The relationship between brightly coloured insects, toxic secondary plant substances and toxic, self-secretions is discussed and described. The results of the chemical analysis of approx. 80 species are tabulated and it is shown that the model butterflies in two famous mimicry complexes sequestered and stored toxins from plants and were thus provided with powerful chemical defence mechanisms. [The SCI] indicates that this paper has been cited in over 80 publications since 1972.

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"From field observations and experiments (during 1950-60) with captive birds, I became convinced that many brightly coloured (aposematic) insects contained toxic defensive substances, some of which were sequestered from their food plants and stored. At this period of my life I hero-worshipped Tadeus Reichstein, whom I regard as one of the most gifted chemists of all time and also one of the most creative and honourable men of his day. I was determined to persuade him to join me in a research project concerned with aposematic insects. Reichstein, however, insisted that he was a steroid chemist and pointed out that up to that time (1956) steroids were unknown in insects. 'In order to have the privilege and pleasure of working with you,' I told him, 'I would find steroids in old boots.'

The first insect I discovered which measured up to his requirements was a desert grasshopper. This insect (Poekilocerus bufo-nius)1 sequestered cardenolides from its food plant and also concentrated the material in the secretions of a defensive spray. I got a good mark for the fact we could collect this material on filter paper, thereby avoiding extraction of the whole insect. Reichstein identified calactin and calotropin and traces of other cardenolides in the fluid ejected. After this propitious start we identified sequestered cardiac glycosides in 23 aposematic insects from 6 different Orders. We also paid special attention to the supposed models of two of the most famous mimicry situations, the Monarch (Danaus plexippus)2 and the Aristolochia-feeding Swallowtail Pachlioptera aristolochiae.3 In both these models we found stored toxic secondary plant substances sequestered from their food plants, cardenolides in the former and aristolochic acids (not steroids!) in the latter, thereby resolving a hundred-year-old controversy.4,5 The hitherto hypothetical defence of the models was thus placed on a sound chemical basis. All our results were tabulated in the paper in question, negative as well as positive findings.

"The popularity of this publication I believe rested on the following points:

1. The defensive role of the secondary plant substances had recently been pointed out by Fraenkel,6,7 and had aroused considerable interest. The first proof of their sequestration and storage by insect herbivores proved topical and stimulating.

2. Reichstein's matchless chemistry (for instance he identified 10 cardenolides in the Monarch Butterfly) could be depended on and other workers besides myself could follow his lead with complete confidence.

3. The general discussion and review of the relationship of warning colouration in insects with toxic plants and toxic self-secretions provided a useful basis for further research.


