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PREFACE

In preparing the 14 papers and ensuing discussions presented at the Insect Biochemistry Symposium, IVth International Congress of Biochemistry, Vienna, 1958, I have exercised to the full my editorial privilege of changing, to a lesser or greater degree, some of the authors' manuscripts. In organizing the Symposium I endeavored to make the gathering truly International, but by tacit agreement, English was the predominant language of the various participants. In my subsequent efforts to ensure that the translated papers composing this book be at least clear to the reader, and all of them grammatically correct, I have taken unwarranted liberties with some of these manuscripts. In fact, I may well have distorted the original meaning of some authors, particularly of those for whom English is not a native tongue. If indeed this be the case, I can only offer my sincerest apologies. I would in mitigation plead that in order to meet the Publisher's deadline, lack of time precluded a desirable correspondence with the authors concerned. For the same reason, I have checked references only in a most perfunctory manner, and hence responsibility for any possible errors in this connection rests largely with the authors themselves.

In a Symposium of this kind a certain amount of overlap in subject matter is perhaps unavoidable; this is patently obvious in the present instance in the case of carbohydrate metabolism. The fact that certain aspects of insect biochemistry were not discussed must not be interpreted as of necessity a lacuna in our knowledge. Thus for example various circumstances prevented any discussion of insect digestion, even though some excellent work has been published on this subject; by contrast, in the field of insect excretion there simply is not sufficient biochemical information available to warrant discussion. If nothing else, the Symposium indicates the present status and future problems of at least some aspects of insect biochemistry.

L. Levenbook

ERÖFFNUNG DES SYMPOSIUMS

A. BUTENANDT

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Vor allem möchte ich im Namen aller Teilnehmen Herrn Dr. Levenbook für die Vorbereitung des Symposiums herzlich danken.

Es ist das erste Mal, dass das Thema "Biochemie der Insekten" zum Gegenstand der Diskussion auf einem Biochemie-Kongress gemacht wird. Damit wird die wachsende Bedeutung dieses neuen biochemischen Arbeitsgebietes unterstrichen. Insekten wurden häufig zur Lösung biologischer Probleme verwendet, auch die Biochemie verdankt den an Insekten durchgeführten Analysen wichtige Entdeckungen grundsätzlicher Art. Es sei daran erinnert, dass die Erforschung der Gen-Wirkkette der Pigmentbildung bei Schmetterlingen und Fliegen erstmalig zu der Erkenntnis führte, dass Gene über Fermente wirken. Im Rahmen dieser Untersuchungen wurden die Ommochrome, charakteristische Pigmente der Arthropoden, in ihrer Struktur geklärt und gezeigt, dass es sich um Phenoxazonfarbstoffe handelt, die bis vor kurzem in der Natur nicht aufgefunden waren. Heute wissen wir, dass die Ommatine und Ommine zu den verbreitetsten Naturfarbstoffen gehören und dass ihr Vorkommen nicht auf die Insekten beschränkt ist. Auch Pilze synthetisieren Ommatin, und die chromophore Gruppe antibiotisch bedeutsamer Actinomycine gehört zu den Phenoxazon-Farbstoffen.

Schon einmal haben Untersuchungen über Insektenpigmente zur Entdeckung einer wichtigen neuen Farbstoffklasse geführt. Der Flügel-Farbstoff der Pieriden erwies sich als Derivat des Pteridins und seine Strukturermittlung eröffnete den Weg zur Entdeckung von Vitaminen der Pteridinreihe vom Typ der Folinsäure, die im Stoffwechsel bei der Übertragung von C_1-Resten eine grosse Rolle spielen. Kürzlich konnte im Biopterin ein neues Pteridin in der Insektenwelt aufgefunden werden, und der Befund, dass der Weiselfuttersaft, das Gelée royale, der Honigbiene sich vom Arbeiterinnenfuttersaft durch seinen Gehalt an Biopterin unterscheidet, eröffnet möglicherweise einen neuen Weg zum Studium von Differenzierungsvorgängen bei Insekten.

Lange Zeit hindurch waren die Insekten nur Gegenstand der deskriptiven Biochemie, aber in den letzten Jahrzehnten wurden in steigendem Masse Probleme der dynamischen Biochemie bearbeitet. Es gilt zu zeigen, welche aus der Physiologie der Wirbeltiere oder der Mikroorganismen bekannten Stoffwechselmechanismen auch bei Insekten vorkommen und wo der Stoffwechsel seine besonderen Wege geht. Die Entdeckung der Trehalose als Blutzucker der Insekten, des hohen Aminosäuregehaltes der Hämolymphe und der besonderen Wege, die im Kohlenhydrat- und Fett-Abbau zur Energie-Gewinnung für die Muskelbewegung der Flug-Insekten beschritten werden, sind Beispiele für die spezifischen Stoffwechselabläufe bei Arthropoden.

Besonders reizvolle Aufgaben stellt die Insektenwelt dem Hormonforscher: wir wissen z.B, dass die Metamorphose der Insekten durch das Zusammenspiel von 3 Hormonen gesteuert wird, von denen eines vom Gehirn, ein zweites von der Prothorax-Drüse und das dritte vom Corpus allatum sezerniert wird. Das Hormon der Prothorax-Drüse, das Häutungshormon Ecdyson, ist als erstes Insektenhormon kristallisiert gewonnen worden. Wir werden während des Symposiums hören, in welch schneller Entwicklung unsere Erkenntnisse auf diesem Sondergebiet der Insektenwelt sind.

Aber nicht nur Hormone im klassischen Sinne sind bei den Insekten zu finden. Ihnen zur Seite treten jene Stoffe, die man als "Ectohormone" oder neuerdings als "Pheromone" bezeichnet hat. Es handelt sich um spezifische Sekrete, die in einem Tier erzeugt werden, aber in einem anderen Individuum ihre spezifische Wirkung erfüllen und oft das soziale Verhalten der Insekten bestimmen. Deshalb spricht man auch von "Sozialhormonen". Wir nennen die sogenannte "Königin-Substanz" der Honigbiene, die von der Königin eines Bienenstaates produziert wird und die Arbeiterinnen darüber verständigt, dass eine Königin anwesend ist; wir nennen die Sexuallockstoffe der Schmetterlinge, von denen der des weiblichen Seidenspinners (*Bombyx mori*) isoliert und als ungesättigter primärer Alkohol erkannt worden ist; wir nennen die Alarmstoffe der Blattschneider-Ameise (*Atta sextens*), die nach neueren Untersuchungen zu einem grossen Teil aus Citral bestehen. Über andere charakteristische Inhaltsstoffe und Gifte der Insekten werden wir in diesem Symposium hören.

Man könnte die Hinweise auf bedeutsame Probleme der Insekten-Biochemie stark erweitern, doch ist es nicht die Aufgabe dieser Einführung, der zur Diskussion stehenden Problematik vorzugreifen. Der Verlauf des Symposiums wird die steigende Bedeutung biochemischer Probleme der Insektenwelt aufweisen und gewiss dazu anregen, dass sich die Biochemie in grösserem Umfange mit dieser interessanten Welt beschäftigt.

ENGLISH TRANSLATION OF PROF. A. BUTENANDT'S INTRODUCTORY ADDRESS

In opening this Symposium, I should like first to offer sincere thanks to Dr. Levenbook for his organization of the Symposium.

This is the first time that the topic of "Insect Biochemistry" has been made the subject of discussion at a Biochemical Congress. This underscores the increasing importance of this new biochemical field of investigation. Insects have frequently been employed to solve biological problems; and biochemistry too owes a debt to analyses performed on insects for important discoveries of a fundamental nature. It may be recalled that investigation of the genetic sequence of events concerned with pigment formation in moths and flies first showed that genes act through enzymes. It was during the course of these investigations that the structure of the ommachromes, pigments characteristic of Arthropods, was elucidated, and they were shown to be phenoxazone pigments which until recently had not been found in nature. We now know that ommatine and ommine pigments are widely distributed in nature, and that their occurrence is not restricted to insects; fungi synthesize ommatine, and the chromophoric group of the actinomycins, important as antibiotics, is also a phenoxazone pigment.

The discovery of an important new group of pigments through examination of insect colouring matter had occurred on a previous occasion. The wing pigment of Pierids was found to be a pteridine derivative, and elucidation of its structure opened the way to the subsequent discovery of the pteridine series of vitamins, such as folic acid. These play an important metabolic role in transferring C_1 fragments. Recently a new pteridine, biopterin, has been found in the insect world; the discovery that honeybee Royal Jelly differs in composition from the diet of the worker bee in its biopterin content may possibly pave the way for studies on processes of differentiation in insects.

For a long time insects were the subject of only a descriptive type of biochemistry, but during the last decades problems of dynamic biochemistry have been investigated to an increasing extent. It will now be necessary to determine which of the general metabolic mechanisms obtaining in mammals and microorganisms occur also in insects, and which are peculiar to the latter. The discovery of trehalose as the blood sugar of insects, the high amino acid content of their hemolymph, and the specialized pathways of carbohydrate and fat metabolism concerned in the utilization of energy for muscular movement by flying insects, all of these are examples of specific metabolic processes in Arthropods.

Insects offer particularly attractive material to the endocrinologist; we know, for instance, that metamorphosis in insects is under the control of three hormones: the first is secreted by the brain, the second by the prothoracic gland and the third by the corpus allatum. The prothoracic gland hormone is the moulting hormone ecdysone, and is the first insect hormone to have been obtained in the crystalline state. During this Symposium we shall hear about the rapid progress being made in our knowledge of this special field of insect biology.

Hormones in the classical sense, however, are not the only ones found in insects; we must now include those substances called "ectohormones" or, more recently, "pheromones". These are specific secretions produced by one animal which fulfill their particular functions in a second individual. They frequently determine the social behavior of insects, for which reason we may speak of "social hormones". Thus we may mention the so-called "queen substance" of the honeybee, a material produced by the queen of a colony which informs the workers of the queen's presence; the sexual attractants of moths, the one from the female silkworm *Bombyx mori* having been isolated and characterized as an unsaturated primary alcohol; and the so-called "alarm substance" of the leaf-cutting ant *Atta sextens* which, according to recent investigations, consists largely of citral. At this Symposium we shall hear more about other characteristic insect constituents and poisons.

One could continue to enlarge upon these allusions to important problems in insect biochemistry, but it is not the purpose of this Introduction to anticipate the problems which will be discussed. As the Symposium proceeds the increasing importance of the biochemical problems in insects will become evident, and biochemistry will surely be stimulated into occupying itself to a greater extent with this interesting field.

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CONTENTS

THE CHEMISTRY OF HOST SPECIFICITY OF PHYTOPHAGOUS INSECTS

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It has been stated that living plants, especially the flowering plants, furnish the food materials for fully half of the living species of insects. Every part of the plant may be eaten, but green leaves no doubt constitute the bulk of vegetable food material. Since leaves are the principal food of insects, and in most cases the only food, it is obvious that they must contain all the food materials which an insect requires. Yet we find that most insects that eat leaves are more or less selective in their choice of food plant. Insects may feed on only one or a few closely related plant species (monophagy), or on a larger group usually confined within a certain plant family (oligophagy), or on a still wider group of plants (polyphagy), but never on all plants. Is host selection in this group of insects governed by the nutritional superiority of the particular plant or region of the plant serving as a food, or rather by the presence or absence of attractants and repellents in plants which are otherwise of more or less uniform food value?

The basic food requirements of all insects seem to be very similar, and very much like those of higher animals. They include the "essential" amino acids, most of the vitamins of the B-group, a sterol and the physiologically important minerals. With only a few exceptions the nutritional requirements of plant feeding insects are not known, but there is no reason to assume that they should be different from those of other types of insects which have been more extensively studied. These basic requirements of insects concern substances which occur in *all* living cells, including, of course, those of plant tissues. Insofar as the occurrence of these substances is concerned, the composition of all leaves is very much alike, and there is little reason to suppose that differences in chemical composition as regards the "primary" substances (which occur in all living matter) can be responsible for the choice of food plant on the part of the insect.[1]

Plants also contain a vast array of what has been called "secondary" plant substances. These can be conveniently grouped under glucosides, saponins, tannins, alkaloids, essential oils, organic acids and others, many thousands of which have been described in the literature. Their occurrence is sporadic, but may be specific for families, subfamilies, genera, and sometimes even species or subspecies. Their role in the metabolism of plants has never been satisfactorily explained, but in view of their sporadic occurrence, and of their differences in chemical constitution, it is almost inconceivable that they play a function in the basic metabolism of plants. For similar reasons it is also highly improbable that they are of nutritional importance for insects in the same sense as are the "primary" substances, namely, that they are metabolized and utilized in tissue synthesis.

It is suggested that the food specificity of insects is solely based on the presence or absence of these odd compounds in plants, which serve as repellents to insects (and other animals) in general, and as attractants to those few which feed on each plant species. The immense variety and number of compounds concerned thus corresponds to the equally immense variety of specific nutritional relationships between insects and plant hosts. The compounds concerned need not play any role in the basic metabolism of either plant or insect, since they serve merely as trigger substances which induce, or prevent, the uptake of the true nutrients. Most, if not all, secondary plant substances possess characteristic odors or tastes and thus may elicit sensory reactions to the food. In contrast, most of the important nutrients like proteins, starch, fats, vitamins or minerals have little or no taste or smell, at least not in amounts in which they are present in plants.

It is suggested then, that leaf-feeding insects could develop equally well on any leaves, provided they ate enough of them. We must assume that early in their evolution plants developed the means by which they became unpalatable to the rising multitude of insects. The unpalatability was accomplished by the production of the vast array of chemical compounds which characterize specific taxonomic groups of plants. In fact, the appearance of the flowering plants in the early Cretaceous period coincides with the various morphological and physiological adaptations in both insects and plants which characterize the interdependence between the insects and flowering plants. This reciprocal adaptive evolution which occurred in the feeding habits of insects and in the biochemical characteristics of plants forms a striking parallel to the better understood relations between the shape, color and scent of flowers, and the sensory responses of insects. It is common knowledge that the pigments and flavoring of blossoms owe their existence solely to their functions as attractants for insects to particular flowers. Is it less logical to assert that the secondary substances in plants exist solely for the purpose of repelling and attracting insects?

Had the plants been entirely successful in their chemical protection against insects, there would be no insect problem in agriculture. In fact, however, insects on their part responded to this chemical control by the plant; a host preference arose when a given insect species, by genetic selection, overcame the repellent effect of such a material, thereby gaining a new source of food. This led to a situation where further selection produced new species or genera of insects that required the former repellent as an attractant to induce feeding.

To establish the ecological relationships between insects and secondary plant substances, the following points should be considered or proven:

1. The active substance should be isolated and identified.
2. The isolated compound, if an attractant, should induce feeding when applied to leaves which are not commonly accepted as a food by a certain insect, or when incorporated in neutral media like filter paper or agar jelly.
3. Members of plant families other than those which commonly contain the attractant in question should be acceptable if they normally contain this compound.
4. A quantitative relationship should exist between concentration of an attractive substance and feeding response.
5. A compound which serves as a repellent in a particular insect–plant relationship should, when incorporated in the normal food plant, make it unattractive.
6. A plant may be attractive and at the same time poisonous, by either possessing separate attractive and poisonous compounds, or by presenting these two effects in one and the same compound.

In the following sections, the situation as it has emerged for some of the principal plant families *viz.* Cruciferae, Umbelliferae, Solanaceae, Leguminosae, Moraceae and Gramineae, will be discussed.

CRUCIFERAE

All members of this family contain glucosides with a mustard oil as the aglycon, some of which, like sinigrin and sinalbin, are widely distributed. Cruciferae have a very characteristic fauna of Lepidoptera, flea-beetles and aphids. The first detailed description of a chemical–insect–hostplant relationship concerned the work of Verschaeffelt[2] on the cabbage white butterflies *Pieris brassicae* and *P. rapae*, which feed almost exclusively on members of this family. His work was, 40 years later, largely confirmed, and extended to the diamond back moth *Plutella maculipennis* by my collaborator, Thorsteinson[3]. These insects feed exclusively on Cruciferae, and on a few species of other plant families which contain similar glucosides. Many other plants were eaten only after they had been treated with sinigrin or sinalbin. A quantitative relationship exists between the glucoside content of the food, and feeding response of *Plutella*.

UMBELLIFERAE

This family is characterized by the presence of essential oils, many of which are known as constituents of spices. According to the investigations of Dethier[4], *Papilio ajax* was found feeding on 18 different plants of this family, containing any of the following crude oils: Carrot, caraway, anise, coriander, celery and angelica. Pieces of filter paper treated with such oils or pure constituents of oils, such as carvone (from caraway), methyl chavicol (from anise) or coriandrol (from coriander) were also attacked. Methyl chavicol is also contained in certain non-umbelliferous plants (Rutaceae: *Dictamus fraxinella*; Compositae: *Solidago* spec. and *Artemisia dracunculoides*) which are eaten by this insect.

LEGUMINOSAE

The Mexican bean beetle, *Epilachna varivestis*, feeds almost exclusively on plants of the genus *Phaseolus*, but has, in recent years, become increasingly adapted to the soybean in the United States. It never feeds on *Vicia faba*. Evidence points to the effect of a glucoside of the nature of a triterpenoid saponine being the attractive factor. This compound has been concentrated, but not yet isolated.[5]

SOLANACEAE

The very extensive work of Kuhn, Schreiber and others on the structure and occurrence of glycoalkaloids in Solanaceae and their effect on the potato beetle *Leptinotarsa decemlineata* has been summarized by Kuhn and Löw[6], and Schreiber[7,8]. These alkaloids, contrary to former expectation, do not make the plant attractive to the beetles, but are the agents which render a species of Solanaceae repellent or toxic. The compound which makes the potato plant attractive to *Leptinotarsa* has never been identified. Glycoalkaloids of related structures occur in Solanaceae in an astonishing diversity of structures, those occurring in the common potato plant, solanine and chaconine, being harmless and of no apparent effect on the potato beetle, and those in other plants, e.g. in tomato, *S. demissum*, *S. chacoense* and tobacco, being repellent and sometimes toxic. Schreiber[7,8] attributed adversely acting properties to the lack of the double bond in the aglycon, to the tetra- (as opposed to the tri-) saccharide component, and the presence of xylose (Table I). Repellent compounds in other Solanaceae included: tomatine (in tomato), the "leptines" in *S. chacoense*,[9] soladulcin in *S. dulcamare*,[7] a tetroside in *S. acaulia*[7] (Table I), and compounds of an entirely different structure such as the burning principle of red pepper, capsaicin (in *S. capsicum*) and nicotine in tobacco.[7]

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