionary significance of gall formation.

As discussions progressed from the "lower" to the "higher" groups of gall-makers, there unfolded a colourful panorama of amazing feats of morphogenesis: brilliant red discolouration and condensation of vegetative shoots by fungi, tufts of leaf folds hiding the larvae of thrips, and a bewildering variety of intricately structured swellings induced by flies and wasps. A corresponding progression followed from simpler, crude modifications of plant organs (as in condensation, folding, or invagination), to the appearance of novel gall-organs, resembling flowers and fruit. So much so that quips on how a brilliant red cluster of leaves induced by the fungus *Exobasidium* on a blueberry shoot is more showy than the flower, or how fleshy galls had come to look like a fruit provoked nervous chuckles. Could so much resemblance between galls and organs of plants be coincidental? That a gall-maker can evoke some "normal" plant trait from a seemingly inexhaustible reservoir of hidden variability provides one explanation. I offer another (Pirozynski, 1988; 1991).

It is not the galls that resemble flowers and fleshy fruits but the converse: galls appeared in the fossil record before the look-alike organs of plants. What would be the adaptive value to the gall-maker, riddled as it is with insect competitors, to induce a gall that lures additional competitors by resembling

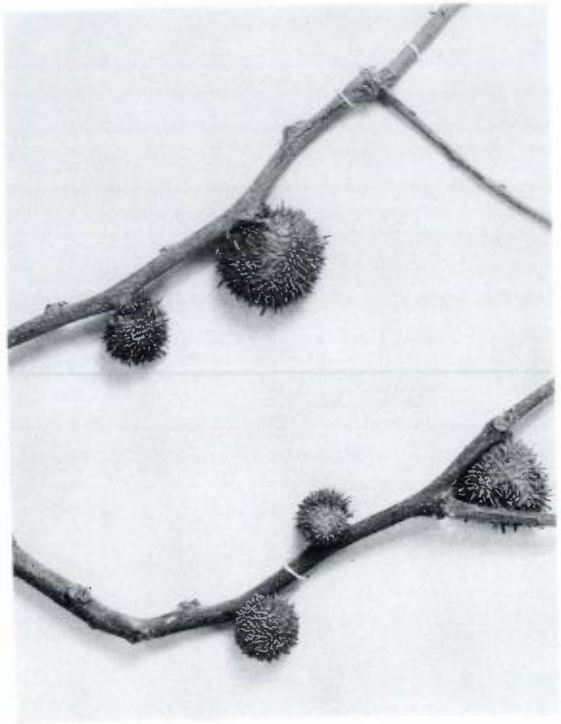

Figure 1

Figure 2.

Galls on *Hopea ponga* (Dennst.) Mabberley (Dipterocarpaceae), caused by an undescribed coccid (Homoptera). Courtesy of V.B. Hosagoudar.

a flower? Moreover, how could a gall evolve to mimic a fleshy fruit when the fruit is intended to be eaten? The conventional wisdom is that the gall protects the occupant, even through mimicry of an immature fruit. A coccid-induced spinose gall (Figs. 1, 2) on the Indian tree *Hopea ponga* (Dipterocarpaceae) was for nearly 300 years mistaken for a fruit and confused with *Artocarpus* (Moraceae). If the spines, as has been implied, offer protection it cannot be against seed-dispersing herbivores: fruits of *Artocarpus* do not shed spines on ripening; they are eaten, spines and all, by large mammals. Furthermore, many galls are brightly coloured to more closely resemble ripe fruit. An unpalatable gall is of no advantage to the occupant when the gall is picked and discarded after the frugivore discovered it had made a mistake.

Dare I suggest that the resemblance of organs of plants to galls is homology? That some traits that once deterred competitors now attract pollinators and frugivores? A condensation and discolouration of a reproductive sporophyll visited by foraging inquilines and parasitoids could have carried a reward of constant or faithful pollination; likewise the incorporation of seeds in a fleshy gall attracting vertebrate consumers could have offered "instant" advantage in seed dispersal. In the conventional view, modification of plants by gall-makers is not heritable; millions of years of gall-making has no evolutionary significance. Instead, plants took millions of years to evolve structures that gall-makers induce in a few days.

This view can now be challenged. The meeting was reminded that the relatively crude agrobacterial crown gall and hairy root hyperplasia transfer and integrate bacterial DNA into the plant's genome, thereby permitting the expression of novel traits for natural selection to act upon.

However, as for the mechanisms by which insects generate the wonderfully elaborate plant galls, we are no wiser now than a hundred years ago. "... what consists the difference in the active irritation that causes so great a divergence in the results?" asked R. McLachlan during the 1889 debate. The answer, he suggested, "... might very materially modify speculative theories based on results only, without a precise knowledge of the agencies that produced those results". It could not be foreseen in 1889 that the precise answer which molecular biology is now capable of providing, goes beyond the issue of the adaptive nature of gall-formation. It could provide proof that the origin of a plant organ and its evolution need not be one and the same thing.

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