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ACTA ZOOLOGICA ACADEMIAE SCIENTIARUM HUNGARICAE

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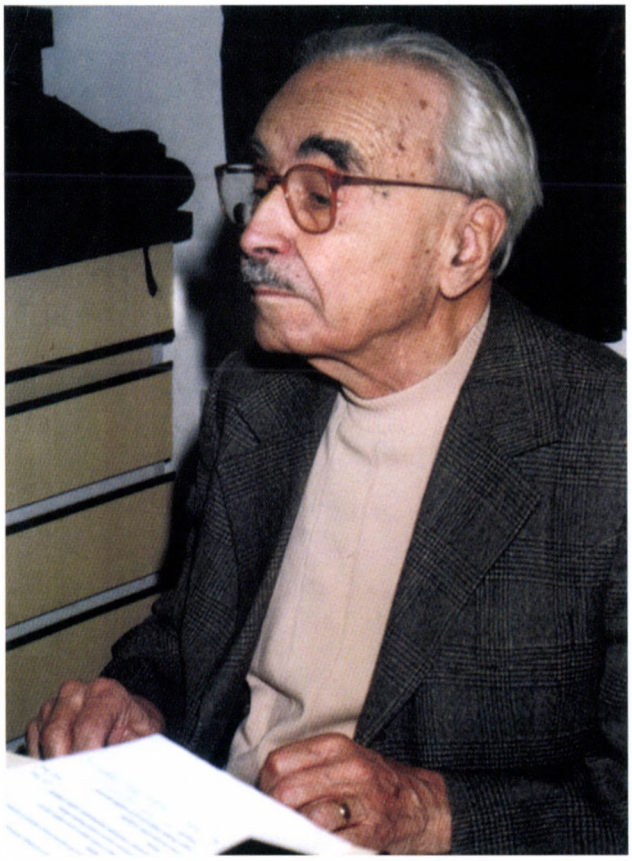

This volume is compiled in honour of Tibor Jermy,
ordinary member of the Hungarian Academy of Sciences,
founder of the Hungarian experimental entomology,
for the occasion of his 85th birthday,
by friends, colleagues and admirers

FOREWORD

Count ISTVÁN SZÉCHENYI, who for his outstanding services to the nation has been called "the greatest Hungarian" bequeathed the admonition to us: "... the nation could only be raised by educated minds". His will is coming true this century: Hungary, relative to her population size and economical resources, had been a scientific super-power before World War II and has upheld a high scientific standard in the post-war world, up to now. Limited funding over several decades hampered research, yet significant results were achieved. The Hungarian Academy of Sciences founded by Count ISTVÁN SZÉCHENYI in 1825, is proud of its elected members who in spite of meagre circumstances did their best to improve the image of the nation and to enhance her reputation. TIBOR JERMY is among these scholars. He, also as past president of the Biology Section of the Hungarian Academy of Sciences, contributed considerably not only to his own special field, but promoted the international recognition of Hungarian science in general.

I believe that the reader who peruses this volume published on the occasion of TIBOR JERMY's 85th birthday, notices the appreciation and respect felt by his students, Hungarian and foreign friends and colleagues. The papers highlight his results obtained in the field of experimental entomology, ecology and evolution. I congratulate and greet TIBOR JERMY on behalf of the Presidium of the Hungarian Academy of Sciences, and wish him good health and scientifically fruitful years to come.

January, 2002

Prof. Péter Friedrich

Ordinary member of the
Hungarian Academy of Sciences
President of the
Biology Section of the HAS

CONTENTS

Acta Zoologica Academiae Scientiarum Hungaricae 48 (Suppl. 1), pp. 9–13, 2002

TIBOR JERMY ACADEMICIAN IS 85 YEARS OLD

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Anyone more or less familiar with the history of science knows that sudden progress in science is always linked with the appearance of a great personality. As opposed to the general view, it can be safely said that even human history has been and is formed by great statesmen, and the masses only play a secondary role.

The 100-year history of agricultural zoology, our field of science, clearly shows that important progress is always associated with the work and influence of an excellent person. The prominent personalities of the 20th century were GÉZA HORVÁTH, until the late twenties JÓZSEF JABLONOWSKI, from the thirties to the end of the fifties GUSZTÁV SZELÉNYI; while from the fifties up to present day TIBOR JERMY, ordinary member of the Hungarian Academy of Sciences has determined the development of agricultural entomology in Hungary.

Prior to expressing our congratulations to the Jubilarian let me – as one who has worked with him more than a quarter of a century – recall in a few words his character.

TIBOR JERMY was born on 31 January 1917 in Lőcse (a town now in Slovakia). His father was an engineer at the Office of State Building who, following the Peace Treaty of Trianon, was employed first in Zalaegerszeg, then in Budapest. TIBOR JERMY's early years were determinative for him as regards languages: at home they spoke German, in the street he was acquainted with the Slovak language, and later, in the elementary school he spoke Hungarian. Between 1928 and 1935, he attended the Ferenc Toldy secondary school for modern languages in Budapest. The late GÁBOR REICHART, one of our colleagues, who had been JERMY's class-mate told me that JERMY was all along a student at the top of his class not only in languages but also in literature, mathematics and physics. He took his final examinations in 1935, then – as he himself told me – after some hesitation did not accede to his father's wish to go to the Technical University, but matriculated at the Péter Pázmány (now Loránd Eötvös) University, Faculty of Natural History-chemistry, since from his early childhood he had been attracted by Nature, whose secrets were unveiled for him by his maternal grandfather, a forest engineer in the Szepesség (a part of the present Slovakia). At the university, under the influence of the impressive personality of ENDRE DUDICH, professor of zoological taxonomy, JERMY chose zoology for his special field. Although his parents were living in Budapest he was admitted to the famous Eötvös College. Professor ALBERT

GYERGYAI, at that time teacher of French literature at the College (who translated works from LA FONTAINE, MONTAIGNE, VILLON, BALZAC, FLAUBERT, PROUST, GIDE into Hungarian) when spending his summer holiday in Nagybajom (Somogy County) in the early fifties asked me where I was working. I told him I worked at the Zoological Department of the Research Institute for Plant Protection Budapest, together with TIBOR JERMY, a former Eötvös collegiate. I cite professor GYERGYAI's answer word by word: "Oh, the TIBOR JERMY, the excellent student." This meant that JERMY distinguished himself by his gift for languages in GYERGYAI professor's French courses too.

He finished his university studies in 1940 acquiring a secondary school teacher's diploma. In 1942 with his dissertation "Taxonomic study on the Plesiocerata of Hungary" he passed a university examination. He won a scholarship to the Sorbonne University but the war situation prevented him from going to Paris. In 1947, he got his doctor's degree *summa cum laude*.

As there was no zoologist's post after graduation he was employed in the National Research Institute of Viti- and Viniculture as wine chemist (1940–1948).

In 1942 JERMY was called up for military service, and as an anti-aircraft artilleryman became a prisoner of war on 31 March 1945. From his captivity in the Soviet Union he returned home on 10 July 1947, and continued his activity in his earlier working place.

In 1948 he went to the Plant Protection Service until in 1949 his old dream came true: he received a zoologist-entomologist post at the Department of Zoology of the Research Institute for Plant Protection. Therefore, he was already 31 years old when starting scientific work in agricultural entomology. It was from here that as director of the Institute between 1969 and 1978 he retired in 1978.

JERMY's scientific activity first consisted of working up the taxonomy and biology of the insect pests of cultivated plants and elaborating control methods. At the very beginning of his career, he had a new approach to these research tasks: he placed the ecological and ethological aspects in the centre of his investigations. In the years following the appearance of the Colorado potato beetle (*Leptinotarsa decemlineata*) in Hungary new investments were made possible. It so happened that on the basis of JERMY's plans the Keszthely Laboratory of the Research Institute for Plant Protection came into existence (1957), and equipped for modern ecological investigations enabled the attainment of greater research results. Until 1967 JERMY regularly spent a considerable part of the growing season (from May to September) in Keszthely. Considering his scientific results, the years in Keszthely were determinative for JERMY's scientific oeuvre.

I should like to list some major fields of plant protection entomology in which internationally acknowledged results were attained by JERMY: the diapause

of *L. decemlineata, Hyphantria cunea* and *Cydia pomonella*; the correlation between temperature and rate of development studied with *C. pomonella* larvae living in apples growing at the northern and southern sides of the apple-tree; theoretical questions of the production biology of terrestrial biocenoses; JERMY was the first in the world who criticized the concept of "biological balance"; with the results obtained while studying the ethological questions of the food specialization of phytophagous insects JERMY became an international authority of the subject; by building up the light-trap network he laid down the bases for the prognosis of insect species flying to light, not to mention his faunistic achievements; by studying the methods of selective control he opened up new areas of research (antifeedants, sex attractants, sterile-male technique, etc.). He was the first to write a general work on biological control in Hungarian; elaborated the Hungarian programme of integrated control methods. He launched agroecosystem investigations in maize fields and apple plantations; on the basis of the results of extensive experimentation as well as by working up critically the relevant literature he established the evolutionary theory of the relation of insect to host plant; upon the request of foreign professional circles he explained his views about the competition among phytophagous insects in a comprehensive study.

Only the major research fields are listed above, in which outstanding results were attained. Looking over the list of his publications, we can see that there is hardly any area of agricultural entomology that JERMY did not touch in the course of his activity. I was lucky to sit for 15 years in the same room with him, so I can say that "everything he touched turned into gold".

We may ask what the secret of this successful career is. The answer can be given by the Roman poet's words: *Philosophus non fit sed nascitur* (The philosopher is not made but is born). JERMY was born to what he is. His brain structure combines the analysing- with the synthesizing type of researcher, that is why he is a creative man, a champion of his science. He is blessed with the faculty of seeing the point, which helped him not only in his profession but in his everyday life too.

We now celebrate the 85th birthday of a scientist who, blessed with an enormous faculty of intuition, recognizes the essence of the problems in an instant. This extraordinary mental quality is associated with an innate manual skill and practical common sense which greatly helped him in elaborating his research methods.

Nevertheless, nobody must think that on interpreting his results TIBOR JERMY contents himself with merely establishing the facts. As a reflective, speculative man, both instinctively and knowing the ontological and epistemological laws he is capable of grasping the ultimate reason of things. For me unforgettable are the pauses during our collecting tours when JERMY in a few words pointed to the uncertainty or even absurdity of statements that I had thought so far incontestable.

As to JERMY's tours abroad it is enough to say that he has visited almost all countries important from a scientific point of view, either when invited as a consultant, or on commission. It was imposing to see him on the speaker's platform at the XVI International Congress on Entomology held in August 1980 in Kyoto, Japan, expounding his views about the coevolution of phytophagous insects before a professional audience gathered from all quarters of the world.

JERMY's major works cover more than 200 Hungarian and foreign scientific papers. His books: JERMY, T. & SÁRINGER, GY. (1955) *A burgonyabogár* [The Colorado potato beetle.] (Leptinotarsa decemlineata Say). Mezőgazdasági Kiadó, Budapest, 188 pp., (translated in German, Russian and Polish); JERMY, T. (1967) *Biológiai védekezés a növények kártevői ellen.* [Biological control against pests of plants.] Mezőgazdasági Kiadó, Budapest, 196 pp.; JERMY, T. (ed.) (1976) *The host-plant is relation to insect behaviour and reproduction.* Symposia Biologica Hungarica 16. Akadémiai Kiadó, Budapest, 322 pp.; JERMY, T. (1983) Multiplicity of insect antifeedants in plants. *In* WHITEHEAD, D. L. & BOWERS, W. S. (eds) *Natural products for innovative pest management.* Pergamon Press, Oxford, pp. 223–236; JERMY, T. (1987) *Gondolatok a koevolúcióról.* [Thoughts on coevolution.] Akadémiai székfoglaló, 1986. március 11. Akadémiai Kiadó, Budapest, 44 pp.; JERMY, T. (1987) The role of experience in the host selection of phytophagous insects. *In* CHAPMAN, R. F., BERNAYS, E. A. & STOFFOLANO, J. G. (eds) *Perspectives in chemoreception and behaviour.* Springer Verlag, New York, pp. 143–157; JERMY, T. & BALÁZS, K. (1988) *A növényvédelmi állattan kézikönyve.* [Handbook of plant protection zoology.] Vol. 1, Akadémiai Kiadó, Budapest, 443 pp.; (1988) Vol. 2, 304 pp., (1989), Vol. 3/A, 322 pp., Vol. 3/B, pp. 329–673 (1990), Vol. 4/A, 1–447, Vol. 4/B, pp. 453–831 (1994), Vol. 5, 376 pp., Vol. 6, 307 pp. (1996); SZENTESI, Á. & JERMY, T. (eds) (1991) *Insects-Plants '89.* Symposia Biologica Hungarica 39, Akadémiai Kiadó, Budapest, 577 pp.

He was honoured with GÉZA HORVÁTH medal (1975) by the Hungarian Association of Agricultural Sciences, IMRE FRIVALDSZKY golden commemorative plaque (1976) by the Hungarian Entomological Society, State Prize (1983), Academy Gold Medal (1992).

He has been member of the editorial board of Acta Zoologica Hung., Acta Phytopath. et Entomol. Hung., Fauna Hungariae (from 1965); Archiv für Pflanzenschutz (Berlin), Entomologica Experimentalis et Applicata (Amsterdam), and a Foreign Correspondence of the Annual Review of Entomology, Palo Alto (USA).

Positions held by him in scientific organizations: vice-president of the Hungarian Society of Biology (MBT), president of the Ecological Section of the MBT, president of the Plant Protection Society of the Hungarian Association of Agricultural Sciences (MAE) (1969–1977), president of the Hungarian Entomological So-

ciety (1969–1972), deputy president, then president of the Biological Section of the Hungarian Academy of Sciences (1980–1990), member of the Zoological and Ecological Committee of the HAS.

From 1990 he has been an associate member of the American Philosophical Society (Philadelphia); the British Ecological Society elected him "Unanimously and enthusiastically" honorary member.

At the special opening board-meeting held on 11 September 1993 the Georgikon Faculty of Agricultural Sciences of the Pannon University conferred on him the degree of Doctor Honoris Causa.

It is regrettable that the Biological Section of the Hungarian Academy of Sciences elected him only in 1976, at the age of 59, corresponding member, then in 1985 ordinary member. However, being in good health he has been able to mark out the new lines of research and assist the young, talented researchers gathering around him.

Finally, let this commemoration by – both in my name and on behalf of the colleagues – an affectionate bow to the 85-year-old TIBOR JERMY.

Acta Zoologica Academiae Scientiarum Hungaricae 48 (Suppl. 1), pp. 15–18, 2002

A SHORT SCIENTIFIC BIOGRAPHY OF TIBOR JERMY

Birth of place and year: Lőcse (today in Slovakia), January 31, 1917
Nationality: Hungarian

Education and scientific degrees

1935–1940	University of Péter Pázmány, Faculty of Arts and Sciences, Eötvös College
1940	Secondary grammar school teacher's diploma
1942	Ph.D. "Sub laurea Almae Matris" in Zoology
1952	Candidate of Science in Agriculture
1973	Doctor of Science
1976	Corresponding member of the Hungarian Academy of Sciences
1985	Ordinary member of the Hungarian Academy of Sciences

Fellowships and positions at host institutes

1966–1967	Ford Foundation Fellow, University of Pennsylvania, Dept of Biology.
1971	Visiting Scientist, Agricultural University, Wageningen, Holland
1978–1979	Visiting Scientist, USD Agricultural Research Laboratory, Yakima, WA

Positions held at Hungarian institutes

1940–1949	Chemist, National Institute for Ampelology, Budapest
1949–1969	Research Scientist, Senior Research Scientist, Head of Department of the Plant Protection Institute
1969–1978	Director of the Plant Protection Institute
1978–	Director Emeritus

Awards

1975	"Horváth Géza" Gold Medal of the Hungarian Agricultural Association
1976	"Frivaldszky Imre" Gold Medal of the Hungarian Entomological Society

1977	Gold Medal of Order of Labour
1983	State Prize
1992	Gold Medal of the Hungarian Academy of Sciences
1993	Dr. honoris causa, Pannon Agricultural University, Keszthely

Scientific societies

1969–1977	President of the Plant Protection Society of the Hungarian Agricultural Association
1977–	Honorary President of the Plant Protection Society of the Hungarian Agricultural Association
1969–1972	President of the Hungarian Entomological Society
1977–	Steering Committee Member of the Hungarian Entomological Society
1980–1987	Vice President, Department of the Biological Sciences of the Hungarian Academy of Sciences
1987–1990	President, Department of the Biological Sciences of the Hungarian Academy of Sciences
1990	Foreign member of the American Philosophical Society, Philadelphia, USA
1992	Honorary member of the British Ecological Society, UK

International organizations

1969–1977	Coordinating Centre for Plant Protection, Comecon Council of Accredited Members
1973–1984	Invited member to the Technical Advisory Board
1976–1992	IUBS, Hungarian National Committee member
1976–1985	UNESCO, Man and Biosphere Program, Hungarian National Committee member
1990–1991	ESF, Network on Insect-Plant Interactions, Coordination Committee Member
1988–1993	Entomologia Experimentalis et Applicata, Amsterdam, Editorial Board Member
1985–1988	Annual Review of Entomology, USA, Foreign Correspondent

Teaching

Invited lecturer at the Szeged University and at various institutions of the agricultural higher education.

Fields of scientific research

Taxonomy. As a university student he was interested in the taxonomy and biogeography of Diplopoda. His Ph.D. dissertation was published by the Hungarian Academy of Sciences. In later years, he dealt with taxonomy only if the target species of research was dubious. He described two species new to science.

Bionomy. The bionomy investigations on many pest insects of agricultural plants allowed the implementation of modern plant protection procedures, as well as the broadening of theoretical bases of applied entomology. In 1954, he organized a countrywide network of light traps that continues operating until today and provides outstandingly complete series of data on changes of insect populations in time. It also gives indications on long-term ecological changes.

Biological control. During the course of biological control against pest insects, he investigated the basic biology of parasitoids. He attempted the introduction of an American predatory bug against the Colorado potato beetle within the framework of the program launched by the International Biological Control Organization. By the support of the International Atomic Energy Agency, he co-ordinated and participated in experiments done to discover the possibilities and feasibility of autocidal method against three pest insects in Hungary.

Experimental insect ecology. In collaboration with colleagues, he established this area of research poorly known and investigated both in Hungary and abroad at the early 50s. Experiments performed with various insect species proved the importance of the joint effects of photoperiodic length and temperature in inducing diapause and in regulating population dynamics.

Biocenology. In dealing with the theory of terrestrial communities he established an analogy between entropy of inorganic systems and the flux of energy of biocenoses. He introduced the laws of "biocenotic minimum" and the "maximum of biocenotic work". He initiated a 10 years long program for the investigation of two major types of agroecosystems. Both in apple orchards and in maize fields, respectively, a surprisingly high species richness was found and there was a wealth of interactions with the surrounding communities, too. The data gained served the foundation of integrated control methods against pests, as well as allowed understanding of some homeostatic processes of agroecosystems.

Insect behaviour. He demonstrated the importance of sun-compass orientation in food finding of insects. Furthermore, he showed the effects of probability of food finding on the population dynamics of insects. When investigating the chemical sensory mechanism of food specialization of phytophagous insects he outlined the two-way specialization of chemoreceptors. Contrary to the earlier and generally accepted concept emphasizing the exclusive importance of phagostimulatory substances, he pointed out the ultimate significance of feeding inhibitory substances of plant origin determining the food plant spectrum of insect species. This latter finding has formed the basis for the application of substances of natural and synthetic origin having inhibitory effects for plant protection purposes. In collaboration with colleagues, he proved the occurrence of learning processes in phytophagous insects for the first time, by discovering the phenomenon of induced preference.

Evolution. The relationship of the two most species-rich groups of organisms, the plants and insects, as perceived since the middle 1960s, is the result of reciprocal selection between the participants, known as coevolution. By analysing numerous insect-plant interactions, he pointed out that, the evolution of all types of presently known interactions can be interpreted properly only by assuming that plant evolution was followed (but not induced) by the phytophagous insects (sequential evolution).

Acta Zoologica Academiae Scientiarum Hungaricae 48 (Suppl. 1), pp. 19–30, 2002

A COMPLETE LIST OF PUBLICATION OF TIBOR JERMY IN A CHRONOLOGICAL ORDER

JERMY, T. (1942) Rendszertani tanulmány a magyarországi Plesioceratákról (Diplopoda) [Taxonomy of the Hungarian Plesiocerata (Diplopoda).] *Matem. Termtud. Közl.* **39**: 1–82.

JERMY, T. (1948) Az amerikai fehér szövőlepkéről. [On the American fall webworm.] *Magyar Bor és Gyümölcs* **3**: 8.

JERMY, T. (1948) Vegyi védekezés az amerikai fehér szövőlepke ellen.[Chemical control against the American fall webworm.] *Kert és Szőlő* **1**: 11–12.

JERMY, T. (1949) A fogasnyakú gabonabogár kártétele salátában. [Damage of the saw-toothed grain beetle in lettuce.] *Növényvédelem* **1**: 9–11.

JERMY, T. (1949) Földicincér lárvájának kártétele salátában. [Damage of larvae of Dorcadion sp. in lettuce.] *Növényvédelem* **1**: 17.

JERMY, T. (1949) A babzsizsik. [The bean weevil.] *Magyar Mezőgazdaság* **4/21**: 6.

JERMY, T. & SZELÉNYI, G. (1949) Irodalmi tájékoztató. [Literature survey.] RUBCOV, A. A.: Biológiai védekezés a kártevő rovarok ellen. [Biological control against pest insects.] *Növényvédelem* **1**: 48–49.

JERMY, T. (1950) Védekezés a bagolypillék hernyói ellen DDT-s csalétekkel. [Control of noctuid larvae by baits containing DDT.] *Növényvédelem* **2**: 6–9.

JERMY, T. (1950) A DDT-permet riasztó hatása Hyphantria hernyókra. [Repellent effect of DDT spray against Hyphantria larvae.] *Növényvédelem* **2**: 13.

JERMY, T. (1950) A sároshátú bogár kártétele. [Damage by Opatrum sabulosum.] *Növényvédelem* **2**: 16.

JERMY, T. (1950) Új eljárás a silóban tárolt gabona gázos zsizsiktelenítésére. [New method for controlling weevils in wheat stored in silo.] *Növényvédelem* **2**: 62–64.

JERMY, T. (1950) Pocokirtás édes folyadékkal megnedvesített cinkfoszfidos szerrel. [Controlling voles by sweet bait containing zinc-phosphide.] *Növényvédelem* **2**: 65–66.

JERMY, T. (1950) Magyarországi kolorádóbogár megfigyelések és tapasztalatok. [Observations and experiences with the Colorado potato weevil in Hungary.] *Növényvédelem* **2**: 51–56.

PODHRADSZKY, J. & JERMY, T. (1950) *Harc a zöldségfélék betegségei és kártevői ellen.* [Fight against pathogens and pests of vegetables.] Mezőgazdasági Kiadó, Budapest, 56 pp.

JERMY, T. (1950) Újrendszerű thermostat. [A new type of temperature-controlled room.] *Növényvédelem* **2**: 51–56.

JERMY, T. (1951) A biológiai védekezés jelentősége a növényvédelemben. [The significance of biological control in plant protection.] *Agrártudomány* **3**: 522–528.

JERMY, T. (1951) Az őszigabona vetésideje és a csikoshátú búzalégy kártétele. [Sowing time of winter wheat and the damage done by the straw fly.] *Növényvédelem* **3**: 1–3.

JERMY, T. (1951) A rizszsizsik elterjedése hazánkban. [The distribution of rice weevil in Hungary.] *Növényvédelem* **3**: 3–4.

JERMY, T. (1951) Magyarországi megfigyelések a kolorádóbogáron. [Observations on the Colorado potato in Hungary.] *MTA Biol. és Agrártud. Oszt. Közl.* **2**: 271–296.

JERMY, T. (1951) Zöldségfélék kártevői. Raktári kártevők. [Pests of vegetable plants. Stored-product pests.]1.kiad. Pp. 467–488, 511–518., 2.kiad. (1953), Pp. 561–568, 620–630. *In* UBRIZSY, G. (ed.) *A növényvédelem gyakorlati kézikönyve.* [Handbook of practical plant protection.] Mezőgazdasági Kiadó, Budapest.

JERMY, T. (1952) Magyarországi megfigyelések kártevő bagolypilléken az 1948–1950. években. [Observations on pest noctuids between 1948–1950 in Hungary.] *Ann. Inst. Prot. Plant. Hung.* **5**: 105–122.

JERMY, T. (1952) Az amerikai fehér szövőlepke (Hyphantria cunea Drury) néhány fürkészlégy (Tachinidae) élősködőjéről. [On some tachinid parasites of Hyphantria cunea Drury.] *Ann. Inst. Prot. Plant. Hung.* **5**: 123–131.

JERMY, T. (1952) A fokhagymapille (Dyspessa ulula Bkh.) (Lep. Cossidae). [A garlic pest – Dyspessa ulula Bkh. (Lep. Cossidae).] *Ann. Inst. Prot. Plant. Hung.* **5**: 133–137.

JERMY, T. (1952) A babzsizsik (Acanthoscelides obtectus Say) táplálékfogyasztása. [The food consumption of the bean weevil, Acanthoscelides obtectus Say.] *Ann. Inst. Prot. Plant. Hung.* **5**: 305.

JERMY, T. & NAGY, B. (1952) A Szelényi-Viktorin-féle rovartoxikológiai módszer kiértékelési részének egyszerűsítése és a leromlás szemléletes ábrázolása. [Simplifying the evaluation of Szelényi-Viktorin-type insect toxicological method and a better demonstration of its death curve.] *Növényvédelem* **4**: 1–3.

JERMY, T. (1952) A gabonaálszú (Rhizopertha dominica Fab.) előfordulása Magyarországon. [Incidence of lesser grain-borer (Rhizopertha dominica Fab.) in Hungary.] *Növényvédelem* **4**: 3–5.

JERMY, T. (1952) Légynyűvek a raktározott burgonyában. [Fly maggots in stored potatoes.] *Növényvédelem* **4**: 17–19.

JERMY, T. (1953) A fekete búzalegyekről (Phorbia securis Tiensuu, Ph. penicillifera n.sp.) (Diptera, Anthomyiidae). [The black wheat flies, Phorbia securis Tiensuu, Ph. penicillifera n.sp. (Diptera, Anthomyiidae).] *Ann. Inst. Prot. Plant. Hung.* **6**: 55–86.

JERMY, T. (1953) A raktározott burgonyát pusztító gyászszúnyog (Lycoria modesta Staeg.). Újabb eredmények a szántóföldi növényvédelem terén. [Damage of Lycoria modesta Staeg. in stored potatoes. New results in plant protection.] *Növényvéd. Kut. Int. Kiadv.* **2**: 38–48.

JERMY, T. (1953) Über einige Raupenfliegen der Hyphantria cunea Drury. *Acta Agron. Hung.* **3**: 25–34.

JERMY, T. (1953) Vrednie szovki Vengrii (nabljudenije gg. 1948–1950.). *Acta Agron. Hung.* **3**: 35–56.

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THEMATIC PART

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THE YEARS SPENT BY TIBOR JERMY ACADEMICIAN IN KESZTHELY (1952–1967)

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PRELIMINARIES

The first occurrence of the Colorado potato beetle (*Leptinotarsa decemlineata*) at Hédervár (Győr County) in 1947 gave impetus to zoological research in Hungary. TIBOR JERMY having returned from captivity on 10 July 1947 was commissioned by the Plant Protection Service of the Ministry of Agriculture to investigate the new pest.

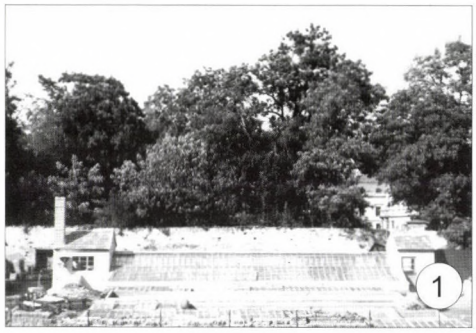
Following its first appearance the pest spread rapidly. At the beginning, it occupied South-Transdanubia, afterward the whole country.

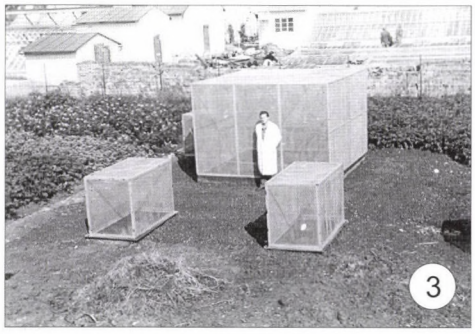
The Zoological Section of the Research Institute of Plant Protection (Budapest) where TIBOR JERMY was nominated for a post in 1949, operated a temporary laboratory in Zalaegerszeg in the summer of 1951 completed with a mobile laboratory mounted on a microbus as suggested and planned by JERMY. With this mobile laboratory the research workers sought out the infested areas and recorded the number of the individuals in different development stages found there. Then they made proposals for the method of control (collecting by hand if the larvae or adults were few; carbon bisulphide (CS_2) to destroy the pupae in the soil; finally, in the case of a large number of larvae and adults dusting or spraying with some pesticide containing DDT or HCH).

THE WORK IN KESZTHELY

The material of the Zalaegerszeg laboratory was transferred on 2 May 1952 to Keszthely, to a glasshouse in the former Festetics garden (Georgikon garden) transformed for entomological purposes (Figs 1–5). In this simple laboratory TIBOR JERMY and GYULA SÁRINGER, for the first time in the world, started investigations on the diapause of *L. decemlineata*.

Making use of the new possibilities offered by the available experimental areas with large numbers of various insect pests, experiments began here. Starting from experience obtained in the course of series of breeding, experimental insect





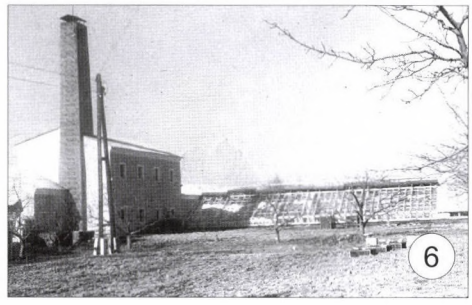


Fig. 1. Temporary greenhouse laboratory in Keszthely in the Georgikon garden (Photo: SÁRINGER, G.)

Fig. 2. Inner space of the temporary greenhouse laboratory (Photo: MÓCZÁR, L.)

Fig. 3. Wire cages for rearing insects in the Georgikon garden (Photo: JERMY, T.)

Fig. 4. Cages for the overwintering of *L. decemlineata* (Photo: JERMY, T.)

Fig. 5. Main building of the new laboratory in Keszthely (Vásártér) (Photo: SÁRINGER, G.)

Fig. 6. A greenhouse of the new laboratory (Photo: SÁRINGER, G.)

ecological research was initiated in Hungary. Compared with the earlier research methods, this meant a real paradigm shift. (On the paradigm see KUHN (1970).)

The glasshouse laboratory in the Georgikon garden functioned until the end of 1957. At a congress held in Moscow in 1954 the socialist countries of that time passed a resolution that the countries infested with *L. decemlineata*, i.e. the German Democratic Republic, Poland and Hungary should establish laboratories specially engaged in *L. decemlineata* research for a specific purpose: results obtained should prevent the dangerous pest from spreading eastward. Those who knew the relevant international literature were fully aware that the eastward invasion of the pest could not be arrested. On JERMY's suggestion the Ministry of Agriculture chose Keszthely as the place where the new laboratory was to be built up, since the Agricultural Academy founded by GYÖRGY FESTETICS in 1797, as well as the West-Transdanubian Agricultural Research Institute also functioned there.

On 2 May 1955 the foundation-stone of the new laboratory was laid in a 4.4 ha mixed orchard at the Vásártér (Keszthely). The ground-plan of building was prepared by ÉVA B. MUELLER, architect, on the basis of JERMY's motions. The building was executed by the State Building Company of Zala County. Owing to the 1956 fight for freedom research work in the new laboratory began only on 9 January 1958. Between 1952 and 1967 TIBOR JERMY worked in the laboratory from early in May to the beginning of September, that is, he spent the growing season in Keszthely. The laboratory was given the name: Keszthely Laboratory of the Research Institute for Plant Protection, Budapest.

The laboratory consisted of 4 work-rooms, 1 photo laboratory, 1 scullery, 3 rooms with controlled temperature, and two 25 × 5 m greenhouses half sunk in the soil, closely attached to the building in west-east direction (Figs 6 and 7). The southern wing of the building was two-storeyed with 2 guest rooms (4 beds) and a shower stall. One of the guest rooms was occupied by TIBOR JERMY and his wife (Fig. 8). For research, it was a great advantage to live next door to the laboratory. In the building, there was a toxicological laboratory opening from outside, where the action of imported pesticides and those produced by domestic factories were studied. The building also contained a room with separate entrance for poisons, a garage and a workshop. At a distance of about 15 m from the building there was a three-room official residence where from 15 October 1956 GYULA SÁRINGER lived with his family.

The controlled temperature rooms were the most valuable rooms of the laboratory. In each room there were 5 so called "photoboxes" adjustable to different day-lengths making the examination of the role of photoperiod possible.

Since the laboratory was surrounded by an orchard, it seemed reasonable for JERMY to examine pests of great economic importance (e.g., *Cydia pomonella*) besides *L. decemlineata*.

The first results of the *L. decemlineata* research were published in 1951 (JERMY 1951). This paper summarized the data of the experiments at Hédervár.

The first summary of *L. decemlineata* investigations carried out in Keszthely is found in the monograph (JERMY & SÁRINGER 1955*a*). This work also contains results of some importance published in the relevant international literature. The work has been translated into German, Polish and Russian as well.

In Keszthely again the diapause of *L. decemlineata* was the first subject we were concerned with. The results are contained in JERMY and SÁRINGER (1956).

According to the data of foreign literature published before the investigations started in Keszthely, it was the senescence of the foliage of potato as a food plant that caused the diapause. At the beginning of August when the foliage of potato began to dry up JERMY fed the young adults with leaves grown from freshly germinated tubers and found that they went into diapause after feeding for 13–14 days. This gave us the idea that something else besides the quality of the food plant was behind the phenomenon. After various possibilities had been taken into consideration, the photoperiod as an abiotic factor remained the only possible reason for beetles entering diapause. The subsequent photoperiod experiments resulted in the above cited paper published in German. At that time it was a conception of so great importance that DE WILDE, J., president of the Holland Royal Academy came to Keszthely and asked me: "when did you realize that the photoperiod was the factor that determined the diapause of *L. decemlineata*?" I answered: "It was in 1952–53. Then you come first, because I found it out only in 1954" – he remarked. However, under the difficult conditions of that time our paper appeared only in 1956. Books and papers on the diapause of *L. decemlineata* have ever since cited the above work.

When the *L. decemlineata* settled finally in Hungary the question of studying the possibility of biological control arose. As the course of development of the pest was known by then, the difficulties of the biological control became clear. Those interested in the subject can find detailed information in the paper JERMY and SÁRINGER (1955*b*).

In the first half of the fifties JERMY's interest turned toward the science of zoocenology. His interest was aroused by the book of BALOGH (1953). Reading the book he made about 50 pages of comments on it and sent them to professor BALOGH, who revised his work accordingly and published it under a new title: Lebensgemeinschaften der Landtiere. Ihre Erforschung unter besonderer Berücksichtigung der zoocönologischen Arbeitsmethoden. Akademie-Verlag, Budapest–Berlin in 1958 on 560 pages. JERMY's thoughts concerning the subject were published in JERMY (1955).

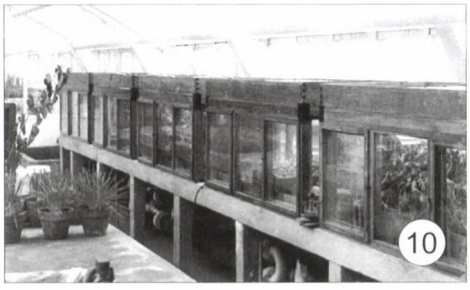


Fig. 7. The new laboratory with official residence as seen from the tower of the Karmelita church (Photo: JERMY, T.)

Fig. 8. TIBOR JERMY and his wife at Héviz (Photo: not known)

Fig. 9. Mass cultures of *Perillus bioculatus* F. on the table of the glasshouse laboratory (Photo: SÁRINGER, G.)

Fig. 10. Mass cultures of *Leptinotarsa decemlineata* SAY on the table of the greenhouse laboratory (Photo: SÁRINGER, G.)

Fig. 11. Some of the numerous foreign visitors (From the left: MANOLACHE, LEBERRE, Ms. JERMY, GHILAROV, BERZSENYI-JANOSITS, CANIA, Ms. DERGOVICS, Ms. SÁRINGER, (Photo: SÁRINGER, G.)

Fig. 12. The laboratory on 17 December, 1977 while cleared (Photo: SÁRINGER, G.)

In the mid-fifties, the cenological view gained ground in the treatment of agricultural zoology subjects too. The paper of JERMY (1956) was written on this subject.

JERMY investigated the zoocenoses from the point of view of production biology as well. The results are summarized in JERMY (1957a).

The *L. decemlineata*, as an animal relatively easy to breed in laboratory, offered opportunity to TIBOR JERMY to set about investigations on the food specialization of insects. He started from the working hypothesis that the relation between an insect pest and its food plant could somehow be disturbed. In experiments carried out with insects he succeeded in inhibiting the effect of stimulants eliciting the feeding reflexes of insects with various substances (e.g., copper compounds, solutions of various alkaloids, sodium tartarate solution). He found out that the resistance to *L. decemlineata* of the different plants could be traced back either to the presence of substances inhibiting the feeding reflexes (e.g., in the case of *Nicandra physaloides*) or to the absence of feeding stimulants (e.g., in the case of *Galinsoga parviflora*). The results are summarized in JERMY (1957*b*). The same subject is treated in the following works: JERMY (1961*a*, 1966), JERMY and MATOLCSY (1967), MATOLCSY *et al.* (1968).

TIBOR JERMY was the first in the world to critically examine the concept of "biological balance". His starting point was that in a given biocenosis this concept could not exactly be defined. His ideas can be read in his paper (JERMY 1957*c*) regrettably published only in Hungarian language.

Of the problems of the production biology of terrestrial biocenoses JERMY gave an account again at the end of the 1950's (JERMY 1958*a*, 1959).

In the late fifties, when hot debates were going on in Hungary between JÁNOS BALOGH professor and GUSZTÁV SZELÉNYI, head of the Department of Zoology of the Plant Protection Institute, on the question of biocenology, was the pioneer work of JERMY and SZELÉNYI (1958) published.

In the same period JERMY summarized his investigations concerning food finding and food choice by *L. decemlineata*, as a result of experiment series carried out in several repetitions in the Keszthely laboratory (JERMY 1958*b*). A paper on the Hungarian food plants of *L. decemlineata* prepared on the basis of exhaustive study by JERMY and SÁRINGER (1959) also appeared in that period.

In the early 1960's further important works gave accounts of JERMY's experiments on the food specialization of insects (JERMY 1961*b, c*).

Pioneer experiments were conducted concerning the orientation of phytophagous insects related with the incidence of the solar radiation. With the aid of a simple swivel chair JERMY pointed out that the *L. decemlineata* always advanced

at a certain angle to the solar ray. In cloudy weather the polarized light helped the insect in orientating. This is the subject of the paper JERMY (1961*d*).

JERMY's investigation on the swarming of insects flying to light, and the realization of his ideas about light-traps came out at the beginning of the 1960's. The first light-trap was set up in 1955 in front of the glasshouse laboratory of the Georgikon Garden (Fig. 1). Seeing the favourable result, he advised setting up light-traps at various sites in the country. The data from this light trapping were worked up in the Hungarian Natural History Museum (Budapest) under the guidance of LAJOS KOVÁCS, lepidopterologist. JERMY's first work on this subject was: JERMY (1961*e*).

On the difficulties of the biological control of *L. decemlineata* we already wrote with TIBOR JERMY a paper at the end of the 1950's. In the same period of time the idea of biological control was again put on the agenda. Prof. Dr. F. M. FRANZ, (Darmstadt) institute leader, brought the carnivorous plant bug *Perillus bioculatus* F. from the USA into Europe. TIBOR JERMY began collaborating with the professor and acquired the bug for the Keszthely laboratory. Egg groups were regularly sent from Darmstadt to Keszthely where they were multiplied (Figs 9–10). The examinations began in 1959. At first, ecological and ethological examinations were carried out. It was found that the bug population placed in the open rapidly dispersed; this showed that the species could be settled only with a large number of individuals placed out. At an international conference held in Czechoslovakia (Smolenice) in September 1962 TIBOR JERMY suggested releasing the larvae obtained from egg groups of *Perillus* bred in the different countries in a single place. Hungary was the country chosen for this purpose, so the egg material came to Keszthely from Belgium, Czechoslovakia, France, Poland, the German Democratic Republic, the German Federal Republic and the Soviet Union. The larvae were released in spring 1964 and 1965 in a severely infected potato field of half of a ha between Keszthely and Fenékpuszta. In the first year 41,831, in the second year 57,633 bug larvae were released. At the site of release and in the neighbourhood not a single overwintered adult was found in the following years. The causes of the prospective failure were indicated by JERMY (JERMY 1962*a*). Further works in this subject are: JERMY (1962*b, c, d*).

Besides the *Perillus* work, TIBOR JERMY started experiments in 1964 with the introduction of *Prospaltella perniciosa* Tower. He thought this parasitoid would be successful against the scale, *Quadraspidiotus perniciosus*, but the experiments gave negative results (JERMY 1967*a*).

From an autoecological point of view, the differences between the temperature at the four cardinal points of the apple-tree are of special importance. The rate of development of *Cydia pomonella* larvae greatly varies according to the side of

the tree where the larvae develop in the apples. The results of the studies on this are contained in the paper JERMY (1964).

Experiments with the sterile male control method, one of the autocide methods, began in the mid-sixties in Hungary. In the Keszthely laboratory, TIBOR JERMY started experiments in this subject with *Cydia pomonella*. The basic condition of the method was the mass production of *C. pomonella* pupae. This required a knowledge of how to stop the diapause of *C. pomonella*. In his experiments JERMY found that the larvae raised under long-day (L:D/17:7) conditions continued developing without diapause. The results of the experiment are found in JERMY (1967*b*).

Besides, the above activities pursued in the Keszthely laboratory TIBOR JERMY was occupied with many minor subjects.

In connection with subjects of higher importance JERMY established contact with many internationally known researcher, European and American scientists of fame visited the laboratory. Some of them even spent months there. Several names from the visitors' book of the laboratory: GHILAROV (1960 Soviet Union), MANOLACHE (1960 Rumania), LABEYRIE (1960 France), SCHWARZ (1961 GDR), ABO-ELGHAR (1963 Egypt), LEBERRE (1964 France), BILIOTTI (1964 France), MOREAU (1964 France) HUBA and JASIČ (1964 Czechoslovakia), SZMIDT (1964 Poland), MOENS (1964 Belgium), OKÁLI (1965 Czechoslovakia), ČAMPRAG (1966 Yugoslavia), CANIA (1967 Poland), BUTT (1971 USA), ALI (1971–74 Egypt), WAHEEB (1973–77 Egypt), HAFEZ (1973 Egypt), YADAR (1972 India), SCHMELZER (1973 GDR), DE WILDE (1973 the Netherlands), WETZEL (1974 GDR) (Fig. 11).

A few words must be said about TIBOR JERMY's working method. He was the one who elaborated the technique of mass breeding for experiments (Fig. 9). The cages and equipments (Fig. 10) required were fabricated under his guidance by the unforgettable jack-of-all-trades GYÖRGY HAJDÚ. Since the beginning, JERMY used statistical methods to evaluate experimental results.

It was in the Keszthely laboratory planned by TIBOR JERMY that the discipline of "experimental insect ecology" came into life in Hungary; it had influence on the research of agricultural entomology all over the country. The results attained in the laboratory led to international appreciation.

I think that for the work in the Keszthely laboratory from 1952 to 1977 TIBOR JERMY deserves permanent credit. The 15 years spent by him always in the laboratory during the growing season will be written in gold letters in the history of agricultural entomology in Hungary.

The Keszthely laboratory planned by him closed down on 31 December 1977 (Fig. 12).

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PERSONAL REMEMBRANCE OF TIBOR JERMY AS A DIRECTOR

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From a perspective of over 30 years, it is not easy to remember those years, months and days when dr. TIBOR JERMY was the director of the Research Institute for Plant Protection under the supervision of the Hungarian Ministry of Agriculture. First, we have to try to go back in time, in terms of our way of thinking, to quite a different era, the so-called 'ancien régime'. At that time, a totally different political system, with other rules, determined our everyday way of life. That era was the period of the construction of socialism and, during that time, directives regarding a centrally planned economy, and the monopolistic role of the Party in the country's politics, had an overwhelming effect on all aspects of life. In fact, 30 or 40 years ago, no one would have dared to think of radical changes of any kind, nor of any real likelihood of Hungary returning to a capitalistic society. No kremlinologists in the United States, nor any historian or policy-maker would have dreamt that, during the early 1990s, the socialistic world system would collapse.

Therefore, it was in 1969, during the time of the construction of socialism and the socialistic transformation of agriculture, that TIBOR JERMY became director of the Research Institute for Plant Protection. The question arises: why did TIBOR JERMY become director? Of course, I do not know – only he could give a reliable answer. However, it seems certain for me that, when GÁBOR UBRIZSY, the academician awarded the Kossuth Prize and then director of the Institute, was dismissed, the responsible authority looked for somebody who would have the necessary professional experience, would be known in the field of plant protection and who might represent, at high level, the plant protection sciences within and outside Hungary. Dr. JERMY was appointed and he accepted the task. It must have been a challenge for him and, in particular, it was important that he continue in the development of this Institute, which already had a good international reputation.

With regard to TIBOR JERMY's activity as a director, the question arises as to whether it was a good strategy to place the burden of complicated and troublesome administration, personnel work (today: human resources) and the labyrinth of Institutional finances on the shoulders of a man who was a researcher to his fingertips. In addition, he had to have a wide knowledge in fields of science other than his own. As director, he had also to follow closely all the manifestations of the party leaders who had complete political control over the country, as well as to consider

the opinions and objections of the trade union. The management also had to deal with such problems as the women's movement, and the youth and the political organisations representing them. Additionally, he had to do the impossible: he had to work out fair wages for something that was not measurable – scientific performance – whilst, at the same time resisting unfair financial demands. And at all times, he had to do all this in such a way as to ensure that he could not be attacked either morally or professionally. This was clearly a significant challenge for director JERMY.

Recalling his period as director thirty years ago, I can safely say that the challenge was met by the right man. Dr. JERMY was director of the Research Institute for Plant Protection between 1969 and 1978 and, as I see it now, it is clear that management was not for him, as he remained a full-time researcher. In retrospect, it appears that he never considered the possibility of stopping his entomological research nor of restricting his tuition of young candidates. At the same time, he purposefully prepared himself to abandon this post on his retirement so that he could return, with all his enthusiasm, to full-time scientific activities.

How could he successfully face this challenge? The answer is in his personality. Though I may be wrong and subjective, I would emphasise the following important factors. Professor JERMY very much loved his scientific vocation and, for him, it was fundamental to share his doubts, to put questions, and to search for answers in biology, in the world of insects and in the complexities of evolution and ethology. For him, being a director could "only" be a part-time job, because he made a conscious return to the scientific world he desired and planned. So, contrary to the ways of many of his contemporaries, management was not a question of prestige. Let us remind ourselves that, should someone have to leave a high position at that time, this would have included a kind of "demotion" or even complete fall from favour.

We know TIBOR JERMY is a modest man. This modesty is reflected in the environment around him, e.g., particularly in his "director's office", which had the simplest but very practical furniture. Of course, the Institute could have afforded some luxury in his office but this was contrary to his personality. Several times, his modesty was noted (of course, not in his eyes) and his colleagues told him that he should put more emphasis on his appearance. At that time, the type, size and colour of the boss's car were very important symbols of authority. You only had to look out of the window when a "big boss" arrived for a visit to know this. Well, these things were of no importance to director JERMY. He considered that the little money available for research should be spent on indispensable matters and the same was true for the trappings of power. We agreed with this attitude but, as a

consequence, our Institute was not the favourite place for visits by the supervisory authority.

Searching in my memory, it is easy to recall another important fact. TIBOR JERMY was fond of order and was very precise. He was very serious about his job as director because he liked the Institute. He knew quite well that there was no direct relationship between scientific performance and the working hours you spent in the Institute. He, nevertheless, expected his colleagues to respect their work place, to like their vocation in spite of the low wages, and to work in the Institute during working hours because of the particular features of our professional field. So, during his era, strict order prevailed in the Institute.

It was not an easy job to be a one-person manager and to try to agree, on a daily basis, with the leaders of the Party, with the trade union and with the youth organisation and to cooperate with the personnel leader. Looking back on those years, I think he did a good job under those conditions, although I suspect that his hairs may have turned increasingly grey at that time.

By that time, the dark years of cold war were already over. Hungary wanted more than just the compulsory relationships with the Eastern block countries and tried to look for contacts towards the West. In our field, this became more and more evident. Nonetheless, in this respect, TIBOR JERMY, with the help of his excellent knowledge of languages, wisdom and human reliability, was again different from many of his contemporaries for, in spite of strongly maintaining scientific co-operation with Western researchers, he never had the slightest thought of neglecting his scientific contacts with Russian-Soviet researchers. There was only one important factor for him in scientific matters: high *scientific value*, and it was therefore just as important for him to know what was being achieved by an excellent Ukrainian or a Russian-Jew as by an American or other Western scientist. I have always greatly highly admired professor JERMY, because he never referred to language barriers, nor (as some researchers do) considered as non-existent research results which were unavailable to him.

I know that he had the courage to support excellent Russian scientists whose significant results were, who knows whether intentionally or not, ignored by the Western world. This showed, in my eyes, that he recognised only one science – neither Hungarian, nor Western, nor Russian, but only that which was called entomology or, in a larger context, biology, ecology, etc.

Director JERMY planned for the future and, as soon as he was 60 years old, he asked for his retirement. Many of his colleagues never noticed a small, narrow "tube office" when they studied the plans for the construction of the laboratories to be built at the Institute near Nagykovácsi. This office was tiny, with just enough room for books, the most important "objects" to director JERMY. Beside the many

comfortable large laboratories and offices, this "tube-office" was also built as designed by professor JERMY, member of the Academy. He had thought that it would be a safe and long lasting work place and that future generations would not envy it. His knowledge of human nature and his wisdom have come true.

Now I want to touch on one of the most important questions. How did the Institute develop while professor JERMY was its director? My older colleagues must remember that the Research Institute for Plant Protection of the 1960s and 1970s differed a lot from that of today. During that time, the Institute had a core of excellent researchers dealing with certain fundamental problems of plant protection. Let me just mention the high quality work done by ZOLTÁN KIRÁLY and his colleagues in phytopathology, by GUSZTÁV SZELÉNYI in cenology, by JÓZSEF VÖRÖS in mycology, by GYULA JOSEPOVITS on the mode of action of fungicides, and by TIBOR JERMY in biological control, insect ethology and the theory of evolution. In addition, and based on long tradition, scientists of the Institute paid much attention to applied research and to the development and evaluation of pest management programmes for pesticide registration, to working out analytical methods for designing new pesticides, to studies on herbicides and mixtures of pesticides, on the economics of plant protection and to practical aspects of farm management and, in general, working out pest management programmes. Much of this work was done under contract with the chemical companies.

In addition to the activities performed in the service of agricultural practice, modern fundamental research was also undertaken at the Institute. However, in the 1970s, great changes took place in both the higher administration and in research on plant protection in Hungary. This was the period of great expansion in the organisational, financial and intellectual life of the Plant Protection Service and its nation-wide organisation. Other research institutes, such as the Institute for Viticulture and Enology and those for Horticulture and Cereal Production, as well as their plant protection sections were greatly improved, while the number of specialists with plant protection degrees has greatly increased.

Director JERMY recognised this changing world and made great efforts to modify the profile of the Institute in relation to the new situation. As a consequence, development and management programmes and servicing activity decreased and so, consequently, the amount of time spent on fundamental research increased. This shift in emphasis to research was of great concern to certain colleagues, whose skill and age were such as to make a change in their career difficult. These changing circumstances also raised another important point. It was necessary for director JERMY to keep good, regular contacts with practices in plant protection and with the official body responsible for plant protection. Thus, he had to establish useful co-operation with the Plant Protection Service and, later, with the

plant protection management within the Ministry of Agriculture. Thus, the leaders of the Institute also took part in the work of the inter-ministerial committee responsible for decision-making in plant protection.

The image of the Institute has also changed. As a result of these changes, the Institute has become integrated into the organisation of the Hungarian Academy of Sciences and has maintained its good reputation within and outside the country. Being an internationally recognised institute of the Hungarian Academy of Sciences, the Research Institute for Plant Protection has survived the shocks of the political changes (which caused major changes to and even the collapse of some non-academic institutes) with relatively little injury.

I really consider that I am totally unqualified to assess TIBOR JERMY's activity as a director and also feel that this insight and remembrance of him is inadequate and incomplete. Nevertheless, I wish to close these few lines by stating that his activity as the director has induced significant, beneficial and lasting changes in the life of the Research Institute for Plant Protection. Even though this position must have been a real challenge for him, I think that he always found a well-balanced solution to each challenge within the framework of the legal possibilities of that time, based on moral directives under the omnipresent political pressure. His only aim was to serve the science of plant protection and to provide good conditions for his fellow scientists to do their research. We have a great deal to thank him for.

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T. JERMY'S CONTRIBUTIONS TO THE FIELD OF BIOLOGICAL CONTROL

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Papers related to the field of biological control make up ca. 10% of TIBOR JERMY's scientific contributions. They date to the period of late 1950s and early 1960s when a renaissance of biological control research started all over the world. The meaning of biological control is used here in its widest sense, i.e., comprising the release of natural enemies and the use of irradiated or otherwise sterilized insects for genetic control purposes.

As research on new ways of pest control has always been on the agenda and specific features of reproductive physiology and feeding habits rendered some insect species more suitable for such purposes than others, many target species have been selected for studies in biological control. Pest species newly introduced to Europe, such as the American fall webworm (*Hyphantria cunea*), and the Colorado potato beetle (*Leptinotarsa decemlineata*) have also stimulated such efforts. The Hungarian Plant Protection Institute has been in charge of implementing new plant protection procedures based on its own research and that adapted from other investigators. Research on one of the promising approaches, the use of sterilized males, was co-ordinated with and partly supported by the International Atomic Energy Agency (IAEA, Vienna). Protocols of techniques were made available and small national projects were financed, thus providing the opportunity for international cooperation and participation in workshops as well as fostering contacts and friendship among scientists.

The success of genetic control in the USA had given an impetus for similar work throughout Europe. Specifically, the sterile insect technique (SIT) held great promise and ambitious programs were started. These programs needed a scientific staff with knowledge in the principles of radioentomology and proper training in dealing with irradiating devices and rearing facilities. Towards this end, TIBOR JERMY obtained training in a radioentomological course held in Florida. With hopes for eradicating serious agricultural pests, the government funded improvements in laboratory instruments and the construction of two insectaries for the Plant Protection Institute. It was at this time (1968) when the Zoology Department, headed by TIBOR JERMY, began a strong scientific development. The prospects for biological control seemed so good that TIBOR JERMY, who became the Director of the Plant Protection Institute in 1969, was given permission by the Ministry of Ag-

riculture to start building a new Institute unit to house the Zoological Department's genetic control programs and insect rearing facilities. The new unit was ca. 9 km distance from the old one, just at the border of Budapest, and was opened in 1973. JERMY not only initiated and organized the construction of the new unit, but greatly influenced the nature of research projects started there. The genetic control projects continued until the late 1970s.

During the period of 1960–1980, there were three major pests considered as subjects of SIT: the European cockchafer (*Melolontha melolontha*), the codling moth (*Cydia pomonella*) and the dry bean weevil (*Acanthoscelides obtectus*). Most of the work on the second species was carried out in the Keszthely laboratories (West Hungary) where occasionally SIT experts from Canada (M. D. PROVERBS) and USA (B. BUTT) – mediated by the IAEA – were also present to help the codling moth project. In addition to reducing the pest populations, the research on all three species provided a wealth of basic biological information. JERMY's own scientific interest and the international trends in biological control were in fortuitous coincidence and at the same time shaped the research profile of the Zoology Department. Besides radioentomological research, JERMY conducted studies on classic biological control by releasing natural enemies. As a summary of the knowledge and experience gained during this period, as well as guidance for future studies, he published the first comprehensive monograph on biological control in Hungarian (JERMY 1967).

INVESTIGATIONS ON NATURAL ENEMIES

JERMY's first investigations on the use of natural enemies were initiated in the 1950s during outbreaks of noctuid moths (*Euxoa* spp.) and the introduced fall webworm (*Hyphantria cunea*). The use of parasitic flies (Tachinidae) against these pests were considered (JERMY 1952, 1953, 1957*a*).

One of the most important pest insects of those times was the Colorado potato beetle (CPB). JERMY started numerous and varied investigations on the species (see also SZENTESI in this volume). Besides ecological and ethological studies, the possibility of using natural enemies against the CPB was also raised (JERMY & SÁRINGER 1955). Through international cooperation embracing mostly Comecon countries from the then communist Eastern Block, a project was launched to assess the potential of *Perillus bioculatus*, a predatory bug species of the CPB. The natural predator was brought in to Europe from the USA. The Keszthely laboratory was selected to coordinate the project because of its previous

research on the CPB (JERMY 1962*a, b, c, d, e*, 1980). TIBOR JERMY and GYULA SÁRINGER lead the efforts to evaluate the impact on the CPB of predatory bugs reared in the neighbouring countries, transferred to and released close to Keszthely in Hungary. The results were disappointing as there was no indication that the natural controlling agent was effective. JERMY evaluated the experiences (JERMY 1962*d, e*, 1967) and his arguments contributed to the abandonment of the project as not being effective. He concluded that the introduced bug was unable to establish a permanent population, partly because it had its own natural enemies.

RESEARCH ON STERILE INSECT TECHNIQUE

During the 1960s, important results were obtained with the SIT against the screw worm (*Cochliomyia hominivorax*) in the USA. As the method seemed economically feasible, similar projects were started worldwide. Hungary also joined in the international trend and at least three species-specific projects were initiated. JERMY took the lion's share of the organizing and research tasks. One of the target species was the cockchafer (JERMY & NAGY 1967*a, b*), another was the apple moth (JERMY 1969, JERMY & NAGY 1969, 1 971), and the third was the dry bean beetle (SZENTESI & JERMY 1973). Discussions about possible solutions to the pest problems and invaluable research information on the biology and ecology of the target species are summarized by JERMY and colleagues (JERMY 1975, 1977, JERMY *et al.* 1978, NAGY & JERMY 1972). Acknowledging the experiences obtained in the SIT, a chapter on autocidal methods was written by Hungarian scientists in the book "Biological Control" edited by the Comecon countries (JERMY & NAGY 1974). This book, originally published in Russian, was subsequently translated into Hungarian (JERMY & NAGY 1975).

TOWARDS INTEGRATED PEST MANAGEMENT

Although the release of natural enemies and SIT programs were of limited success economically (JERMY *et al.* 1976), important biological and ecological knowledge was gathered that helped further the development of theories and even the start of new disciplines. These contributions were summarized by JERMY (1951, 1958, 1969, 1984, 1987). In his important essays on biological balance (JERMY 1957*b*, 1977), he pointed out and explained why, contrary to popular belief, a so-called "balance of nature" did not and would not exist. Another major

contribution was his book on biological control (JERMY 1967) that not only summarized contemporary data and findings, but for the first time, surveyed the history and early literature of Hungarian biological control. Finally, JERMY updated and summarized these concepts in his landmark essay on the meaning and applicability of integrated pest management in Hungary (JERMY 1975).

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INSECT–PLANT RELATIONSHIP – CHANCE AND NECESSITY

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From the early 1920s, Europe was furiously struggling with the invasion of the Colorado potato beetle and then soon took cognisance of its inevitable triumph with resignation. All over Europe, laboratories were established and talented entomologists attempted to discover the "Achilles-heel" of the new pest devastating potato fields and threatening the potato industry.

In 1947, the first scouts of the species were noticed in Western Hungary too. Authorities quickly established a temporary laboratory in the local mansion house at Hédervár and measures were taken to eliminate spots of infestation. The first elementary studies with the species were made by two entomologists who worked while being closely watched by officials of the Hungarian KGB! One of them was TIBOR JERMY.

In spite of the atmosphere of paranoia of those years (the communist authorities insisted that the turn up of the Colorado potato beetle in Hungary was the result of the cover action of the American "war-mongers"), the first connection with the Colorado potato beetle resulted in a lifetime bond and stimulated a research rich in ideas and results. TIBOR JERMY's special and most important scientific field was born then and there. Although he was a tremendously busy writer on very varied topics at that time (see his complete publication list at the end of this volume), important experimental and theoretical achievements were frequently connected with this particular species. The most important results concerning how insects use host plants, including behavioural and developmental observations, were born by studying the Colorado potato beetle. One cannot also dismiss the idea that the conceptual flourishing of later years must have been rooted in those times.

Based on TIBOR JERMY's suggestions and plans, a permanent laboratory was opened in Keszthely (West Hungary) in 1958 where quieter atmosphere and fine colleagues helped him to further deepen knowledge about the Colorado potato beetle, as well as basic biology and autecology of several other insect species. Other entomologists, as well as the papers published from this period, univocally prove that he was full of clever ideas, which then were manifested in very simple experiments. His proverbial patience, and endurance under harsh conditions, led to the production of heaps of notebooks full of results, but these were never published; once knowing the outcome of an experiment he was too eager to carry on with the next, instead of writing yet another paper.

Nevertheless, the first major result of the period was a book about the Colorado potato beetle, co-authored with a close colleague, G. SÁRINGER (JERMY & SÁRINGER 1955). In the book, translated into three languages, but unfortunately not into English, a separate chapter deals with the food plants, feeding behaviour and food consumption of various developmental stadia. In the course of detailed investigations the suitability of solanaceous plant species as potential food or as plants supporting maturation and/or the ability to diapause are evaluated and discussed. A similarly detailed study (JERMY & SÁRINGER 1959) further expands the circle of plant species potentially associated with the species. In addition, the book is the first place where simple, but important methods in studying host-plant relations, such as *leaf-disk* and "*sandwich*"-tests are briefly mentioned.

In spite of the very diverse interests (ranging from the Colorado potato beetle's biological control and sterile male technique to methodology and even to philosophical issues) the central line of TIBOR JERMY's scientific work has been, and still is, the many facets of insect-plant interactions. If one would like to find the major milestones along this road (although admittedly every classification is subjective), one could distinguish three overlapping and intermingling areas:

(1) the food finding process which includes orientation to host- and non-host-plants, including movement on bare soil surfaces

(2) causes of host-plant specialisation of phytophagous insects, including processes of host recognition, the importance of inhibitory stimuli, as well as how experience modifies host-related behaviour

(3) evolutionary considerations and theories of the relationship between phytophagous insects and plants.

All three areas are embedded into a solid behavioural and ecological matrix. [TIBOR JERMY realized the importance of an ethological approach in entomology very early and the use of behaviour-modifying methods in plant protection entomology in particular (JERMY 1971*a*). See other chapters in this volume.]

HOST-PLANT FINDING BY PHYTOPHAGOUS INSECTS

Considering the fast spread of the Colorado potato beetle through the European continent, frequently covering large distances, and the remarkable mobility of adults in agricultural habitats, it was self-evident to raise the questions: (a) how does the Colorado potato beetle find its host-plant, and (b) how accurate is its host-finding?

The observations on long distance migration soon provided evidence that there was no connection with host finding, as arrival to a particular area was a ran-

dom event, and even if it terminated on a host, this fact did not negate the conclusion (JERMY & SÁRINGER 1955). It was a very challenging task to understand whether short distance orientation to (host-) plants was governed by stimuli provided by the plant specific to the relationship with the beetle. Evidently, prime candidates for a clue could be chemical factors emanating from the plant. MCINDOO's (1926) olfactometer experiments and the impetus provided by VINCENT DETHIER's (1947) important book considerably influenced contemporary thinking, allowing much conceptual space for chemical factors. The general ambition to find compounds responsible for spotting a host-plant has not since died out with phytophagous insects and with the Colorado potato beetle in particular, although results are scanty and support only close range effects.

Assuming that beetles orient to host-plants by the sense of smell, JERMY placed young, vigorously feeding adults (starved for one day prior to the experiment) into a wire mesh tube of 3 m long and 10 cm diam. size closed at both ends. The tube was lying on the soil surface so that one half of its length was among potato plants and the other half on bare ground. The hypothesis was that the beetles would gather at the tube-end placed under the plants. The result was, however, different. The beetles occupied no preferred site and distributed themselves everywhere within the tube. Laboratory tests strengthened these results (JERMY 1954–1956). JERMY not only hinted at his scepticism regarding olfaction-based host-finding for walking and especially for flying insects (JERMY 1954–1956, JERMY & SÁRINGER 1955), but as a corollary of observations he collected, he began experiments on the orientation to host-plant of the Colorado potato beetle. Using SANCHI's mirror test and in numerous additional ingenious ways he proved (JERMY 1958, 1961a) that keeping directionality by the sun-compass orientation was the most profitable way for walking beetles to encounter a host. Keeping a more or less straight path decreases the likelihood of circular movement in a place. He had also made suggestions for the possible involvement of polarized light and the silhouettes of plants in the orientation of the Colorado potato beetle. His conclusion was that host finding in the beetle was a chance event and the directional movement on bare soil surface or among vegetation provide the highest probability of meeting a potato plant. Upon encountering vegetation numerous contacts are made with individual plants. Thus, close examination and/or possible short-distance olfactory orientation help identify food.

When reading TIBOR JERMY's papers on this and other subjects one is amazed by the humble simplicity, yet nevertheless strict "Ockhamian logic" of his experiments and conclusions. In addition, from the early works on with insects he noted the high level of inefficiency of (mostly behavioural) functions that phytophagous insects demonstrate, e.g., in host finding. He gradually deepened the idea

that stochastic processes are an important part of insect functioning from genetic to phenotypic levels equally. One can easily agree with him in the importance of accidental events after watching a hungry Colorado potato beetle passing a potato stem within 5 cm. Or recognising that large numbers of eggs, laid by the Colorado potato beetle females, can be collected from totally unsuitable plant species or from objects in a potato stand. There is absolutely no chance for the young larvae to get to the nearby host-plants from these substrates. Then how adaptive is egg-laying with the Colorado potato beetle? These and yet other similar experiences led him to oppose that each phenotypic character is necessarily adaptive.

The conclusions formed from the results of the works on orientation were a guideline for JERMY's understanding of this fundamental step in host finding. Still he re-initiated similar studies in the mid-1980s to obtain results that are even more convincing. The orientation topic was upset by contradictory results from elsewhere and most importantly by the uncritical acceptance and generalisation of results from papers methodologically flowed. The unproven importance of olfactory guidance to the host-plant was still the dogmatic idea in the field of plant-insect interactions, although experiments showed orientation by chemical cues for half a meter at most, in the case of the Colorado potato beetle. The new experiments (JERMY *et al.* 1988) corroborated JERMY's former findings and conclusions. Whereas his earlier works were a collection of observational and experimental mosaics, this study was well planned and coherent enough to serve as a proof of the hypothesis. A "leptodrome" was formed [named by him with a good deal of humour after the ancient circus-arena combined with the genus name (*Leptinotarsa*) of the Colorado beetle] where day-after-day hundreds of adults were allowed to walk towards plants and silhouettes in most varied experimental situations. There were exceedingly hot days also when the temperature put to the test observers and animals alike.

In the results again, a strong directionality showed up with walking beetles that was based on photo-menotaxis, whereas a high turning rate became prevalent once the beetles arrived at a host-plant stand. However, host odour and visual input were not effective from distance greater than 40 cm. Therefore, not only is arrival at a host-plant stand accidental (we do not know of any influential visual factor specific to the potato foliage), but finding a particular host individual in a non-host matrix must also be so.

HOST SPECIALISATION OF PHYTOPHAGOUS INSECTS

Although host finding, recognition, acceptance, rejection of a plant, initiation and maintenance of feeding, and oviposition site selection mean very different actions, they have one thing in common, namely that each represents an event for which inputs are conveyed at the behavioural level. This is an important condition at this level of resolution, although it is assumed that physiological feedback, e.g., experience modifies behaviour.

From experiments with the Colorado potato beetle, it was clear (and it was outlined several times, e.g., in JERMY 1983, 1993) that host-specificity is a behavioural phenomenon and can be influenced and modified also at this level. The realisation gave him possibilities to conduct research in two major directions: (1) conceptual questions of food selection, and (2) practical use of the knowledge so obtained. The first gave him an opportunity to review and re-evaluate dominant theories of food selection and to develop his own idea named the two-way, or as more frequently used later, the asymmetric specialisation of chemoreceptors. The second provided a viable opportunity, attractive to many scientists, to demonstrate the power and usefulness of a scientific idea for the society. [The latter point was a built-in imperative in the Hungarian society at that time, however, flavoured with a schizophrenic thinking, i.e., impeding the realisation of the same idea by all means! This is how science earned a scornfully created picture of uselessness as opposed to values of plain physical work.] The experience that many/most substances present in plants are capable of interfering with or stopping the normal process of feeding has led to the recognition of potential use of *feeding inhibitors*. The idea was not totally new but it did receive very strong support from his experiments.

Stimuli governing host selection

In order to get closer to substances governing host acceptance or rejection three methods were applied (JERMY 1954–1956):

- spraying potato leaves with a substance then cutting out leaf-disks,
- vacuum infiltrating of substances into potato leaf-disks,
- "sandwich test", for which among two potato leaf-disks a third, the test-plant disk, was pasted.

The usual arrangement of disks for such a test was checkerboard-type or circular, alternating with control disks. Several young and hungry beetles were placed in a dish containing the disks. The most important results were (JERMY 1954–1956, 1958, 1961*b*):

- 1% Bordeaux mixture (a complex compound containing Cu^{2+} ions) sprayed on potato disks inhibited feeding,
- potato disks infiltrated with leaf-sap of the solanaceous plant species *Nicandra physaloides* or the opposite, *Nicandra* disks with potato leaf-sap, were not consumed by the beetles. Thus, *Nicandra* contained compounds capable of masking positive feeding stimuli of potato. Similar effects were experienced when pure alkaloids were used instead of plant saps,
- by the sandwich test the sphere of plant species inhibiting feeding of potato beetles to different extents could be mapped. He named the figure representing the preference distribution of plants the "triangle of food preferences" (see figure in JERMY 1961*c*). The plant species could be grouped into three categories corresponding to the DE BOER and HANSON's (1984) classification: (1) host-plants, (2) acceptable non-hosts, and (3) unacceptable non-hosts. The first had feeding stimulants, but no deterrents, the second group contained neither stimulants, nor deterrents, and the third one was dominated by deterrent substances.

Soon extensive laboratory experiments were carried out (JERMY 1961*b*, c) to find our more about the array of substances, mostly inorganic compounds, capable of influencing feeding of the potato beetle. Besides testing several cations (Cu^{2+}, Mg^{2+}, Fe^{2+}, Na^{+} and Ba^{2+}) on feeding, effects of these were also tried out on oviposition behaviour and larval mortality. It turned out that with the exception of Cu^{2+}, other ions did not affect feeding. The copper compound caused a decrease in feeding, and therefore – due to malnutrition of females – egg-maturation depression and lower number of eggs laid, as well as a high level of mortality of young larvae through the process of starvation. Cu^{2+} application on potato foliage resulted in emigration of mobile stadia, mortality of young larvae and decreased egg laying, adding up to a considerable population dynamic effect.

These observations and experiments not only prepared the bases of practical application of feeding deterrents (see following section), but also deeply influenced further development of the food specialisation concept of TIBOR JERMY.

The attempt to form a theory of food specialisation based on the significance of negative (inhibitory) stimuli first evaluated the existing concepts from a historical perspective (JERMY 1961*d*, 1966, 1972). As relatively more information was available on stimulating substances, the prevalence of (1) *phagostimulatory* concept was inevitable [represented by such authors as LANGERHEIM (1900), VERSCHAFFELT (1910), and THORSTEINSON (1960)] holding the view that food specialisation of phytophagous species is basically determined by the botanical distribution of specific phagostimulants and attractants. Opposing it, DETHIER (1954),

HARLEY and THORSTEINSON (1967) developed the (2) *inhibition* theory, which considered the importance of inhibitory substances in shaping the host-range of polyphagous insects. The last one (3) named *symmetric two-way specialisation* concept was formed on the bases of presence and/or absence of both types of compounds (LIPKE & FRAENKEL (1956)). A modification of the latter is the (4) *asymmetric two-way specialisation*, which can be attributed to TIBOR JERMY's experience gained with inhibitory compounds on oligophagous species (mostly on the Colorado potato beetle). This theory declared that although specialisation depended on the ratio of both positive and negative compounds, it occurred in an asymmetric way, i.e., inhibitory stimuli would always be more powerful and able to block feeding even on the optimal host once applied on it. Secondary plant substances participate in both roles. Stimulatory compounds become sign (token) stimuli for some groups of oligophagous insects indicating proper host.

His arguments ran in this way:

- many oligophagous species can be maintained on diets not containing specific phagostimulatory substances,
- increasing food specialisation results in increased sensitivity to inhibitory substances,
- the two types of stimuli is in an asymmetric relationship,
- most stimulatory substances prove to be simple (primary) plant compounds, which means a limited botanical specificity,
- more inhibitory receptor cells are known than stimulatory ones.

The same concept of asymmetric importance of inhibitory substances was later extended to the then (and unfortunately today also) less known *oviposition* specialisation (JERMY 1965, MUSCHINEK *et al.* 1976, JERMY & SZENTESI 1978) with some reservations. One was the relative autonomy of receptors situated on the ovipositor. They most probably are subordinate to the ones on the palps/antennae. Second, the range of hosts selected by ovipositing insects seemed to be narrower than that of the ones suitable for larval development, at least in some insect species. It is tempting to note that the theory places two basic important behavioural processes into a unified frame.

Simple experimental arrangements, yet an outstanding ability to see much deeper and further than the actual work's periphery, lend the scientific merits to one of his best acknowledged and cited paper (cited well over 100 times) written with professors FRANK HANSON and Vincent DETHIER (JERMY *et al.* 1968). Prior to this paper, JERMY had made one preceding attempt to demonstrate long lasting effects of host plants on the subsequent food choice (JERMY 1961*c*). He fed 4 larval groups of the Colorado potato beetles to adulthood with tomato and potato leaves in an experimental arrangement (Table 1), and following metamorphosis he tested

Table 1. The effect of larval nutrition on the host selection of young adults (JERMY (1961)). (Number of replicates = 10)

Group	Larval nutrition	Acceptability of tomato leaves to young adults (mean and standard error)
1	L1–L4 tomato leaves	21.1±6.5
2	L1–L2 tomato leaves	
	L3–L4 potato leaves	27.8±12.3
3	L1–L2 potato leaves	
	L3–L4 tomato leaves	8.9±3.9
4	L1–L4 potato leaves	7.9±3.5

the resulting beetles on tomato leaves. Larval feeding had no influence on subsequent host selection of the adults (the difference were not significant), although there was a tendency for accepting tomato at adult stage if larvae had been raised on it either throughout the larval development or during L1 and L2. He called the effect *conditioning* clearly referring to central nervous system processes that would last and be retained through time, as well as substantial physiological changes. Whether the inability to condition the Colorado potato beetle is connected with its oligophagy remains to be demonstrated.

Behavioural observations have always been and still are one of JERMY's most important tools for understanding processes at a given level of complexity. (Among others, the title of his academic doctorate dissertation proves this: "Ethology of food specialisation of phytophagous insects".) In the paper mentioned above (JERMY *et al.* 1968), the authors studied the induction of specific food preferences and demonstrated that in some insect species experience with a given acceptable host plant in a larval stage would generate a long-lasting preference for that food. The induction of preference can be evidenced by choice experiments in later larval stages. Although the phenomenon did not fit into any then known learning processes, its connection with central nervous system events was not denied. It resulted in a narrowing-down of the potential host-range, a sort of "tunnel-vision", sometimes so rigidly formed that larvae died of starvation than accepting any of the alternative host-plants. The many facets of the phenomenon they investigated generated a wealth of further intriguing questions and this paper remained, perhaps, one of the most interesting scientific topics of the field. Extending the area of experience-modified behaviours into the host selection of phytophagous insects TIBOR JERMY reviewed the main phenomena in a succinct paper (JERMY 1987*a*) published in a book dedicated to VINCENT DETHIER's 70th birthday. This paper discusses the occurrence of and the behaviours involved in the factors influencing the induction process, as well as oviposition induction, habituation to deterrents

and food aversion learning. For the first time it also treats *adaptive significance* of the above-mentioned phenomena. He states that the adaptive advantage of aversion learning and habituation is obvious, as the former prevents consuming deleterious amount of poisonous food, and the second allows utilising unusual, nevertheless still suitable food. It is more difficult to explain the adaptive significance of induced preference. Among the lots of assumptions none is adequate, if one considers the narrowing of food specialisation which is the core event of induction.

The practical use of antifeedants

Steps for practical approaches to utilising information gained about food specialisation soon brought successes. Many reports based on experiments under laboratory conditions (and less frequently performed in the fields) proved the feasibility of application of feeding inhibitors against pests. These were mostly empirical achievements and they supported TIBOR JERMY's asymmetric specialisation theory nicely, though inadvertently. By cooperating with chemists (JERMY & MATOLCSY 1967, MATOLCSY *et al.* 1968, JERMY *et al.* 1981) a wealth of very different compounds showed remarkable inhibitory effects on many phytophagous pest species.

Today it seems that there were basically two types of approach to get efficient antifeedants at that time: (a) testing natural plant substances or synthetics ("sweeping down shelves in chemical laboratories"), and (b) planned selection of structurally related compounds (or designing structures) to catch correlation between phagostimulatory effect and molecular structure. However, only limited successes of the second approach are known, e.g., SZURDOKI *et al.* (1991). None of the ways has given a happy solution for several reasons. Without attempting to list all reasons, JERMY (1971*b*, 1990) highlighted two important ones: (1) it can be *a priori* predicted that a great variety of compounds would play inhibitory roles for any insect species, and (2) it is not likely that one will find a universal antifeedant, active on all insect species.

It was very timely at this point (end of 1970s) to unite two methodologies and attempt to give answers to such questions: (a) whether *behavioural* and *electrophysiological* approaches corroborate each other's findings considering actions of antifeedants, and (b) how, and how widely, inhibitory effects are represented at the receptor level? Of the two approaches (SCHOONHOVEN & JERMY 1977), no doubt, electrophysiology was the younger, and therefore, could hopefully provide different insights. Feeding deterrents could act on the sensory system either by stimulating specialised deterrent receptor cells, or modifying the activity of cells reacting to stimulants. There were some deterrent receptor cells known with a few insect

species, however, no coherent picture of their response range could be formed. The alternative mode of action seemed equally plausible, but even more complex. For instance, although feeding deterrent action of Cu^{2+} ions has been proven behaviourally with the Colorado potato beetle several times, no receptor response could be found. A better understanding of how receptor information is interpreted in the central nervous system of insects would help substantially in conceiving other phenomena accompanying application of feeding deterrents.

One such behaviour-level representation of deterrent-effect was the clear distinction of central excitatory state from *central inhibitory state* (CIS, JERMY 1971*b*). The CIS was evoked by the presence of deterrent, and its decay-time, as well as events accompanying it depended on the type and concentration of substance and on the insect species. The results of a CIS elicited by Cu^{2+} ions with Colorado potato beetle larvae was manifested in cessation of feeding for as long as 30 min, slow backing or total freezing, vomiting then walking away from the site.

As with insecticides, the question of adaptation to and resistance against feeding inhibitors had inevitably to be raised (JERMY 1971*b*, 1983). Considering the low probability of correlated changes in chemoreceptor function and behavioural responses, TIBOR JERMY concluded that it must be an unlikely event. One of the factors he (JERMY 1983) emphasized was the immense diversity of compounds providing an "inhibitory biochemical profile" in plants that would make even less probable adaptive changes at both receptor and behavioural levels. Nevertheless, the possibility of *habituation* to deterrents, as distinct from receptor adaptation, was duly discussed and experimentally demonstrated (SCHOONHOVEN & JERMY 1977). Larvae of at least two oligophagous insect species, *Leptinotarsa decemlineata*, and *Pieris brassicae*, did not decrease "feeding pauses" during repeated presentations of feeding deterrents. However, as information was limited on habituation regarding species number, food specialisation and substances, LIZ BERNAYS and TIBOR JERMY, during the time of a Nairobi conference, agreed on starting an in-depth research into habituation to feeding deterrents. The useful cooperation resulted in a wider perspective about the phenomenon, among others, in obtaining evidence through complicated testing procedures that habituation to feeding deterrents was a more likely event with polyphagous insect species (JERMY *et al.* 1982). Later experiments using a more natural approach, using plant leaves instead of pure and single chemicals with a polyphagous insect species, *Mamestra brassicae*, provided a more sophisticated picture that was difficult to explain (JERMY *et al.* 1987). Nevertheless, the results seemed to strengthen the earlier assumption (JERMY 1983) that insects might be less prone to habituate to the multitude of chemicals present in live plant tissues.

EVOLUTIONARY QUESTIONS OF INSECT PLANT RELATIONSHIPS

Studies of the evolutionary questions of insect plant relationships were a natural consequence of studies on food specialisation. The earliest written version where TIBOR JERMY addresses such questions of insect-plant relationship is a text of oral presentation given in Wageningen (The Netherlands) in 1971 (JERMY 1971*c*). It is obvious that he knew EHRLICH and RAVEN's (1964) paper by that time, as he refers to it. However, it is remarkable that he detected similar thoughts on evolution (although not named coevolution or meaning reciprocity) with DETHIER (1954) who besides his own treatments referred to PAINTER (1951). JERMY's own idea for the evolution of the relationship is also named differently in comparison with later versions. However, the logic and argument of subsequent papers were already present. The fallacy of the main premise of coevolutionary relations according to which congruent phyletic lines among plants and insects are the dominant case was also clearly stated here. He listed all major important insect-plant relations too, and argued that the other points of the coevolutionary theory, such as competition among phytophagous insects and the role of secondary plant substances also fail to stand firm. The idea of "subsequent evolution" then described and its cardinal theses are listed in eight points. Reading these points one can only conclude with considerable surprise that the core arguments are almost as complete as in the later published versions, although not presented in a as eloquent, elegant and elaborated way as in later papers.

Over the years, the critique of coevolutionary theory between plants and insects became increasingly refined and elaborated (JERMY 1976, 1984*a, b,* 1991, 1993, 1994, JERMY *et al.* 1990). The essence of the two theories is this: the driving force behind coevolution is the *reciprocal* selective response of (usually) two participants, the plants and insects. Insects exert selective pressure on plants by feeding and forcing them to change, most of all, biochemically. The altered plants, released from the herbivore pressure, however, will soon be recolonised by the adapted insect species once again capable of utilising the new plant species. Then the cycle repeats (EHRLICH & RAVEN 1964). The theory opposing the above scenario (JERMY 1976 and further) is that of *sequential* evolution, which states that, plants change biochemically for reasons other than herbivore pressure, such as climatic, soil, or competitive elements. These changes free them from herbivory momentarily, however, the altered plants will be followed by those insects whose genetic variability were fortunate enough to have mutations from which selection would pick up those capable of utilising the new plant lineage. In other words,

whereas insects do not select new plant lineages, plants select for those of insects' sequentially. This makes the relationship basically asymmetric.

Since the propounding of insect-plant coevolutionary theory, at least two other theories emerged modifying the basic tenets to some extent. The *diffuse coevolution* (VAN VALEN 1973) or *community coevolution* implies that all members of a community affect each other's evolution. The *geographic mosaic theory of coevolution* (THOMPSON 1994) assumes that, due to differences in outcome of interspecific interactions, the nature of relationships can alter through time, space and strength. This creates a mosaic of relationships where levels of intimacy may dynamically change along environmental gradients between the endpoints of mutualism-antagonism.

JERMY gives a very detailed and comprehensive criticism of these and related ideas in SCHOONHOVEN *et al.* (1998). Several factors such as the problem of competition among phytophagous insects, evolution of stenophagy, the importance of attack by herbivores and defence (resistance) by plants in the evolution of the relationship, the palaeobotanical and palaeoentomological evidence, alternative hypotheses of oligophagy, the role of secondary plant substances, the reasons for the overdominance of specialized phytophagous species, etc. make the relationship extremely complex. JERMY treats them one-by-one in various papers and to different extents.

One or perhaps the critical point in insect-plant evolutionary considerations is the explanation for the preponderance of specialisation of herbivorous insects (assumed to be at 75–80% of all plant feeding species). According to the co-evolutionary hypothesis, host specialisation is a natural consequence of the coevolutionary process as it promotes niche segregation and decreases interspecific competition. It is also correlated with several environmental and developmental factors (BERNAYS & CHAPMAN 1994). JERMY (1976, 1984*a*, 1985) has long been dealing with the importance of interspecific competition among herbivorous insects, among others devoted an entire paper to it (JERMY 1985). His major arguments are based on

- the "conspicuous rarity" of most phytophagous insects;
- the almost unlimited availability of plant material as a resource;
- the importance of plant phenology, its patchy distribution, and the specific preference of herbivorous insects for particular plant parts which all contribute to decreased trophic competition;
- the weakness of "evidence" such as "competition past".

He concluded that interspecific competition was of minor importance in driving evolution of stenophagy. Alternative theories, such as the enemy-free space hypothesis (BERNAYS & GRAHAM 1988 and others) according to which specialisa-

tion in host preference could be the result of predation pressure from generalist predators, seemed also less likely to him (JERMY 1988, 1993, 1994).

In contrast, JERMY (1971*c*) clearly states that evolutionary changes in host specificity are the result of hereditary changes. In later works, (e.g., JERMY 1993) he emphasizes that it happens as an *autonomous* evolutionary event. JERMY *et al.* (1990) expounded that stenophagy is more frequent than the polyphagous strategy because (1) it reflects the relatively higher rates of speciation and extinction among oligophages, (2) it indicates the evolutionary irreversibility of specialisation (specialists evolve specialists), and (3) it refers to some constraints on the evolution of the insect nervous system.

Most treatments of plant-pollinator systems take for granted that such a relationship can only be the result of reciprocal mutualism. In fact, apart from some very specific cases, such as e.g., fig and fig-wasp mutualism, the overwhelming majority of pollination relationships, as pointed out by JERMY (pers. comm.), SCHOONHOVEN *et al.* (1998) and others, are asymmetric, i.e., it is accompanied by morphological changes only on the plant's side, whereas plants hardly influence evolution of pollinators. In a recent debate over the question of what factors influenced the evolution of the long tongue of hawk moths, and in particular, of *Xanthopan morgani praedicta*, the Malagasy hawk-moth, JERMY (1999 and see references there) again stressed that there was no mutual dependence between the moth and its orchid (*Angraecum sesquipedale*) partner. The long tongue does not imply exclusive specificity for the orchid as shallow flowers are also visited, and long-tongued hawk-moth species are frequent in geographic regions where deep flowers are rare. Thus, the long tongue might be an ancient character, a result of genetic changes of hawk-moth speciation, which can also question its adaptive significance. It seems that the evolutionary relationship between the orchid and its assumed pollinator is one-sided meaning adaptation to the long tongue and not *vice versa*.

Although adaptation is an important element of the evolutionary process, it often creates traps for the evolutionary thinking too (GOULD & LEWONTIN 1979). For instance, JERMY (1987) concluded that induced preference is *nonadaptive* and "...may simply reflect the limited flexibility of the insects' neural systems which might even reduce fitness in certain ecological situations" (p. 154). It is the 1971 Wageningen lecture (JERMY 1971*c*) which is the first in the series of evolutionary papers that explicitly criticises our inability to get rid of deterministic thinking invoking adaptationism. The sceptical remarks about Nature as being a great destroyer and only a feeble creator, so characteristic of his later papers and discussions also pop up here for the first time: "...evolution is a domino play with the genetic code." (p. 5.) We should, instead, accept Nature where chance events domi-

nate over deterministic ones (JERMY 1998) with many unpredictable and unpurposive events. The sources from where he received support in form of analogous thinking and strengthened his own sceptic view of Nature, and specifically of adaptive evolutionary processes, are the works of two great French scientists, MONOD (1972) and JACOB (1981). JERMY's approach is not enforcing one's imaginations upon Nature, but instead assembling seemingly unrelated facts collected by quiet contemplation. It is aptly described by a sentence of his inauguration speech (JERMY 1987*b*) that he delivered on the occasion of his election as a member of the Hungarian Academy of Sciences:

> "*Scientific mentality vigorously resists accepting that Nature is like an engineering product masterminded with mathematical accuracy; instead, it is similar to an artistic object created by evolution with rambling fantasy and largely by random processes. For Man, it is an arduous task to decipher the causality of phenomena; yet, it is Nature's* random *character that may offer so much aesthetic pleasure for the contemplating Man.*" (p. 38, emphasis from the translator.)

POSTSCRIPT

The author of the present account only wanted to be a humble chronicler of a slice of a prosperous scientific life and by no means an evaluator or a critic of TIBOR JERMY's or others' ideas. This should be done by a scientist adequate to the task. All along during TIBOR JERMY's life the classic "one-against-all"-type game has been and still is played. It is still being played at his age of 85. From the most authentic source, from TIBOR JERMY himself, the author knows that he is preparing an even more comprehensive treatise of his evolutionary thoughts in his usual "devil's advocate" manner. This again, there is no doubt, will be fuelling new debates. It is a further personal remark of the author that, although he has tried it, he probably failed to get rid of subjectivism due to the fact that he spent 30 years – it was his good fortune – with TIBOR JERMY sharing his views.

*

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TIBOR JERMY, FOUNDER OF RESEARCHES IN AGRO-ECOSYSTEMS IN HUNGARY*

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Late summer in 1975, an enthusiastic group of specialists, led by Dr. TIBOR JERMY, member of the Hungarian Academy of Sciences, visited the sand-dunes of the Nyírség region. The specialists worked at the Research Institute for Plant Protection of the Hungarian Academy of Sciences (HAS), the Plant Protection and Agrochemistry Centre of the Ministry of Agriculture and Food, the Plant Protection and Agrochemistry Station of county Szabolcs-Szatmár, the Újfehértó Experimental Station of the Research and Development Institute for Fruit Growing and Ornamentals, the Training Farm of the College of Agriculture at Nyíregyháza. Their objective was to find apple orchards of various sizes and with different production practices which would allow them to make regular and reliable detections as well as multiple studies meeting the requirements of agro-ecosystem researches for at least 10 years.

Following the survey in the Nyírség region, we selected 4 areas of different types in this apple growing district: small plots untreated for several years (0.2 ha), treated home gardens (0.5 ha), conventional commercial orchards (5 ha) and intensive large-scale apple fields (100 ha). In addition, there was the 5.8 ha apple orchard in the vicinity of a woodland, belonging to the Research Institute for Plant Protection of the HAS in county Pest: it was split into a treated and an untreated part.

Similar survey preceded the selection of fields in the maize growing area of Mezőföld where researches on maize grown in monoculture and in crop rotation could start thanks to the leaders of the Agricultural Holding of Agárd and the Cooperative Farm of Kápolnásnyék. Of course, these surveys and selection of areas were preceded by several activities, the most important being that Dr. JERMY had reacted, with good sense and in due time, to the challenges of the era. He knew that a thorough ecological study of the agricultural areas was needed and justified, because, on the one hand, over 70% of the country was under agricultural cultivation and, on the other hand, the ecological effects of the new methods used in agricultural production were not known at all. We had not studied and understood the ef-

* As a sign of respect, by a short presentation of results, collaborators of the agro-ecosystem projects greet TIBOR JERMY on the occasion of his 85th birthday.

fects, on the communities of the agricultural areas, of new management programmes (i.e., monocultural production on large growing areas, intensive nutrition, mechanisation, chemical pest control, etc.) of the production systems introduced and operated in compliance with the social and economic philosophy of the period, however such knowledge and information were necessary to work out, then to apply the new production methods which seemed to be optimal both economically and environmentally.

TIBOR JERMY not only recognised that no modern agricultural production could exist without the exhaustive knowledge of conditions prevailing in the agro-ecosystems, but he also convinced the professional public of its necessity and importance. Following his proposal, the Committee on Zoology and the Committee on Plant Protection of the HAS initiated an overall ecological exploration of the agro-ecosystems of the two major crops grown in Hungary, i.e., winter apple and maize. The programme coordinated by the Research Institute for Plant Protection was completed between 1976 and 1985, financed by the Central Research Funds of the HAS.

He personally worded the most important objectives of the programme stating that people could only make use of the essential elements of the ecosystem for the purpose of modern agriculture if they knew well the conditions of the landscape altered by human interventions. For this, the structure, the species composition (if possible) of the agro-ecosystems, the system of relationship among the pest populations and the conditions of population dynamics had to be explored. Furthermore, the mechanisms regulating the agricultural areas, the ecological problems of changes in the sector and the possibilities of sustainability had to be studied.

It was clear at the very beginning of the programme that a close working cooperation among specialists of biology, zoology, taxonomy, plant protection, botany, ecology and plant production had to be established for several years. Following the convincing arguments by TIBOR JERMY, several institutions, research groups and specialists of the country joined the programme and participated in its effective implementation.

In order to completely explore the living associations of agricultural areas, several methods for investigation and collection were used: light traps, suction traps, soil traps, yellow plates, sexual pheromone traps, traps for arthropods walking on the twigs and trunks, mash traps, gleaning, beating, sweep-netting, individual plant inspecting, mite brushing, placing out nesting boxes for birds, fixing corrugated cardboards on trunks, and extracting specimens from the gathered materials by various means. Catches were removed daily (light traps) and weekly, while the various surveys were made weekly or biweekly from April to the end of October.

The results of this research confirmed that a much higher number of animal species lived on the agricultural area than it had ever been imagined. It was found that the agricultural areas in Hungary and even the plantations under intensive cultivation do not belong to the notion of "cultural desert".

As many as 1759 animal species were identified in the apple plantations, twice as much as OATMAN identified on the apple growing areas of the USA in 1964. The number of species living in apple orchards decreased with increase in the intensity of crop production and plant protection, although the number was nevertheless very significant (467 species) on the more intensively cultivated areas. A similar trend was found in the density of pest species with density being highest in the untreated scattered areas and gradually decreasing with increase in the size of the area and the intensity of the cultivation. On the contrary, some insects (e.g., leaf miners) reached their highest population density under the most intensive cultivation, but the number of the pest species then significantly decreased.

The presence of 582 species was detected in maize fields. It was found that no great difference existed in either the number of species or the population density between maize plants grown in monoculture or in crop rotation. The monoculture induced neither reduction in the fauna nor great increase of the insect population inhibiting plant production. The observations and the studied relationship are of great importance, because no similar work had ever been done before.

On the basis of these studies it was concluded that the establishment of and changes in the composition of species in the agro-ecosystems were primarily influenced by human activity, more precisely by the impact of the plant protection programmes and other methods used in the plantations. The effects of weather and environmental conditions were only secondary. We demonstrated that only a small proportion of the species (2.1–4.4%) living in a particular area consisted of harmful organisms. On the other hand, the density of potential pests was much higher, capable even of being 25% of the identified fauna. The typical annual agricultural crops (field crops) and their vicinity were much poorer than the more diversified biotopes of the several-decade-old apple orchards and their environment. Under more natural conditions with minor direct influence of the human factors, the weather, the environment and the natural elements (parasitoids, predators) were the most significant population regulating factors.

It was confirmed at the same time that large populations of several species of beneficial insects prevailed on the agricultural areas, even in the regions with intensive cultivation. The possibilities offered by them were recognised in the very first years of research. We started to investigate the host-parasitoid relationship (leaf rollers, leaf miners, chalcidoid wasps, braconid wasps, etc.), the host-predator relationship (spider mites – predatory mites, aphids – lacewings, *Stethorus* species,

syrphids, etc.) and the role of parasitoids in the population dynamics of the pests. Relative equilibrium established under natural conditions (e.g., in patchily distributed untreated apple plantations). There was a greater balance in the number of phytophagous and zoophagous species. But, the characteristic of areas with intensive cultivation was that certain pest species were completely eliminated (e.g., leaf rollers with one generation), or reduced to an insignificant density (e.g., codling moth, San José scale), while other species had an increased population density (e.g., leaf miners). In these situations, the increase in the population density of a particular pest might create advantageous conditions for the increase of the parasitoids to such an extent that they became an important factor in regulating the population. Thus, a relative balance was created and maintained until a new harmful effect was generated for the ecosystem.

We found in our investigations that the aerial zooplanktons, being independent of the production conditions, had a great role in both populating the agricultural areas and establishing the insect associations. Chemical treatments focusing on the fields or the plantations had no or only slight effect on this aerial fauna, and therefore the original situation is rapidly recreated following the chemical interventions. This introduction and establishment increased the diversity of species on the area and had advantageous impact on the biocenosis as only certain elements of the species were harmful. These facts confirmed the opinion that the agro-ecosystems and the natural ones had close relationship with each other.

We studied the relationship between the agro-ecosystems and the natural ecosystems. The role of the environment was equally very important for ruderal, woodland ecosystems and in orchard ecosystems. It was noticed that the spatial establishment of the pests and their parasitoids originated in the more diverse environment. The direction of their introduction was, therefore, not constant, depending mostly on the position and vicinity of the plantations. That of the leaf miners was of one direction and spreading, while that of the leaf rollers was patchy. Their parasitoids showed a "follower" distribution.

We concluded that the harmful effects of human interventions might still be reversed on the agricultural areas. The best examples were taken from the beneficial insects. If the unfavourable effect on the area ceased to exist, the ecosystem was capable of replenishing itself from the populations present in the air or in the environment. To achieve this, we had to maintain the diversity of species in the spatial, ruderal areas, in the woodlands and other areas. With this in mind, we worked out a pest management programme for leaf miners which protected the parasitoids. The method was widely used in practice.

In the investigations of the plant communities in the orchards, we had the opportunity to study the effects of pesticide rotation on plantations with IPM and conventional management or under no-treatment, no-cultivation scheme.

It was found that the established good host-parasitoid relationship was disturbed on the area previously under IPM scheme if no pest control regime had been applied. In the first year of the change the relatively small parasitoid population was not able to regulate the increasing pest population, in the same way. We called therefore the attention to the fact that the disadvantages of even one growing season could destroy the advantageous impacts of the IPM practices implemented for leaf miners during four years.

Results of the agro-ecosystem research were published in at least 180 articles (the most important ones are cited), over 100 of which is in a foreign language. We lectured several times both in Hungary and abroad. Records were published in the book by BALÁZS, K. & MÉSZÁROS, Z. (eds) (1989) *Biological control with natural enemies* (Mezőgazdasági Kiadó, Budapest), also in volumes 1–6 of the manual by JERMY, T. & BALÁZS, K. (eds) (1988–1996) *Plant protection entomology* (Akadémiai Kiadó, Budapest) and in the book by JENSER, G., MÉSZÁROS, Z. & SÁRINGER, GY. (eds) (1998) *Pests of field and horticultural crops* (Mezőgazda Kiadó, Budapest).

The agro-ecosystem research resulted in several academic and scientific degrees and allowed us to participate in several national (National Council for Research Development, Hungarian Scientific Research Fund, National Committee for Technical Development) and international projects (German–Hungarian Intergovernmental Cooperation, US–Hungarian Cooperation).

I think that now all of us having participated in the agro-ecosystem research started in 1976 recall, with pleasure, the joint field work made weekly, several times in extremely hot weather or in heavy rain, or even the processing of huge mass of data with calculator and, later, with computer and mainly the obtained results, the successes at domestic and international conferences and the reactions to the articles and publications. We were also pleased to see that the domestic fruit production rapidly implemented our results in practice.

The experience obtained in the agro-ecosystem research, the knowledge of the regularities determining the agro-ecosystems turned our interests to the integrated, environmentally friendly pest management and to the integrated fruit production. The mechanisms prevailing in the agro-ecosystems, the exploration of host-parasitoid and host-predator relationships resulted in the establishment of pest management programmes safe for the parasitoids and predators. Since it has also been confirmed that our early statements are still valid and that the natural reg-

ularities determining the mechanisms of the agro-ecosystems are almost independent of the production systems.

Results of the agro-ecosystem research have contributed to establishing the integrated pest management in apples and the integrated apple production. The information obtained was used to develop the integrated fruit production for sour cherry and small fruits.

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FIFTY-YEAR-LONG INSECT SURVEY IN HUNGARY: T. JERMY'S CONTRIBUTIONS TO LIGHT-TRAPPING

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INTRODUCTION

The use of different trapping methods has an important role in field samplings of insect populations and assemblages. Taking into consideration that the majority of insect species are active at night, a regular and quantitative survey of their abundance may only be conducted with traps operating automatically. Light trapping is one of the most frequent and most popular sampling methods. Hundreds of light traps are working around the world mainly to forecast agricultural and forest pests. The possible uses of data on the identified species from these collections are wide ranging, and may serve taxonomic-faunistic, zoogeographic or insect-ecological studies to name a few. In most cases, only a single light trap is operated at or near the observed crop field or forest stand. There are only a few places, where several (5–15) light traps are operated simultaneously in order to produce pest forecasting generally on a smaller area. Only two countries are known worldwide where there is an existing national light trap network, >50 stations, that has been operating for decades. One of these is in the UK (Rothamsted Insect Survey: R.I.S.), the other one is in Hungary (Hungarian Light-trap Network). Simultaneous samplings with such networks of light traps can be carried out according to landscape, or even at a larger spatial (regional, national) scale to forecast insect pest densities. In addition, they are able to make synoptic monitoring of spatio-temporal dynamics of complete insect assemblages. Such survey systems are fundamental to modern research fields, e.g., for the study of effects of climate change on habitats and communities, or for the long-term monitoring of biodiversity changes and their trends.

Hungarian entomology celebrates two important events in 2002: Professor JERMY's 85th birthday and the 50th anniversary of the installation of the light trap type, which was designed and first operated by him in 1952 and has been used by the National Light-trap Network ever since. After a 6-year-experience of trapping and managing the caught insect material from six different sites in the country, JERMY launched a widespread use of his traps. At his suggestion, a national-wide network of light traps started to operate in Hungary in 1958. The network, established with the intention of forecasting for plant protection purposes, grew to more

than 100 traps a decade later, and even today about 60 stations are operating. Below I review the birth of the so-called "JERMY-type" trap; how and at what degree JERMY has contributed to the development and current knowledge of the use of light trapping in Central Europe with the establishment of this long-term-operating network, unsurpassed so far.

ESTABLISHMENT OF THE "JERMY-TYPE" LIGHT TRAP

To understand the need for JERMY's splendid idea, i.e. the development and long-term operation of a continuous sampling device, we need to cast light on the circumstances 50 years ago: requirements of plant protection practice, the available literature on foreign light trapping experiences, and last the professional and economical background of the times.

Necessity for countrywide forecasting of pests

In the late 1940s and early 1950s, before the use of light traps, post-war Hungarian plant protection was faced with the countrywide outbreaks and heavy damage by serious insect pests. These were either the recently introduced invader species, like Colorado potato beetle (*Leptinotarsa decemlineata*), and the American fall webworm (*Hyphantria cunea*), both spreading in Hungary from 1947. On the other hand, outbreaks of endemic noctuid species (cutworms) between 1948–1950 caused extensive damage in arable field crops. The outbreaks of these important pests begged for countrywide forecasting of pests. In that period, JERMY investigated both under field and laboratory conditions the control of these pests. He also studied the behaviour and the ecological characteristics of these pests. He clearly saw that the foundation of a forecasting system, with greater spatial scale and different temporal scales, was needed to prevent insect damage at the national or regional level. Having an extensive knowledge of literature, he knew about the results of foreign studies reporting that light traps are capable of collecting a high number of individuals, especially noctuid moths. These results suggested him the use of light traps for monitoring. But what could be found in the foreign literature at that time?

Experiences on light trappings in the first half of the 20th century

The phenomenon that night-active insects are attracted toward artificial light sources was probably familiar to our ancestors who built fire. According to de-

scriptions between 1st century BC and 4th century AD, the first primitive light traps operating with oil lantern were used by Roman beekeepers to protect against wax moths (STEINER 1991). Engravings illustrating beekeepers or people with oil lamps or burning torches killing moths with persist from the 17th and 18th centuries (HOBERG 1682). Hungarian forestry literature in the 19th-century also advises that great fires must be lit at forest edges to suppress moth pests (like *Lymantria dispar, Operophtera brumata, Malacosoma neustria* or *Euproctis chrysorrhoea*) causing defoliation, because many of them would be attracted and burnt by the flames. A generally applied insect collecting method was 'lamping' with the aid of a white sheet placed in front of a light source (KOVÁCS 1958, LÖDL 1989). The first electronic lamps appeared around the turn of the century. In the second half of the 1910s, a wider availability of electricity made possible the development of several trap types with this light source that allowed automatic insect collection. From that time until the end of WWII, an increasing number of studies were published annually throughout the world on light trapping in the international agricultural entomology literature. These revealed that the improvement and operation of traps were restricted mainly to plant protection in agriculture, the control of major pests of the most important economic crop plants. These agricultural cultivated plants included sugarcane, tea, jute, rice, palms, tobacco, cotton, maize, fruit trees, vine and vegetables. From the list of these crop plants, it is evident that a considerable proportion (35%) of these light trap experiments took place in subtropical-tropical colonial areas of European countries. Most studies were conducted in USA and Canada (51%), while only a smaller proportion (14%) of the light trapping was published in European literature. Pioneer investigators of light trapping analysed thoroughly the catching efficiency of the traps, because in most cases the aim of this collecting method was to strongly decrease pest population level in stands of the crop plant. The large number of individuals, especially in the case of moths (mainly noctuids) and beetles, captured by light traps within a relatively short period of time, encouraged these researchers. These numbers often meant captures of hundreds of individuals per night or even 500 000 individuals per year in case of certain species (cutworms, vine moths, leaf rollers, sugarcane beetle, cockchafers). Efforts to use light traps to eliminate pest insect populations from plant stands (orchards, arable fields) were doomed to failure, and by the 1950s it became obvious that the light trap method is not suitable for pest control. Nevertheless, these experiments greatly contributed in the development of different trap types: several constructions were tested; furthermore, capture changes due to different spectral composition of light sources were also discovered and comparative studies were made on the light sensitivity of different insect orders. During trapping of different target pests, it was discovered that from nearly all winged insect orders, a huge number of

species flies toward light, e.g. moths, beetles, leafhoppers, flies, mosquitoes, crickets, hymenopteran parasitoids, etc. Identification of all collected materials, especially from the macrolepidoptera, often yielded hundreds of species from a given locality. So by the middle of 20th century light trapping had become one of the most preferred insect sampling methods, producing both quantitative and qualitative data on individuals and species in a relatively short period of time. In the literature published by the end of the 1930s, most of the issues regarding insects light trapping had already been discussed, and these issues have appeared in studies of light trapping or are of concern to us until today. For example, effects of weather elements on daily flight activity, effects of moonlight and moon phases, characteristics of night flight behaviour, changes of male:female ratio, seasonality characteristics, nocturnal flight distribution, relationship between egg-laying and flight to light, effect of light trap location and surrounding habitats on captures, etc.

In relation to the identification of complete moth assemblages, being even nowadays an issue, the effect of climate fluctuation was also revealed. It was reported that in the 1920s in the State of Montana (USA), within the noctuid moth assemblages collected with light traps, the proportion of prairie (xerothermous) species had increased during years of strongly dry weather.

During the four decades before 1950, more than 600 papers referring to light trapping were published. Was JERMY familiar with the results of these investigations before he devised his light trap? The answer is yes, because his collection of articles includes numerous reprints and photocopies referring to light trap experiments from that period. These and the conversations I had with him suggest that he was very familiar with the literature on light trapping, published in English, German, French, and Russian, thanks to his extensive knowledge of foreign languages. He was most influenced by the works of C. B. WILLIAMS, inventor of the famous type Rothamsted light trap. WILLIAMS' articles published from the mid-1930s have been among the most cited works of light trap literature until today. Regular investigations of light trap catches with modern, statistical evaluation started with C. B. WILLIAMS' activity. In the 1910s and 1920s, WILLIAMS light-trapped several important economic pests (froghopper, cotton and pink bollworm) in tropical areas (Surinam, Trinidad and Egypt, respectively), and during this work he developed a new type of light trap design which he continuously kept modifying to increase its efficiency. This was the precursor of the famous Rothamsted type light trap (WILLIAMS 1948), which is still in operation at R.I.S. These experiments led him to the important observation that successful light trapping should be carried out over a long-term period with continuous record and under standard conditions. WILLIAMS accomplished two famous trapping series, the first one between 1933–1936 and the other one between 1946–1949 in the experimental field of

Rothamsted Experimental Station. During these continuous collecting periods he used his above-mentioned self-constructed light trap type. His results were published in a series of articles (WILLIAMS 1935, 1936*a*, 1939, 1940, 1948, 1951, 1953, 1964). From the captured insect materials, he identified the complete macrolepidoptera group, so his analyses mainly refer to moths, especially the family Noctuidae. The aim of his light trapping experiment series was to indicate the rate of all potential environmental effects influencing captures (meteorological factors, moonlight, and electricity of the atmosphere). The true importance of these works, in my opinion, is that he was the first one who introduced the statistical methods (e.g., correlation and regression analyses, ANOVA) and species diversity (α-diversity) for the analyses of light trap data (WILLIAMS 1936*b*, 1953, 1964). Information in WILLIAMS' articles had a major role in forming JERMY's favourable opinion about light trapping methods. The question was, however, whether he should completely apply the same WILLIAMS-type light trap under the conditions in Hungary?

Technical background and the construction of "Jermy-type" trap in 1952

In the early 1950s, following the Soviet examples, a socialist planned economy was introduced in all branches of production in Hungary. A characteristic of this type of productions was that only a few kinds of industrial goods were made, but in enormous quantities. So the assortment in light bulbs was also limited. As JERMY intended his light trap to forecasting of insect pests, his idea was to operate it in a long-term national network. His great technical talent, which he has proved many times with his experiments, helped him to make a very clever selection of all the materials and tools: all of them could be bought then and were expected to remain commercially available for decades. So, as a light source, he chose a 100 W incandescent, tungsten filament light bulb for his trap. (This bulb type is still available in Hungary.) Due to network operation, in case of malfunction or bulb exchange, all the components must have been quickly purchasable at any point of the country. Our network is still operating with the "JERMY-type" traps, being the best proof of the grandiosity of this conception. Although minor technical modifications on the trap have been made based on experience while running the network (BENEDEK *et al.* 1974), its main structure, the arrangement of technical elements determining the way and level of catches has remained.

In 1952, JERMY constructed his light trap from very simple components, while taking into consideration practical point of view. As a part of the trap, there is a circular roof made of aluminium with a diameter of 1 meter fixed to a column at two meters above ground level. The light source (light bulb and lamp-holder) is

hung on the lower side of the roof. The function of the roof is to protect of the lamp and captured insect material from rain. Below the light source is a metal funnel placed 40 cm below the roof. The upper end of the funnel is 50 cm in diameter and it tapers to 5 cm in diameter, and then it continues in a 10-cm-long tube, leading to the killing jar. The funnel directs the attracted insects flying around the light bulb to the connected killing jar. Balls of cotton wool are placed on the floor of this glass jar, to prevent damage to the insects as they fall into the jar. Chloroform (sometimes carbon tetrachloride) has been used as poison in the traps, because it proved to be less dangerous to the operating personnel than the formerly applied hydrogen-cyanide. In addition, since its vapour is heavier than air, a sufficient concentration stays in the glass to produce a killing effect. JERMY provided detailed descriptions and drawings of each structural components of his trap, with the intention of standardising construction and manufacturing. He also preferred a light source with white light, because he knew from published data that other light sources with shorter wavelength (e.g., UV light) attract high numbers of insects (JERMY 1961). Processing large numbers of individuals caught by more efficient light sources would have required a lot more labour and costs, and it often could have resulted in less valuable scientific material because large bodied species would damage more delicate ones (JERMY 1961, 1974, KOVÁCS 1962). This was aptly demonstrated, when more traps were experimentally operated with UV light source at stations of the Hungarian Plant Protection Service in 1963 (MÉSZÁROS 1966*a*). JERMY did not install boards (baffles) around the bulb, resulting in a further reduction in the amount of collected material. Baffles were used in several trap types (e.g., Minnesota type) in order to increase level of catch through increasing collision of insects with these boards.

Outlining light trap operation

Besides structure, use or operation also had to be standardised to insure that operators would work the same way at each station of the national network, and that the traps would produce the same quality of insect material required for identification. The thoroughly detailed directions for the operation of the light trap (JERMY 1961) were developed based on a 6-year trial period (1952–57) in close association with a team of taxonomic specialists for identification.

Experimental period of material handling and network operation (1952–1957)

Manufacture and testing of the prototype of light trap in 1952 was conducted in the Department of Zoology in the Plant Protection Institute, Budapest. The trap

was placed and operated in the garden of a rural experimental laboratory of the Institute located at Keszthely, Western Hungary. After the favourable results of the first year, another four traps began operation in 1953. In 1957, the test operation of six light traps was running through the whole season. JERMY was well aware of the fact that light traps would probably collect a large number of individual insects (hundreds of thousands), especially in case of a network with many stations working continuously. Identifying this huge collected material requires a team of taxonomic experts. As a practical man, JERMY probably would not have started the light trap network, if there had not been suitable taxonomic expertise available at that time. He managed to convince several colleagues at the Department of Zoology of the Hungarian Natural History Museum to participate in this extraordinary task. Among others, he recruited the two most exceptional lepideptorologists of that time, L. KOVÁCS (Macrolepidoptera) and J. SZŐCS (Microlepidoptera). JERMY clearly saw that the success of his forecasting network depended on the complete and reliable identification of moth assemblages collected annually with individuals numbering in the hundreds of thousands. The scientific knowledge of the above mentioned taxonomists matched the grandiosity of the task. LAJOS KOVÁCS worked fanatically on the huge moth collection until his death. They gradually perfected the national light trapping method (JERMY 1961, KOVÁCS 1958) as they were continuously communicating with each other. The fact that JERMY, while co-operating with others, examined the possibilities and efficiency of his trap through a test period of six years, demonstrates his incredibly persistent and experimenting personality, observing and recording even tiny details. Thanks to their co-operation, they had all the necessary experience by the end of 1957 to start the extension of the light trap network at the stations of the Plant Protection Service in 19 counties.

Development of light trap network

The plant protection stations were state-controlled and they were distributed all across the whole country. Therefore, they seemed ideal for the extension of the light trap network. In 1958, two stations, and in 1959 all plant protection field stations were supplied with light traps. The number of light traps working in agricultural areas suddenly increased until the late 1960s, because from 1963 onwards, additional regional light traps were set up (4–6 traps/county) for local forecasting. From 1963, the collected insect material of nearly 30 traps operating at the stations and institutes was processed centrally in the Department of Zoology of the Hungarian Natural History Museum by its Identification Group, which included younger taxonomic experts as well. In 1961–62, a forest light trap network with 12 sta-

tions was also established under the direction of PÁL TALLÓS and PÁL SZONTÁGH (LESKÓ & SZABÓKY 1998). The Plant Protection Identification Group had also processed catches of these forest traps until 1971. By this time 25 forest traps had been operating. With this rate of extension of the forecasting network, JERMY's dream had been fulfilled by the end of the 1960s. Following the death of L. KOVÁCS in 1971, identification of the forest and agricultural light trap materials was separated locally also. Experts of Forest Protective Monitoring-forecasting Service in the Forest Research Institute processed the collections of the forest light trap network with the aid of outside professional and amateur entomologists. The complete Lepidoptera collection was processed again from the mid-1970s (for some years following the death of KOVÁCS, only major forest pest species were identified regularly). There were some fluctuations in the number of forest traps in the 1970s and 1980s. Today there are 25 traps operating.

From the agricultural light traps, the material of so-called central traps that work at plant protection stations (one trap per county), was processed in a centralised forecasting system from the 1970s, but only major moth and beetle pests were identified. The number of all the agricultural traps is recently around 50.

History, structural changes, and managing materials of the Hungarian light trap network have been reviewed in detail by several authors. For information about the initiation, development, and later periods of the network and a thorough review of the history of the forest light trap network in Hungary, see the works of JERMY (1961), KOVÁCS (1962), MÉSZÁROS (1966*b*), MÉSZÁROS and VOJNITS (1968), VOJNITS (1968*b*), BENEDEK (1970), HERCZIG (1983), NOWINSZKY (2000), LESKÓ and SZABÓKY (1998).

JERMY'S DIRECT AND INDIRECT CONTRIBUTIONS TO LIGHT TRAPPING

The technical development

It is obvious from the above review that one of the most important direct contributions of JERMY to this traditional and popular insect sampling method was that, by recognising the conditions and requirements, he devised a simple, but efficient light trap type for practical use, which is still successfully operated today. In addition, in collaboration with taxonomic experts, he also developed the still valid standard sampling methods in detail.

The network development

From the very first moment, JERMY intended to use his trap as part of a nation-wide network, with the aim of forecasting insect populations. After a trial period of six years, he gradually increased the number of light trap stations and gathered information about possible operational errors, and laid the foundation for the successful long-term operation of a forecasting network.

His publications about light trapping

JERMY had only a few publications specifically on light trapping. The reason for this is that the study of other entomological problems was in the focus of his broad-ranging scientific activity, as is illustrated by the list of his publications in this book.

In 1961, he published the description of his successfully tested light trap type, its directions for use, and the short history of the 10-year-long development of the network (JERMY 1961). In 1974, at an international symposium on the use of light traps, held in Budapest, he reviewed the results that had been reached so far and discussed the importance and utility of traps in faunistic, ethological, ecological, forecasting and migration investigations (JERMY 1974). In spite of the small amount of publications, he has always paid attention to the smooth functioning of the light trap network. He referred to the importance of analyses of light trap data series in numerous writings and lectures on plant protection studies, and he warned about the necessity to preserve the light trap network. It was evident to him that the data series, with decades-long observation, are eventually becoming more valuable in monitoring such large-scale processes as effects of climatic change on insects or bioindication of species and diversity changes. He also published his views on this (JERMY 1998).

Foreign reception of Jermy's light trapping improvements

Scientists abroad also took notice of the results obtained by the "JERMY-type" light trap. During the 1960s, there were numerous light trapping experiments and developments performed, especially in Germany (e.g., CLEVE 1964), where a trapping had already been going on for 10 years by the time JERMY began testing his model (HAEGER 1957). JERMY's light trap type was tested mainly in the surrounding countries, e.g., in Austria (MALICZKY 1965), but was also used in France (GAGNEPAIN 1974), and it was thoroughly described and compared with other traps in Germany (MESCH 1965). L. RÉZBÁNYAI, who applied this method for his Hungarian lepidopterological investigations (RÉZBÁNYAI 1974), introduced Hun-

garian light trapping techniques to Switzerland and applied this method for his investigations there (RÉZBÁNYAI 1974). Meanwhile, JERMY's (JERMY 1961, 1974) and other Hungarian scientists' work and publications on light trapping were frequently referred to by several outstanding foreign scientists using the method (e.g., WOLDA 1978, 1981).

Jermy's influence on Hungarian light trapping investigations

JERMY's careful, critical but always encouraging thoughts and his demands on himself and of others, inspired a number of studies on light trapping in the case of scientists who had personal contact with him. There are few publications about data of Hungarian light trap networks that would not refer to "JERMY-type" traps. The important direct influence of the trap constructed by JERMY and the long operation of the initiated network on light trap studies would be difficult even to estimate. On the basis of publication lists (e.g., LESKÓ & SZABÓKY 1998, MÉSZÁROS & VOJNITS 1968, NOWINSZKY 1994, 1997, 2000, 2001) and other literature surveys, there are at least 600 publications that were written by Hungarian researchers using data collected by "JERMY-type" light traps. In my opinion, the greatest impact of JERMY and his light trap is documented in this large public undertaking. It is impossible to entirely present now the 50 years of the Hungarian light trap studies with all its diverse fields based on the study of insect samples and data series produced by the successful trap type and the well-working networks. So I only illustrate this with some examples from more important light trap studies, without striving for completeness. Literature search of the themes referring to light trapping illustrated the tremendously wide ranging, countless potential groupings that exist (LÖDL 1987). Data produced by the Hungarian light trap network may be analysed at different temporal and spatial scales. Data coming from the method of light trapping might aid the analyses of daily (e.g., influence of weather elements on night activity), seasonal (e.g., flight pattern of insects from catches summed weekly), and long-term year-to-year (e.g., fluctuations in population dynamics, biodiversity) temporal changes. Data might be spatially analysed at local (1-trap-station), regional, or national scale. As for sampled insects, light trap data may refer to a given species or groups of species (e.g., taxonomic or ecological assemblages). From a combination of the above points of view, many studies of new fields of light trapping were created. I mention these briefly to attempt to arrange in chronological order and by topic the light trapping studies of past decades.

MAJOR RESEARCH FIELDS AND RESULTS OF THE HUNGARIAN LIGHT-TRAPPING

Faunistics

Even in the very first years of light trapping, our lepidopterologists discovered several moth species new to the Hungarian fauna and new to science (KOVÁCS 1962, MÉSZÁROS & VOJNITS 1968, 1974). With the accumulation of data, description of a moth fauna within a larger region became possible (LESKÓ & SZABÓKY 1997). Processing the light trap materials proved to be useful in the case of other insect taxa besides Lepidoptera. In the 1960s, Neuroptera (STEINMANN 1963, ÚJHELYI 1968), Heteroptera and Homoptera (JÁSZAINÉ 1964–66) were also identified in light trap catches. Since 1969, J. TÓTH identified the major portion of the collected Coleoptera from the traps operating in the forest, and he also produced valuable faunistic data (TÓTH 1972, 1973). Large numbers of species from the order Trichoptera were also found among the light trap caught species. Trichopterologists frequently used the light trap method of collecting to gather faunistic data (e.g., KISS 1984, KISS & SCHMERA 1997, 1999, NÓGRÁDI 2000, NÓGRÁDI & UHERKOVICH 1988, 1990, 1994, SCHMERA 1999, 2000, UHERKOVICH & NÓGRÁDI 1990).

Forecasting of pestiferous moths

Even during testing phase of light trap network, flight pattern analysis of certain moth pest species began, in order to solve its forecasting as soon as possible. Some of the earliest similar works were done on the cutworms (*Heliothis maritima*, *H. dipsacea*) (NAGY 1957), on the European corn borer (NAGY 1960), and on *Loxostege sticticalis*, *Homoeosoma nebulellum* and *Etiella zinckenella* (REICHART & SZŐCS 1961). Experts at the Identification Group needed to do the pioneering work in working out the forecasting methods built on the network. It is necessary to emphasise here the name of ZOLTÁN MÉSZÁROS, who published his results on forecasting in a series of articles (e.g., MÉSZÁROS 1963–1965, 1966*a, b*, MÉSZÁROS & VOJNITS, 1967, 1974). He grouped moths according to their characteristics of life history, and he invented new indices on the basis of population dynamics according to generation number, which had a predictive value of possible outbreaks for the following year. With these characteristics, he prepared the first long-term population dynamics analysis of some noctuid species (MÉSZÁROS *et al.* 1979). Parallel with this, flight dynamics, characterising the seasonality of most studied moth species, were described. According to network catches, first forecasting

maps were also drawn, which supported the preparations for landscape level forecasting with the aim of protection (MÉSZÁROS & VOJNITS 1967, KOVÁCS & DRASKOVITS 1967). Transformation of numerical data to distribution maps was useful in the analysis of spreading and migration of species (KOVÁCS 1971, MÉSZÁROS & VOJNITS 1967, VOJNITS 1966, 1968*a*), and even in the study of biogeographical analysis of outbreaks (VARGA & UHERKOVICH 1974). It must be mentioned, however, that besides moths, light trap data of other representatives of insect orders were used to temporally characterise their flight activity. Light traps provided useful information for seasonality description of Heteroptera (JÁSZAINÉ & BENEDEK 1968, BENEDEK & JÁSZAI 1973, ERDÉLYI & BENEDEK 1974), cockchafers (HOMONNAY 1977), and certain leafhopper species (*Macrosteles* spp.) (JÁSZAINÉ 1977).

Forecasting results of light trapping concerning agricultural pests were summarised by MÉSZÁROS & VOJNITS (1968, 1974), and NOWINSZKY (2000). Finally, these early forecasting methods became part of the every day practice in plant protection (BENEDEK *et al.* 1974).

Forecasting of forest pests

From the establishment of the network (1961–62), light trap catch data played an important role in the yearly forecast of forest pests (LESKÓ & SZABÓKY 1998). Those research results, which were based upon the simultaneous analyses of light trap and damage data series of forest defoliating moth pests, were usually built into the yearly published forecasting works (e.g., SZONTAGH 1974, 1976, 1980, 1987, LESKÓ *et al.* 1994, 1995, 1997–1999). In this respect, at landscape level, light trap catches did indicate outbreaks of several important pests generally a year earlier.

Abiotic environmental factors influencing light trap catches

Even in the beginning phases of light trapping, the study of abiotic factors started using data series of daily captures of traps. From foreign studies, the different effects of weather elements or moonlight phases on flight activity of insects had been known by the 1950s. In Hungary, it was WÉBER (1959*a, b,* 1960) who, for the first time, studied the effects of weather elements on light trap catches, and many others followed him (NOWINSZKY 1994, 1997, 2000, 2001). The pioneer WÉBER was also the first to demonstrate the changes in light trap captures occurring as the weather fronts passed by. Later, it was shown by the light trapping data of KÁDÁR & SZENTKIRÁLYI (1984, 1992) that an increase in flight activity of

ground beetles preceded cold fronts, whereas it decreased before the onset of warm fronts. Impacts of various types of weather fronts on moths flights were analysed in detail by NOWINSZKY and his colleagues (NOWINSZKY 1997, 2000, 2001, PUSKÁS *et al.* 1997) as well as by LESKÓ *et al.* (1998). Using Hungarian light trap data NOWINSZKY (1994, 1997, 2000, 2001) together with an interdisciplinary team, achieved new noteworthy results in demonstrating the effects of major abiotic factors in the environment as follows: weather factors, moon phases, intensity of polarised moon light, periodic solar activity, solar flares, geomagnetic disturbances, ionospheric disturbances, cosmic radiation, atmospheric electricity, macrosynoptic weather situations, thunderstorms, twilight polarisation phenomena, interplanetary magnetic field sector boundary, gravitational potential by the Moon and Sun, and earthquakes (NOWINSZKY 1994, 1997, 2000, 2001).

Long-term monitoring of insect population and the climate change

Long-term monitoring systems can be used for studying the impacts of global and regional environmental changes on living organisms. The several decades long data sets collected by the Hungarian light trap network were used to monitor changes in insect populations (SZENTKIRÁLYI 1999, SZENTKIRÁLYI *et al.* 2001).

The biological effects of climate change have an increasing importance since 1980s (TRACY 1992). There are numerous predictions for expected influences of the increasing temperature ("global warming") on abundance, life cycle and phenology of insects, interspecific relationships in food chains of insects, and geographical distribution of some pests (WATT *et al.* 1990, HARRINGTON & WOIWOD 1995). According to the possible scenarios, the climate would become drier associated with more frequent droughty years in Hungary. Various hypotheses regarding direct and indirect effects of arid, warm climate on insects (Plant Stress Hypothesis, Climate Release Hypothesis, Plant Vigour Hypothesis) exist that may explain the insects' outbreaks (MARTINAT 1987, MATTSON & HAACK 1987, PRICE 1991). In particular, lepidopterous forest defoliator species produce damaging outbreaks for time to time in Hungary whose fluctuations can be monitored sufficiently by light traps. Different climate elements and aridity indices were used in time series analysis of data sets of yearly moth catches by LESKÓ *et al.* (1994, 1995, 1997–1999) and SZENTKIRÁLYI *et al.* (1995, 1998). They detected decreasing tendencies of yearly amount of precipitation in climatic data series. A series of stronger droughty years has been detected since early 1980s until the mid-1990s. The outbreak patterns of each studied species were synchronised at a nation-wide scale

and those were recorded in drought years. In the analysis of time series of moth pests, no significant periodicity was detected.

Increase in the abundance of *Lygus* species caused by arid years could be proved by long-term light trapping (RÁCZ & BERNÁTH 1993). The spatial spreading of an invader moth pest (cotton bollworm) was extended in dry and warm years also in Hungary as it was confirmed by light trap catches (SZABÓKY & SZENTKIRÁLYI 1995). KÁDÁR and SZENTKIRÁLYI (1997) demonstrated the emigration of hygrophilous species by flight from the drying habitats in arid seasons by long-term fluctuation patterns of carabids.

The long-term data series of light trappings can be implemented not only in the analysis of population dynamics but also in the description or characterisation of seasonal flight patterns of less abundant, rarer species. In this way over many years of trapping sufficient number of data could be collected for seasonality analysis of certain ground beetles (KÁDÁR & SZENTKIRÁLYI 1998), brown lacewings (SZENTKIRÁLYI 1992, 1997) and antlions (SZENTKIRÁLYI & KAZINCZY 2001).

Long-term monitoring of insect biodiversity by light trapping

Adverse trends of biodiversity changes are experienced all over the world. For this reason, their long-term monitoring possibilities have a great importance. The National Biodiversity-monitoring System (LÁNG & TÖRÖK 1997) also includes numerous light trap stations to obtain data on species diversity changes through the identification of entire collected materials of some insect orders. The fluctuations of diversity patterns of insect assemblages sampled by light traps may indicate the changes in habitat conditions.

LESKÓ *et al.* (2000) and SZENTKIRÁLYI *et al.* (2000, 2001) analysed the changes and long-term trends in time series of yearly number of individuals, richness of species, and species diversity statistics of macrolepidopteran assemblages sampled by light traps located in various forests over four decades. Their results proved that there is a definitive, significant decreasing trend of moth assemblages in time series of each structural character at certain trap stations. According to similarity analyses, sudden changes and transformations happened in the species composition and structure of moth assemblages from time to time (during a 5–10-year period). For instance, data series of a trap station from lowland region with sandy area characterised by xerothermous habitats can be read in Figure 1. The fluctuations and decreasing trends of number of individuals and number of species could be explained by changes in environment at trap site, such as forest settling, disappearance of natural grassland, increase of arable fields, drainage, droughty years, decreasing water tables and the decline of old-growth oak forests.

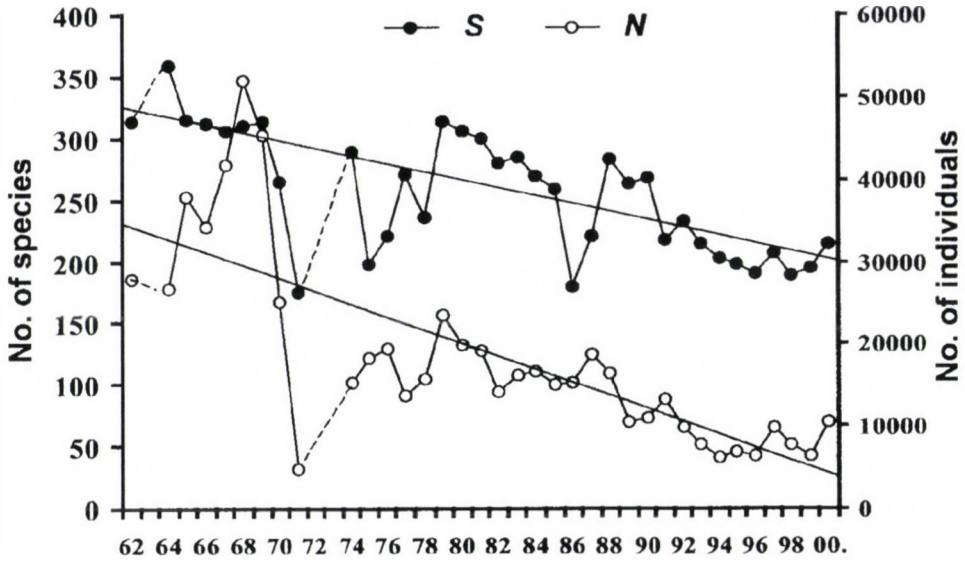

Fig. 1. Long-term fluctuation pattern and trend of the yearly total number of species (*S*) and number of individual (*N*) of macrolepidopteran assemblage sampled by a forestry light trap in southern part of Hungary (near Tompa) between 1962 and 2000. (Equation of trend for *S*: y = 326.50 – 3.30x, and for *N*: y = 34920.43 – 789.67x) (after SZENTKIRÁLYI *et al.* 2001)

Since 1981, a long-term light trap monitoring has been going on some predatory insect groups (lacewings, antlions, ground beetles) at the Department of Zoology of the Plant Protection Institute. It was found that the level of species diversity of green and brown lacewings strongly depended on the vegetation at the light trap sites. The long-term time series of species richness and abundance level significantly fluctuated depending on winter mean temperature and summer drought levels (SZENTKIRÁLYI 1992, 1998). Only the carabids produced fluctuations with smaller amplitudes in structural characteristics of assemblages (KÁDÁR & SZÉL 1999).

Another long-term insect monitoring has been operated by R.I.S. light trap network in Great Britain (TAYLOR 1986). TAYLOR *et al.* (1978), TAYLOR (1986) and WOIWOD (1987) informed us that the land-use changes (mechanization of agriculture, increase of intensity of farm practice, "hedging and ditching", forest clearing, intensive field margin management, widespread use of pesticides) reduced the total number of moths by about 60 percent between 1950 and 1960. In parallel, the α-diversity of the moth assemblages was also decreasing.

CLOSING WORDS

I hope that I have illustrated how the established Hungarian light trapping system has provided various experimental opportunities for many researchers for decades. Allow me to close this overview with sentences from a manuscript prepared by JERMY in 1993. "The Hungarian light trap network – due to its spatial density of traps, time period of data series, as well as to the number of insect groups under taxonomic identification – is unique all over the world. There can be only in a few countries, such as in Great Britain found a system more or less similar to it. For many reasons we must do all our best in order to maintain the network for the future."

*

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PHEROMONE STUDIES AT THE PLANT PROTECTION INSTITUTE, BUDAPEST, DURING THE LAST QUARTER OF THE PAST CENTURY

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It goes without saying that the international boom in pheromone research which began in the late nineteen-sixties and early seventies would excite the interest of such a keen ethologist as TIBOR JERMY. Consequently, behavioural observations and trapping with female-baited traps were soon initiated on several pest Lepidoptera at both the Budapest and Keszthely laboratories of the Institute. Monitoring trials with already known synthetic pheromones (i.e., the codling moth *Cydia pomonella* L.; Lepidoptera, Tortricidae) were conducted in the early seventies in connection with a large sterile-male project supported in part by the International Atomic Energy Agency.

Having joined the Institute in 1974, the research topic of pheromones was suggested to me as a line of study in 1975 by TIBOR JERMY. During the first years, I was lucky to be able to conduct the first experiments under his personal supervision – in some cases in his own garden. TIBOR JERMY's acute observational prowess and the thorough organization of experimental design, omitting no detail however unimportant it might seem to be, impressed me deeply and had a highly determining impact on my later scientific career as well, for which influence I cannot be too grateful.

Observations on the natural behaviour of the target insect is of crucial importance in pheromone studies. An outstanding example of how direct observation of behavioural events can lead to novel understanding of pheromonal regulation of mating, even after several decades of intensive studies, is readily shown by the work on the Colorado potato beetle (*Leptinotarsa decemlineata* SAY; Coleoptera, Chrysomelidae) by JERMY and BUTT (1991).

Consequently the main objective of the studies at our laboratory during those early years was the description of behavioural processes connected with pheromone production and response in several lepidopteran (mainly noctuid) pests, in order to gain evidence for the presence and possible role of pheromones in the courtship process. The first publishable results were obtained with the cabbage armyworm, *Mamestra brassicae* L. (Lepidoptera, Noctuidae), where the presence of both a long-range female-produced pheromone, and a male-produced hair-pencil pheromone could be demonstrated (SZENTESI *et al.* 1975).

In addition, considerable efforts were dedicated to the study of role of hair pencils in the courtship of the oriental fruit moth, *Grapholita molesta* BUSCK. (Lepidoptera, Tortricidae) (ISTVÁNOVICS & TÓTH unpubl. data), and quite extensive tests were run using the known pheromone inhibitor dodecyl acetate (ROTHSCHILD & MINKS 1977). In fact, successful suppression of mating and also of damage levels was achieved in preliminary air-permeation trials with this compound; however, the industrial sponsor (EGYT Pharmaceutical Co., Budapest, Hungary) never allowed these studies to be published.

In the following years, pheromone extracts were prepared from several moth species, and simple laboratory bioassays were developed for monitoring the activity of these extracts (TÓTH 1979, SZŐCS & TÓTH 1979). The extraction and bioassay of the sex pheromone of the winter moth (*Operophtera brumata* L.; Lepidoptera, Geometridae) is of special interest in this respect because it was among the first pheromone papers on this family (SZŐCS & TÓTH 1978). Interest in geometrids was enhanced by a contribution of my friend GÁBOR SZŐCS when he joined the laboratory in the late seventies. He had specialized in this group of Lepidoptera in his student years as moth collector. As we shall see, the study of geometrid sex pheromones became a significant research area in our laboratory.

Further progress towards the chemical identification of the pheromones which had been extracted was hampered by the unavailability of sensitive equipment and special expertise inside Hungary. A breakthrough became possible when international contacts with laboratories specializing in the structure elucidation of hitherto unknown pheromones was established. In this respect, the most significant partners and professors were G. H. L. ROTHSCHILD from CSIRO, Canberra, H. ARN from the Wädenswil Federal Station, W. FRANCKE from Hamburg University and C. LÖFSTEDT from Lund University, to whom the author is greatly indebted for the invaluable training and assistance they provided. Consequently, a row of joint pheromone identifications were completed in the early eighties on important pest noctuids (TÓTH *et al.* 1983, 1986) and tortricids (GUERIN *et al.* 1986*a, b*). Of special taxonomic and chemical interest is the identification of the ketone pheromone component from the grapevine pest geometrid *Peribatodes rhomboidaria* SCHIFF. (Lepidoptera, Geometridae) (BUSER *et al.* 1985, TÓTH *et al.* 1987). Through further structure elucidation of several other geometrid pheromones (HANSSON *et al.* 1990*a*, TÓTH *et al.* 1991, TÓTH *et al.* 1992*a*), it became clear that this group of insects uses a polyene-derived set of compounds (mostly epoxides) crucially different from the usual mono- or dienic acetates and alcohols of well-known tortricid or noctuid pheromonal structures. The importance of the chiral composition of these epoxides in maintaining species-selective pheromonal communication channels was amply demonstrated in geometrid species sharing

the same habitat and general flight season (SZŐCS *et al.* 1993, TÓTH *et al.* 1994*b*, LANDOLT *et al.* 1996).

Epoxide structures seem to prevail also in the family Arctiidae. In the fall webworm (*Hyphantria cunea* DRURY; Lepidoptera, Arctiidae), the presence of linoleic and linolenic aldehydes, together with a dienic C21 epoxide, *was shown out?* from pheromone extracts by North American and French scientists. However, no field activity was observed by any combination of the above three compounds (HILL *et al.* 1982, EINHORN *et al.* 1982). Cooperating with Swiss, Japanese, Russian and Spanish scientists (TÓTH *et al.* 1989*b*), we identified two further trienic epoxide components from the pheromone of the fall webworm, and the first baits active in field trapping tests were formulated with the novel trienic epoxide (3*Z*,6*Z*)-1,3,6-(9S,10R)-9,10-epoxy-heneicosatriene. Later studies revealed that a ternary mixture of linolenic aldehyde, (3*Z*,6*Z*)-3,6-(9S,10R)-9,10-epoxyheneicosadiene and (3*Z*,6*Z*)-1,3,6-(9S,10R)-9,10-epoxyheneicosatriene is needed for optimal field activity (BINDA *et al.* 1990).

A third structural type of moth pheromone is presented by branched hydrocarbons. Dimethylalkanes were identified for the first time by us in the mountain-ash bentwing *Leucoptera scitella* L. and the closely related coffee leafminer *Perileucoptera coffeella* GUÉR. – MÉNEV. (Lepidoptera, Leucopteridae) (FRANCKE *et al.* 1987, 1988). Later studies revealed that only one of the four possible enantiomers was responsible for biological activity in *L. scitella*, although the presence of other enantiomers did not interfere with activity (TÓTH *et al.* 1989*a*).

A secondary alcohol, a novel structural type for Lepidoptera, was discovered by us when studying the pheromone composition of *Stigmella malella* STAINTON (Lepidoptera, Nepticulidae) (TÓTH *et al.* 1995). The pheromone of this species consists of (6*E*)- and (6*Z*)-6,8-nonadien-2-ol and the only biologically active form of the molecule is the pure (S) enantiomer. Similar, but monounsaturated secondary alcohols and ketone derivatives, have since been identified exclusively from some ancient monotrysian Lepidoptera (ZHU *et al.* 1995, KOZLOV *et al.* 1996) and from Trichoptera (LÖFSTEDT *et al.* 1994, BJOSTAD *et al.* 1996, JEWETT *et al.* 1996, LARSSON & HANSSON 1998), suggesting that the seemingly ancient pheromonal pattern of secondary alcohols may reflect the presence of an evolutionary link between the orders Trichoptera and Lepidoptera.

In some cases, in the course of our pheromone identification projects, geographical differences in pheromone composition have been discovered within the target species. In the currant borer, *Synanthedon tipuliformis* CLERCK (Lepidoptera, Sesiidae), for example, the main pheromone component is (2*E*,13*Z*)-2,13-octadecadienyl acetate (VOERMAN *et al.* 1984, SZŐCS *et al.* 1985). The minor component (3*E*,13*Z*)-3,13-octadecadienyl acetate significantly synergizes biological

activity when added at 3–5% (SZŐCS *et al.* 1990). This striking synergism was observed in currant borer populations in several countries in Europe (SZŐCS *et al.* 1991), New Zealand (SZŐCS *et al.* 1990) and Canada (SZŐCS *et al.* 1998). However, in tests conducted in Tasmania, no biological activity of the 3,13 dienic acetate was observed (SZŐCS *et al.* 1990).

Three components, (5*Z*)-5-decenyl acetate, (7*Z*)-7-dodecenyl acetate and (9*Z*)-9-tetradecenyl acetate, have been identified from the pheromone of the turnip moth (*Agrotis segetum* SCHIFF.; Lepidoptera, Noctuidae) by several authors (BESTMANN *et al.* 1978, ARN *et al.* 1980, TÓTH *et al.* 1980, LÖFSTEDT *et al.* 1982). Usually the presence of all three components is needed for maximal biological activity in Europe, although it appeared that the relative importance of the components may shift according to geographical region (ARN *et al.* 1983, LÖFSTEDT *et al.* 1986) – the decenyl compound being more important towards the west and the tetradecenyl compound towards the east (HANSSON *et al.* 1990*b*). In a field trapping study of several Eurasian and African sites, we found that the ternary mixture was working well at all sites in Eurasia and North Africa, while at the two sites south of the Equator in Africa, only the decenyl compound showed some field activity and the addition of the two others did not influence attractive activity (TÓTH *et al.* 1992*b*). This suggested the evolution of pheromonally distinct strains of the turnip moth in Africa south of the Equator. This idea was supported in a direct comparative study of Swedish and Zimbabwean turnip moth populations by the Lund (Sweden) pheromone group (WU *et al.* 1999).

The third example of geographical differences in pheromone composition came from a phycitid, the lima-bean pod borer *Etiella zinckenella* TR. (Lepidoptera, Phycitidae). From Hungarian and Egyptian populations, several tetradecenyl pheromone components have been identified (TÓTH *et al.* 1989*c*), among which the mixture of (*Z*)-9-tetradecenyl and (*Z*)-11-tetradecenyl acetates showed maximal biological activity (TÓTH *et al.* 1996*a*). This blend attracted male lima-bean pod borers in trapping tests at sites in several European countries, Egypt, Northern India, but no activity was observed in Taiwan, Japan, Australia or North America, suggesting a crucially different pheromone composition for pod borer populations in these latter regions (TÓTH *et al.* 1996*a, b*).

Apart from the scientific importance, such comparative studies of populations of widespread pests in several geographical regions can be very significant from the practical point of view. Naturally, the best results for agricultural monitoring or forecasting can be expected when the optimal pheromone composition for the given region is used.

More recently, the scientific interest in our laboratory shifted somewhat from Lepidoptera to the Coleoptera, which offer new and exciting challenges for the

pheromone scientist. In the early nineties, we started to study the pheromones of click beetles (Coleoptera, Elateridae), discovering new pheromone components for several central and western European click beetle pest species (FURLAN *et al.* 1996, TÓTH & FURLAN unpubl. data), and optimising the activity of known pheromone components in the region for species where some information is already known about the pheromone composition (TÓTH *et al.* 1999).

Also in the Coleoptera, we have discovered attractants for several scarab beetle pests (i.e., *Epicometis hirta* PODA, *Anomala* spp., etc.) (TÓTH *et al.* unpubl. data) in the second half of the nineteen-nineties. Most recently, promising results were obtained in a preliminary mass-trapping test on *Anomala vitis* FABR. and *A. dubia* SCOP. (Coleoptera, Scarabaeidae, Melolonthinae) in peach and sour cherry orchards (VOIGT & TÓTH 2002) using the highly potent sex attractant discovered previously (TÓTH *et al.* 1994*a*).

Having discussed the main lines and results of pheromone studies of the past quarter of a century in our Institute, it just remains for me to offer these results as a tribute to the initiator of these studies, to TIBOR JERMY, as a humble contribution from this laboratory on his 85th birthday.

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CONTRASTED FORAGING TACTICS IN TWO SPECIES OF POLYPHAGOUS CATERPILLARS

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Polyphagy can occur at the level of species, population or individual. We analyzed foraging by two polyphagous species of caterpillar in the field and laboratory in a first investigation of the differences between polyphagy at different levels. We sought to obtain details that would inform different regulatory mechanisms and different adaptive bases. The fast-growing noctuid, *Trichoplusia ni* is known to be polyphagous at the level of species and population, while the slower-growing arctiid, *Grammia geneura*, is additionally polyphagous at the level of the individual. *T. ni* individuals showed greater uniformity in time spent feeding, had longer but fewer feeding bouts, and moved very little, compared with *G. geneura*. While *T. ni* rested on the food, *G. geneura* more commonly rested off it. *T. ni* individuals rarely mixed food items but rather showed increased preference for the rearing food, while *G. geneura* individuals habitually took a mixture of food items. We relate the differences to several potential physiological and ecological factors that are contrasted, including the crypsis of *T. ni* which alters with the food plant, and to the probable aposematism of *G. geneura*.

Key words: foraging, generalist, food-mixing, Lepidoptera

INTRODUCTION

The term polyphagous, as applied to a species of herbivorous insect, does not necessarily imply that individual insects of that species are polyphagous. To begin with, polyphagous insect herbivore species may be made up of populations having relatively narrow host ranges (FOX & MORROW 1981, THOMPSON 1994), and a relatively polyphagous population of insects may be made up of specialist individuals (BERNAYS & MINKENBERG 1997). Among the major phytophagous orders of insects, examples of these different levels of polyphagy may be found but they vary in relative abundance. For example, among orthopterans studied, individuals of most species feed on multiple foods, while among lepidopterans, it is more common for individuals to feed on only one plant species. Here, larvae remain on the host chosen by their ovipositing mothers. In only a small minority of species do individuals habitually move from plant to plant (MERZ 1959, DETHIER 1988*a*, SINGER 2000).

Even among individuals of food-mixing taxa there are contrasts between those that mix little and move little on the one hand, and those that move continuously between different food plants and eat many species in the course of a day.

For example, individuals of some grasshopper species may feed on dozens of species in a day, while others, that may be equally polyphagous over their lifetime, feed on only two or three in a day (CHAMBERS *et al.* 1996). There is little known about the costs and benefits of these different strategies, although data on grasshoppers indicate that individuals mixing their food plants have a faster growth rate than those that do not, and thus benefit individually from taking the mixture (BERNAYS *et al.* 1994, BERNAYS & MINKENBERG 1997).

Among Lepidoptera mixtures tend not to be beneficial (BERNAYS & MINKENBERG 1997, HAGELE & ROWELL-RAHIER 1999, SINGER 2000) except over long time frames, where the normal food of first instar larvae is different from that of the later stages (GASTON *et al.* 1991). On the contrary, it is not uncommon for individuals to increase their fidelity to a plant that has been fed upon, the phenomenon of "induction of preference" (JERMY *et al.* 1968, JERMY 1987), and in some cases at least, individuals benefit physiologically from remaining with a single host species (KAROWE 1989). Thus, many species are relatively immobile and more or less restricted to the host plant chosen by the mother. A typically sedentary species is the noctuid, *Trichoplusia ni*. The mobility of some generalists is necessitated by other types of constraints. For example, armyworms (*Spodoptera* spp.) that feed mainly at night and must find shelter off the plant during the day, may move to different plants on different days. Also, restricted food patches may dictate movement, as with *Heliothis virescens* feeding on tobacco, where each flower (the preferred tissue) is too small to support much feeding, at least of the later stadia. In some cases large species that feed on small herbaceous plants finish individual plants and must then search for additional ones (JONES 1977). At high population densities, some species such as *Lymantria dispar* and *Spodoptera* spp. move extensively, while the most extreme strategy is found in a number of generalist arctiids that spend relatively long periods moving, especially in the later stadia, when they encounter and feed upon many different foods. They may eat parts of up to 20 different plant species in the course of a day. Such is the case with *Grammia geneura* (SINGER 2000).

This study is an experimental analysis of foraging by caterpillars of two species of polyphagous Lepidoptera that appear to be at the extremes of the possible foraging strategies, the noctuid *Trichoplusia ni*, and the woolly bear arctiid, *Grammia geneura*. Using field and laboratory observations we asked a) how do generalists at the species level differ in individual foraging tactics? b) does induction of preference play a role in the patterns observed? c) what physiological or ecological factors might influence such differences?

MATERIALS AND METHODS

The study organisms

Grammia geneura (STRECKER) (Arctiidae) is a species occurring in arid savanna of SW United States and Mexico. There are two generations each year in SE Arizona where we studied them. Adult females do not feed and have little flight ability. They lay large numbers of eggs in loose batches onto the substrate, which is sometimes simply the leaf litter. They do not place eggs on plants. Newly hatched larvae must find their food plants, and in some seasons they may have to wait for the germination of plants after rain. Larvae are dark, covered in long setae, and apparently distasteful, at least to some predators. Populations used for this study were from southern Arizona. They have one generation of larvae that develop over a period of several weeks on herbaceous plants available after the summer rains. A second generation of larvae begin their development in the fall, then, after sheltering during winter, they resume development on the herbaceous plants (mostly different species) that appear in spring.

Trichoplusia ni (HÜBNER) (Noctuidae, Plusiinae) is a worldwide pest of many vegetables and other plants. It is fast-growing, multivoltine and highly polyphagous on herbaceous plants (SUTHERLAND & GREEN 1984). Adult females are competent fliers and lay single eggs on many different plant species to which they are attracted; individuals readily lay on more than one plant species (LANDOLT & MOLINA 1996). Larvae initiate feeding beside the egg and typically remain on the same plant until pupation. They are green and apparently cryptic on their host plants and known to be palatable to numerous different predators. Populations used in this study were from southern Arizona. They have been found on vegetables in gardens and on numerous wild plants including several species of Asteraceae.

Field observations

In this work we report on individuals observed in nature during daylight hours when most foraging occurs. Temperatures at foliage level varied from approximately 25 to 30°C. Eleven final stage larvae of *G. geneura* were continuously observed for periods of at least six hours. Most records of last stage *T. ni* indivuals were of two to three hours but these were supplemented with one six-hour observation, and intermittent observations on nine individuals over five days (four on *Ocimum basilicum*, three on *Mentha spicata*, one on *Lactuca sativa* and one on *Encelia farinosa*).

During continuous observations we recorded manually all feeding and locomotor events as well as plant species fed upon. Budgets were constructed for time spent feeding and walking. Survivorship analyses were used to examine the distribution of feeding bout lengths and interbout lengths (SIMPSON 1982). It was necessary to pool both of these for each species, to obtain sufficient numbers of each.

Laboratory observations of foraging patterns

Grammia geneura larvae were reared individually in plastic containers (8 cm high × 16 cm diameter) with screened ventilation holes. The bottom of each container was lined with filter paper. Three food plants were provided in symmetrically arranged vials of water in quantities such that caterpillars could feed *ad libidum*. The species were *Plantago insularis* (Plantaginaceae), *Malva parviflora* (Malvaceae) and *Tithonia fruticosa* (Asteraceae). One treatment had three vials with one

of each plant species available, while the other treatments had three vials, each with a sprig of the same food. All plants were acceptable and supported development (SINGER 2000). Containers were kept in an environmental chamber with L:D cycle of 12:12 and temperatures of 28:24°C. Mean durations of development, from hatching to silking, were 39±2, 43±2 and 80±4 days respectively. The foods were replaced on alternate days but always refreshed prior to observations. A total of 10 or 11 individuals was observed in each of the four treatments for a period of four hours early in the final larval stadium when feeding is maximal. Fluorescent lights provided illumination and the temperature was kept at 26 to 28°C. We recorded feeding, movement and location using the Observer program (NOLDUS 1991) loaded onto a Dell laptop computer.

Trichoplusia ni larvae were reared in groups of twenty in plastic cups (7 cm high × 8 cm diameter) with cut sprigs of three foods available *ad libidum*. The food plants were *Mentha spicata* (Lamiaceae), *Lactuca sativa* (Asteraceae) and *Ocimum basilicum* (Lamiaceae). The foliage of the three species in the mixed-food treatment was intermingled to allow movement between foods, and though not placed in vials of water, it was repaced daily. Larvae have been found on all three foods in nature and these species are known to support quite rapid development (BERNAYS & MINKENBERG 1997). Containers were kept in an environmental chamber with L:D cycle of 12:12 and temperatures of 26:23°C. There were significant differences in development rates. Mean durations of development, from hatching to wandering, were 8±1, 10±1 and 9±1 days for *Mentha*, *Lactuca* and *Ocimum* respectively. On day two of the final larval stadium the insects were transferred to individual plastic boxes (11×11×4 cm) with screened ventilation holes. They were provided with a mixture of the same three foods, or only one. In either case, they were in three vials, one of each species, or all three of the same species, in three symmetrically arranged vials of water, again, *ad libidum*. Six individuals were observed for six hours on each of the four treatments. Fluorescent lights provided illumination and the temperature was kept at 27°C. We recorded all feeding, locomotion and resting positions using an HP hand-held computer programmed as an event recorder.

Experiment on induction of preference

The results clearly indicated that *G. geneura* could not be exhibiting any induced preference for previously eaten food because larvae moved between food plant species too frequently. However, to determine if there were restrictions in food acceptability due to experience in *T. ni*, the following experiment was carried out with the offspring of three adult females reared from field-collected larvae. Newly hatched larvae were separated into three groups of approximately 50 and reared in plastic containers (28 cm high × 15 cm diameter) with one of three foods, *Mentha spicata*, *Lactuca sativa* or *Ocimum basilicum*. An hour before the experiment food was removed from the rearing containers. Sixteen individual larvae of the same age (±2 d) from each treatment were placed singly in Petri dishes (8 cm diameter). These were lined on the bottom with damp filter paper on which was placed a single freshly cut disk of leaf (1 cm diameter) of each of the three foods, arranged symmetrically round the periphery. Caterpillars were taken singly from their rearing containers and each placed centrally in a test dish. Individuals took between five minutes and an hour to initiate movements. We recorded the first food contacted and the first food upon which the caterpillar fed continuously for 30 seconds or more.

Finally, first instar larvae from one female *T. ni* were placed on *Mentha*, *Ocimum* or *Encelia farinosa* in the field. There were approximately thirty of each. Most were lost, presumably due to predation, but one on *Mentha*, two on *Ocimum* and two on *Encelia farinosa* survived, and these were photographed to record morphological differences observed.

RESULTS

Field observations

There was a marked contrast in the foraging patterns of the two species of caterpillars in the field. Average percent of time spent walking was 0.4±0.1 in *T. ni* and 14±4 in *G. geneura*. Average percent of time spent feeding was 21±3 for *T. ni* and 15±2 for *G. geneura*. Of the nine individual *T. ni* followed for five days, none moved from the branch of the plant upon which it was first seen, and moves to new

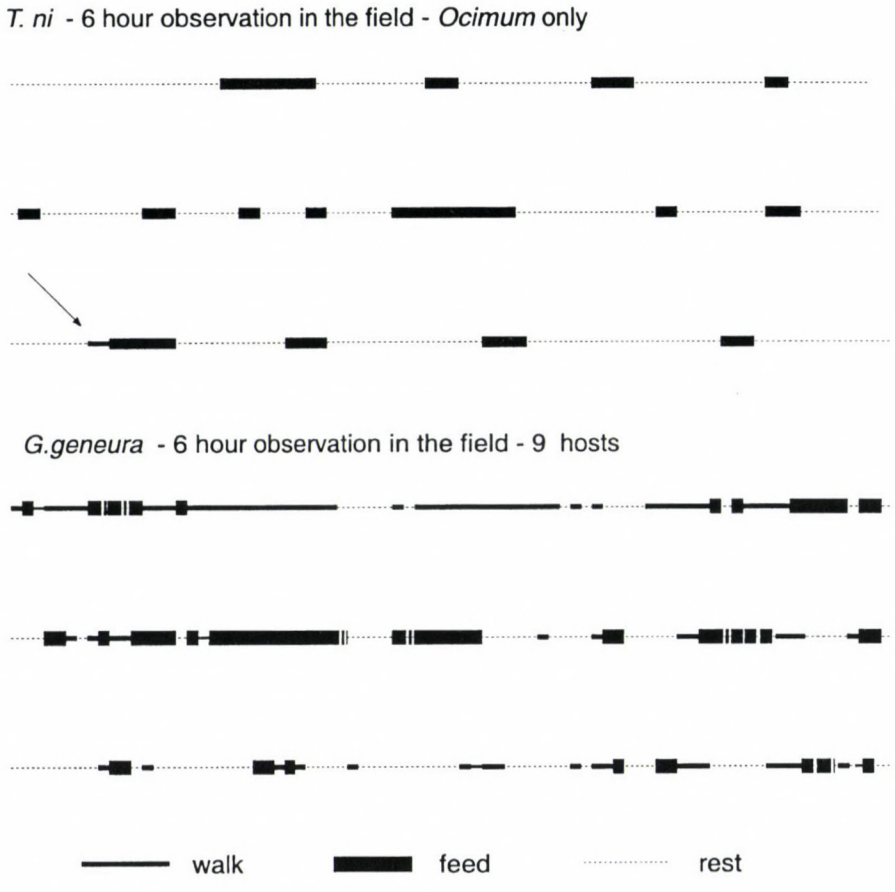

Fig. 1. Examples of data from field observation of last instar larvae of *Trichoplusia ni* and *Grammia geneura* demonstrate the contrast in patterns of foraging. Note the absence of locomotor activity in *T. ni* except for the small walk before a meal during hour five (arrow)

leaves were generally initiated when a leaf was completely eaten, apart from the petiole and parts of the midrib. This involved a maximum move of eight cm. On one occasion, a larva on *E. farinosa* moved to a new leaf after eating less than half of another. All individuals of *G. geneura* moved between plants with numbers of individual plants eaten in a six-hour period varying from eight to 41, and numbers of different species eaten varying from two to nine. In no case was a whole leaf eaten. Figure 1 gives the pattern of feeding, walking and resting in one individual early in the final larval instar of each species watched for six hours in the field. The *T. ni* larva remained on the host, *Ocimum*, feeding at intervals but without moving from the same leaf. There was one short interval of movement (arrow) when it crossed the mid vein and fed on the other side of the leaf. The *G. geneura* larva, by contrast, moved frequently and had many feeds on nine different plant species.

Field conditions are variable and the food plants of the two species differed in size and distribution so that it is difficult to determine the extent to which the different foraging patterns were truly intrinsic. Furthermore, the precise stage of development of individual caterpillars in the field was unknown. Laboratory observations carried out under very similar conditions for the two species and in similarly-sized containers with standard insects, indicate that the differences are maintained in large degree.

Laboratory observations

Proportion of time spent feeding was similar overall in the two species. However, larvae of *G. geneura* varied in the amount of time spent feeding on different plants, with *Plantago* being eaten for a much greater proportion of the time than either of the other single foods or the mixture (Fig. 2a). *G. geneura* individuals spent more time moving than *T. ni* (Fig. 2b), and had more feeding bouts (Fig. 2c) of shorter duration (Fig. 2d) on all three plants individually and in the mixture.

Survivorship analysis of the feeding bout lengths demonstrates differences in the pattern of bouts more fully (Fig. 3). On all host plants, *G. geneura* had larger proportions of shorter feeding bouts than *T. ni* (Fig. 3a) while the differences were much more extreme in the field (Fig. 3b). Here, more than 50% of bouts taken by *G. geneura* were of durations less than one minute, whereas most bouts of *T. ni* were of ten minutes duration or longer. In the survivorship analysis of the interbout lengths we found that *G. geneura* has a continuum of interbout intervals with no clear break between short and long intervals (Fig. 4). By contrast, with *T. ni* we found that there was a population of short interbouts and a population of longer interbouts (Fig. 4). This suggests that the feeding bouts in this species are grouped together to form meals. This was not an artifact of different behavior by different

individuals or of different behavior on different foods, because all individuals showed similar patterns and appeared to do so on the different foods. However, data were too few to statistically compare behavior on the different foods.

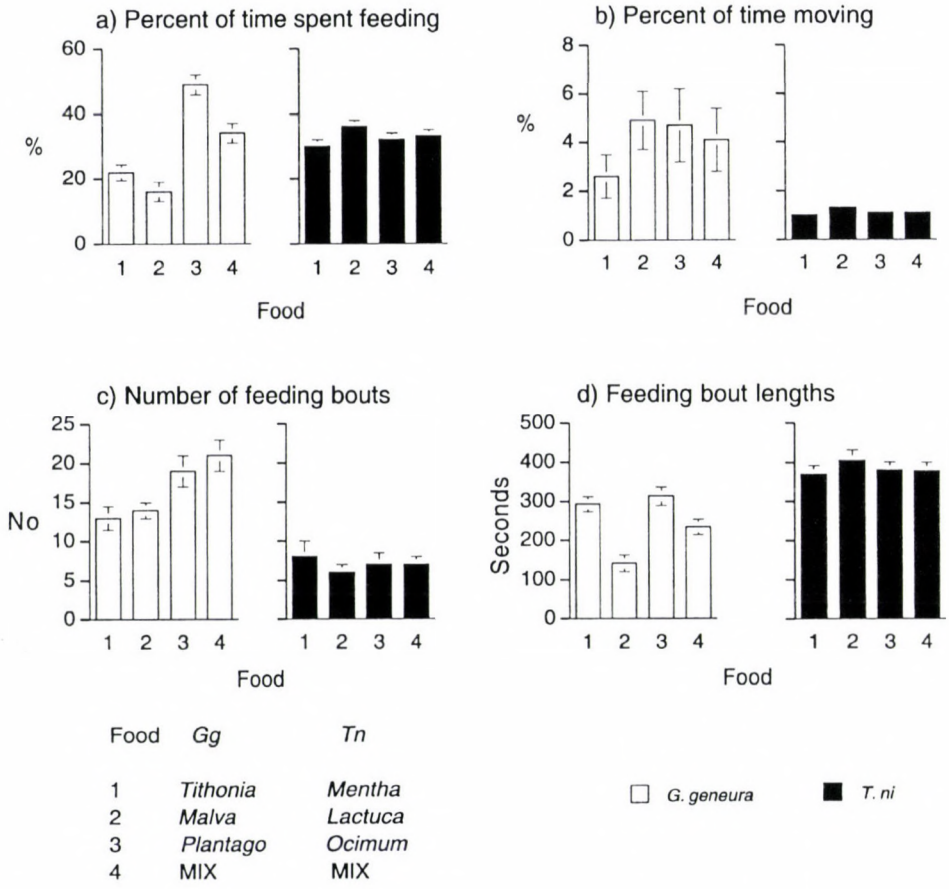

Fig. 2. Activity budgets of last instar larvae of *Trichoplusia ni* and *Grammia geneura* in laboratory observations on various food plants. Mean and standard errors given. 2a. Percent of time spent feeding: *G. geneura* significantly different among treatments (Kruskal-Wallis test, $P < 0.01$); *T. ni* no significant differences (Kruskal-Wallis test, $P > 0.9$). 2b. Percent of time spent moving: no significant differences among treatments for either *G. geneura* or *T. ni* (Kruskal-Wallis tests, $P > 0.5$). 2c. Number of feeding bouts. *G. geneura* significantly different among treatments (Kruskal-Wallis test, $P < 0.01$); *T. ni* no significant differences (Kruskal-Wallis test, $P > 0.5$). 2d. Feeding bout lengths. *G. geneura* significantly different among treatments (Kruskal-Wallis test, $P < 0.01$); *T. ni* no significant differences (Kruskal-Wallis test, $P > 0.3$)

Four variables were used to demonstrate other major differences in foraging pattern by the two species in the laboratory. First, the likelihood of rejection of host plants that are encountered during locomotion. In all four treatments, *G. geneura* often rejected the available host(s), especially *Malva*, although this was highly

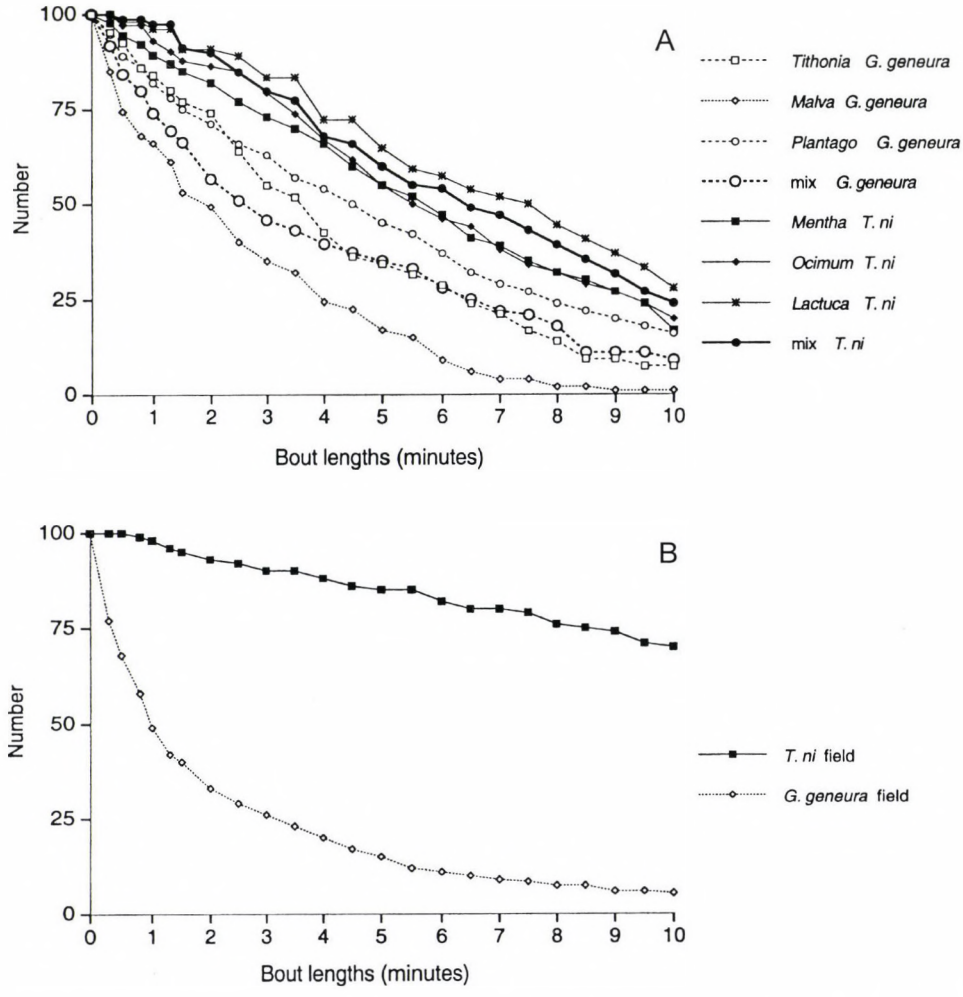

Fig. 3. Survivorship curves of feeding bout lengths of last instar larvae of *Trichoplusia ni* and *Grammia geneura* in observations on various food plants. All values are presented as percentages so that treatments and species can be compared. 3a. Laboratory observations on three single plant species and a mixture for each species. 3b. Field observations with *T. ni* feeding on a single plant and *G. geneura* feeding on a mixture

suitable for development (SINGER 2000). By contrast, *T. ni* rarely rejected a plant encountered although encounters with new foods were relatively uncommon (Fig. 5a). This is demonstrated also by the number of switches between food eaten during observations (Fig. 5b). It reflects a generally higher level of activity and transitions between behavioral states (Fig. 5c). Interestingly, *G. geneura* caterpillars spent much of their resting time off the plants while *T. ni* caterpillars rested at their feeding sites (Fig. 5d).

T. ni caterpillars showed different host-related behaviors after being reared on single hosts, showing a preference for the rearing plant. Those reared on any one of the three test plants oriented toward, and made contact first with the rearing host when given a choice (Fig. 6a). Some individuals moved after an initial encounter, so that the first feeding bout was on a different plant, but in most cases, the first feeding bout of 30 seconds or more was on the rearing plant (Fig. 6b).

There was a marked difference in appearance of full grown *T. ni* caterpillars reared on different hosts. On the very bright green *Ocimum*, individuals were of the same bright green hue and rested lengthwise along the leaf; on the dark green *Mentha*, they were closely matched to the colour of veins along which they rested; on the grey *Encelia*, caterpillars were also grey, and rested in looped fashion on the leaf surface (see Fig. 7). The most extreme, on *Ocimum* and *Encelia farinosa,* are shown in Fig. 7. Clearly, the individuals are more cryptic on their rearing hosts, but would not be on the other host.

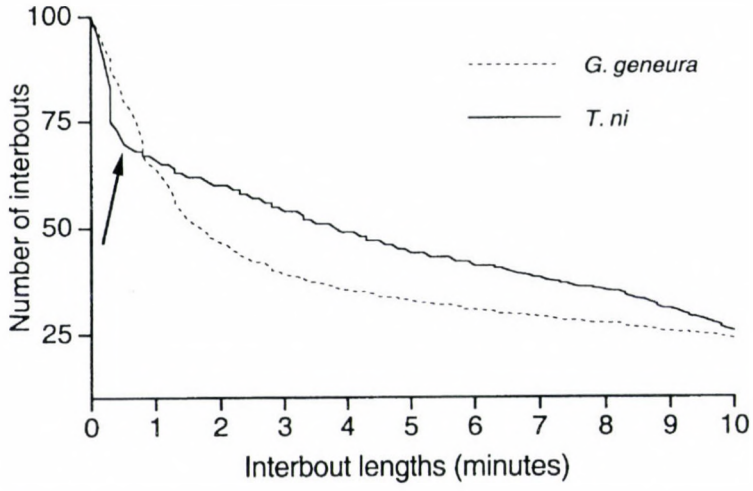

Fig. 4. Survivorship curves of interbout lengths of last instar larvae of *Trichoplusia ni* and *Grammia geneura* in observations on various food plants in the laboratory. All values are presented as percentages so that species can be compared. Note that there is a break (arrow) in the curve for *T. ni* indicating two populations of interbouts, shorter ones that are within a meal and longer ones between meals

DISCUSSION

We have shown that caterpillars of two generalist species of Lepidoptera have highly contrasted foraging patterns in nature; one with great mobility and short feeding bouts on sequences of different foods, the other with restricted mobility, and clear fidelity to a single food. All of the behavioral parameters measured emphasize the marked difference in foraging strategy of these caterpillars, such

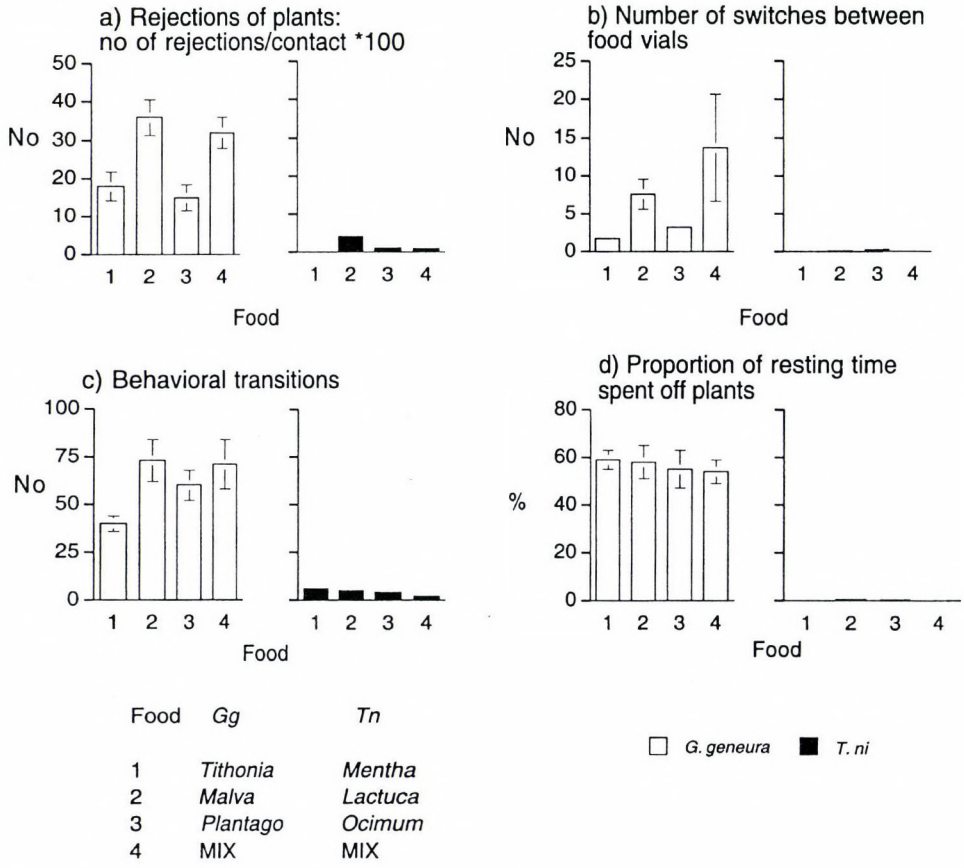

Fig. 5. Foraging details of last instar larvae of *Trichoplusia ni* and *Grammia geneura* in laboratory observations on various food plants. Mean and standard errors given. 5a. Rejections of host plants. 5b. Switches between food vials. 5c. Behavioral transitions: between feeding, walking and resting. 5d. Resting time on or off food plants

that the two cannot be considered together in foraging models, even though both are polyphagous species.

Of the three foods tested singly in the laboratory, *G. geneura* fed for very different periods on each one, with the time spent feeding on *Plantago* being three times that spent feeding on *Malva*. Growth and development of *G. geneura* is similar on these two plant species (SINGER 2000), and amounts eaten per unit time are similar (BERNAYS & SINGER 1998), suggesting that differences in feeding time reflect nutritional compensatory behavior. By contrast, *T. ni* spent similar amounts of time feeding (about 30%) on all three plant species tested although *Mentha* supported a significantly faster growth rate than either *Lactuca* or *Ocimum* (BERNAYS

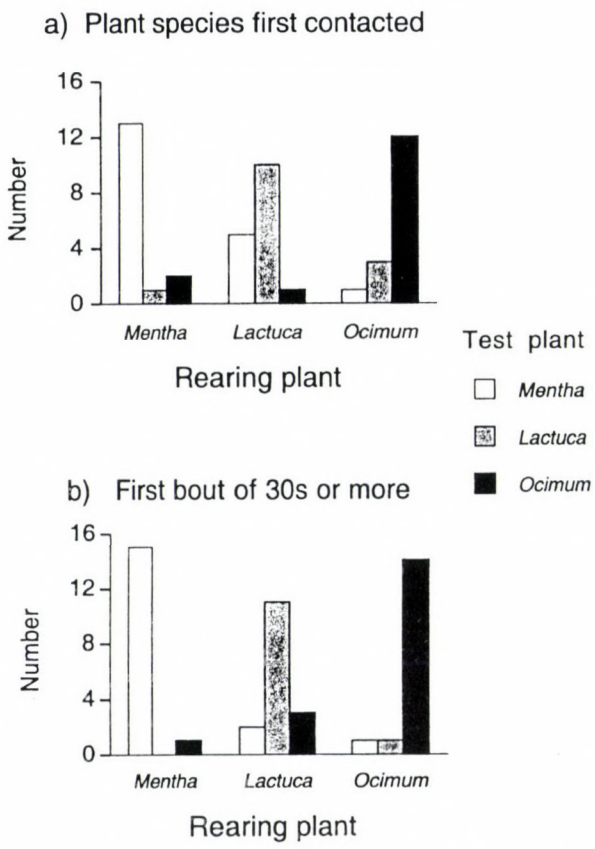

Fig. 6. Induction of preference in *Trichoplusia ni*: a = Plant species first contacted after rearing on *Mentha*, *Lactuca* or *Ocimum* and then given a choice of all three; b = Plant species upon which the first feeding bout is at least 30 seconds after rearing on *Mentha*, *Lactuca* or *Ocimum* and then given a choice of all three

& MINKENBERG 1997). Rates of food intake were not measured but all three plants are soft and eaten with apparent ease. There could be differences in rate of intake, however, relating to differences in palatability. Alternatively, this species may eat all acceptable foods maximally, optimizing intake rate rather than balancing specific nutrient requirements. Perhaps with its rapid development rate, obtaining sufficient nutrition for growth is generally a limiting factor, so that any foods that are of reduced nutrient value cannot be eaten in quantities that allow optimum development rate.

On the mixture of foods, both caterpillar species fed for 30% of the time in the laboratory. *G. geneura* individuals mixed the foods eaten and 30% is actually similar to the mean of the different individual values obtained with the three treatments in which single plant species were provided. *T. ni* caterpillars fed almost entirely on a single food, even when offered the mixture, and the time spent feeding was not different from that found with each of the treatments with a single food plant species.

Percent of time spent moving in laboratory experiments was also relatively high (at about 4% of time) in *G. geneura*, although much less than in the field. It was somewhat less on *Tithonia*, at least during the period of observation. Growth rates are relatively low on *Tithonia* (SINGER 2000) and it is possible that feeding on this plant also reduced activity for some reason. The limited time spent feeding on *Tithonia* was due to relatively few feeding bouts. The small proportion of time spent feeding on *Malva* however, was due to both few feeding bouts as well as their shorter duration. Since *Malva* contains high levels of protein (SINGER unpubl.), the reduced time spent feeding is further support for the idea that *G. geneura* limits intake when need is satisfied. Number of feeding bouts and the average lengths of feeding bouts were similar across foods, including the mix for *T. ni*, although protein levels varied (single measurements on pooled plant material gave approximate values of 4, 3 and 2% fresh weight for *Mentha* and *Ocimum* and *Lactuca* respec-

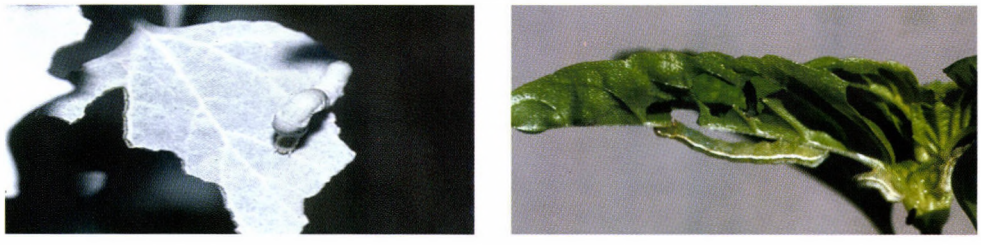

Fig. 7. Photographs of *Trichoplusia ni* reared in the field on either *Mentha* (left) or *Encelia* (right)

tively, BERNAYS unpubl.). The similarity in behavior on the three foods is consistent with a strategy of maximizing food intake irrespective of protein content.

On all foods tested in the lab *T. ni* bout lengths were longer than those of *G. geneura*, but the difference between the species is considerably greater when bout lengths in the field are examined. The reasons for this are not known, but several factors may contribute. Individuals reared in the laboratory experienced none of the disturbances from environmental change or presence of potential natural enemies that might enhance adaptive patterns of risk avoidance such as selective attention to food (causing longer bouts) in the case of *T. ni* (BERNAYS 2001) or movement away from damaged plants (causing shorter bouts) in the case of *G. geneura* (SINGER 2000). It is also possible that the state of the plants (cut vs growing) had an effect, for example if cut plants become less palatable to *T. ni* and more palatable to *G. geneura*. Finally, the arrangement of the foods may have contributed to the differences. In nature, we found *T. ni* on food resources of substantial size, where perhaps there is little else to perceive, whereas in the lab experiments, the bouquets of food were small. By contrast, in nature, *G. geneura* commonly feeds upon very small food items such as young seedlings or plants stunted under arid conditions, while the bouquets of food in the laboratory were often larger. What ever the reason, it demonstrates the importance of using field data as well as laboratory data in any study of foraging tactics.

With respect to interbout lengths there was a major difference between the two species. *T. ni* larvae showed a clustering of feeding bouts with small interbouts between them, as well as many longer interbouts. This distinction is shown by the survivorship analysis of interbout lengths, in which there is a marked break in the curve providing a criterion for describing two populations of interbout lengths, and thus meals, made up of more than one feeding bout. No such criterion was found for *G. geneura*. The differing patterns were brought about by the fact that most *T. ni* caterpillars often had one or more small interbouts following a long feeding bout. Thus a meal often consisted of a long bout followed by a short interbout and another short bout. The underlying cause of such a pattern may be the declining level of excitation during a meal as has been described for grasshoppers and various other animals (SIMPSON *et al.* 1988). The reason for not seeing this in *G. geneura* may relate to the overall pattern of short bouts and the related effects of relatively high levels of locomotor activity.

Larvae of *T. ni* rarely rejected a food after mouthpart contact, or switched to a new food when alternatives were available. When resting they stayed at or near the feeding site. By contrast, *G. geneura* commonly rejected plants, even those that were highly favorable and that led to relatively fast development when presented alone. Furthermore, *G. geneura* generally rested away from the food after a post-

prandial walk. The physiological bases for these differences are unknown, but perhaps involve variation in levels of, or sensitivity to, octopamine (ROEDER 1999). An ultradian rhythm in activity appears to be important in the postprandial locomotion of *G. geneura* (BERNAYS & SINGER 1998). The functional aspects of the differences can also only be speculated upon, but it is clear that *T. ni*, being cryptic on its food, would be better served to move little and feed decisively. The defensive strategies of *G. geneura* appear to involve chemical defenses (and possible aposematism – M. S. SINGER unpubl. results) and active movement away from plants they have recently fed upon.

Finally, *T. ni* exhibited strong induction of preference. That is, there was clear evidence that the rearing plant was strongly preferred over other acceptable alternatives. Previous work on this species is equivocal; LEE (1990) found evidence of induction while M. WEISS (unpubl. data) found none. In the present study induction was very clearly demonstrated by both orientation activity in the presence of a choice and acceptability after contact. The behavior of *G. geneura* precludes induction of this sort and the question remains, why does *T. ni* show induction? There is no clear answer and JERMY (1987) has even questioned the adaptive value of the phenomenon in general.

Many have suspected that induction is a phenomenon whose function is explained physiologically. Thus, if detoxification enzymes or specific proteases are induced by experience of certain metabolites or proteins, it is surely safer and more economical to remain with one host plant species. Although such enzymic induction is well known (YU 1986), its adaptive value is still uncertain. Growth may be improved by staying with the rearing host (e.g., KAROWE 1989), or it may not (e.g.,ESCADOR 1993). Certainly, induction of specific detoxification enzymes caused by ingestion of a particular toxin may then allow a food containing the toxin to be eaten with impunity (GLENDINNING & SLANSKY 1995, SNYDER & GLENDINNING 1996), and this alone may be the functional value of induced enzyme production.

Other aspects of the biology of the insect may be relevant however, though a survey of the literature on induction provided little help: among the species where it has been reported as absent, weakly present, or strong, we found no correlates with respect to phylogeny, diet breadth, egg clustering, or crypsis [the analysis involved the species reported in JERMY (1987) and all references found since, see appendix 1]. However, among the reports available it seems that most lepidopteran species tested show it to some extent, at least in some populations. In the behavior of *G. geneura* and other food-mixing species we have reason to believe that induction of food preference does not occur. It is possible that sequestering the larvae with single high quality foods may induce an increased preference for that food,

but in nature such restriction does not occur. Analyses of bout lenghts in the field also shows that these decline on a food that is eaten for several bouts, but that longer bouts occur following a switch to a new food (SINGER 2000). This further implies an absence of induced preference for the experienced food.

We suggest that induction has some general value in focusing of attention on foods currently available (BERNAYS 2001) but that, in the case of *G. geneura*, where the problem of predation is apparently low, other factors mitigate against induction. For example, mixing may be important for reducing the risk of ingesting high levels of a toxin or of feeding extensively on a plant with a nutrient imbalance. Such factors may be important in an exceedingly diverse plant community with great chemical variability among species (SINGER 2000).

Caterpillars are extremely vulnerable to predation and parasitism (e.g., HEINRICH 1993, MONTLLOR & BERNAYS 1993, WESELOH 1993, BERNAYS 1997) with mortality levels that may exceed 99.5% (e.g., MIRA & BERNAYS 2002), and the relationship between caterpillars and their host plants is surely influenced by higher trophic levels (e.g., BERNAYS 1988, BOWERS 1993, STAMP & WILKINS 1993, DYER & FLOYD 1993, SINGER 2000). It is important therefore to consider the foraging strategies in the light of risk from natural enemies, and the tactics used by the caterpillar species for avoidance of predation and parasitism.

Grammia geneura and *Trichoplusia ni* provide a marked contrast in their adaptations for avoiding predation, which are probably not unrelated to foraging strategy. *G. geneura* is a member of the subfamily Arctiinae in which species are often aposematic, and larvae are all hirsute. We have no information on chemical defenses of *G. geneura*, although there are indications of unpalatability (SINGER 2000). In addition, some secondary metabolites stimulate the same taste cell as sugars and amino acids (BERNAYS *et al.* 2000), suggesting that they are of particular value. Larvae are often aggregated and conspicuous to humans. From these characters we believe that *G. geneura* is aposematic and that this allows it to be conspicuously mobile and protected from much predator attack.

In contrast, *T. ni* typifies many species of cryptic caterpillar with its smooth cuticle and general green coloration. Its behavior appears to be cryptic also. On larger leaves with a conspicuous main vein, such as *Ocimum*, it commonly rests along the vein; on plants with smaller leaves with a network of veins, such as *Mentha,* it more often rests in the looped position. It is acceptable to many predators (BERNAYS 1988, BERNAYS & CORNELIUS 1989) and parasitoids (FLINT 1987) so that its only defense is to be inconspicuous. For this to be effective, mobility must be restricted (HEINRICH 1993) and feeding should be both rapid and efficient (BERNAYS 1997). Food mixing is not compatible with these constraints.

Restricted acceptability of potential foods is thought to improve decisiveness, and thus improve feeding efficiency and crypsis in specialists (BERNAYS 1996, 1998). A similar benefit may accrue to generalists that show an induction of preference. In addition, if feeding on different plant species can lead to morphological changes that enhance crypsis, as we found here, one would expect selection for behavior that improves fidelity to the plant already experienced. Such morphological plasticity has been reported in other contexts (POULTON 1885, GRAYSON & EDMONDS 1989, GREENE 1989), but it would be interesting to examine its occurrence in relation to the occurrence of induced preference in other species. As well as visual crypsis, chemical crypsis has been demonstrated (ESPELIE & BROWN 1990) and it is known that the chemistry of the caterpillar cuticle varies with its food in *Manduca sexta* (ESPELIE & BERNAYS 1989, CORNELIUS & BERNAYS 1995). Recently, this has been demonstrated to be important in predator avoidance (PORTUGAL 2000). There is thus the possibility that induced preference for a particular food plant may be accompanied by chemical crypsis.

In conclusion, we emphasize a major contrast in foraging strategies of the caterpillars of two generalist species of Lepidoptera, including the propensity for induction of preference. The contrast suggests a relationship with several aspects of the biology of the two species, including growth rates and detoxification needs on the one hand, and divergent strategies for avoiding risk of attack from natural enemies on the other. Whether the two species fit into two clear alternative categories will require studies on a range of other polyphagous species.

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APPENDIX 1

Analysis of lepidopteran species tested for induction of preference includes all species listed in JERMY (1987) and the following:

Colias philodice (KAROWE 1989)
Thyridopteryx ephemeraeformis (WARD *et al.* 1990)
Diacrisia virginica (DETHIER 1988)
Pseudaletia unipuncta (USHER *et al.* 1988)
Pieris rapae (RENWICK & HUANG 1995)
Mamestra brassicae (JERMY *et al.* 1987)
Vanessa cardui, *Heliothis virescens* (BERNAYS unpubl.)

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ON THE STRUCTURE OF THE PANNONIAN FOREST STEPPE: GRASSLANDS ON SAND

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The paper discusses the floristic and coenological structure of the Pannonian part of the Eurasian forest steppe biome. The vegetation of the sand landscapes of the Hungarian lowlands is examined where a climate gradient was detected with decreasing annual precipitation from NW to SE. For studying the effect of the gradient, sites in three different sand landscapes were selected. With increasing aridity, semidesert-like communities become dominant and the steppe grassland, *Festucetum wagneri* loses almost all of its steppe characteristic. Among the soil factors it is the organic matter content that explains the closed steppe-open grassland trend. The chorological analysis of the forest and steppe grassland species does not support – despite previous expectations – an opposite distributional trend for the two groups.

Key words: climate gradient, forest and steppe flora gradient, landscape mosaic, raster vegetation map

INTRODUCTION

The forest steppe can be defined as a separate vegetation belt developed in the transitional climate between the zones of closed forests and steppe grasslands. In this belt, more or less closed forests alternate with closed grasslands, forming a landscape of mosaic appearance (WALTER 1943, BERG 1958). Abiotic conditions, herbivores, and fires together are responsible for this mosaic determining whether at a given locality forest or grassland appears.

The zone of the forest steppe is extensive and runs in Eurasia from the Pannonian lowland to China. During its history, the Pannonian part of this belt used to be in close connection with other parts of the zone through flora corridors. At present it is isolated from those. The great richness of this biome is affected by the several landscapes of the Carpathian Basin as documented by the extensive floristic and geobotanical literature.

Due to the transitional climate of this belt, a late summer-early autumn semiarid period lasts for at least two months in certain years (VARGA *et al.* 2000). Recently, statistical analysis showed that the climate of the Pannonian forest steppe is far from being uniform. In the Great Hungarian Plain, e.g., in the Duna–Tisza Interfluve (the area between the Danube and Tisza rivers) a NW–SE climate gradient exists (BORHIDI 1993).

Accordingly, vegetation scientists should question whether the effect of the climate gradient manifests itself in the vegetation, and if so, how (cf. KOVÁCS-LÁNG *et al.* 1999). As the gradient intersects the forest steppe belt, one may get insights into the structure of this biome as well.

First, the forest component of the zone was investigated. As the forest stands remained few in number, instead of studying the gradient in forest structure, the individual distributional data of forest species was examined (FEKETE *et al.* 1999). A conclusion was reached that there is a common trend in the distribution of forest trees, shrubs and understorey species in the Danube–Tisza Interfluve. The chorological pictures reveal an unequivocal diminishing of forest flora from north to south. Two different phenomena appear here simultaneously: both the number and abundance of forest species decreases continuously to the south.

In this paper the grassland component of the mosaic will be analyzed and discussed.

MATERIAL AND FIELD METHODS

Among the abiotic conditions influencing the formation of the vegetation pattern of this zone, the substrate has one of the strongest impacts. Two kinds of substrate, loess and sand are widely distributed in the interior of the Carpathian Basin. The vegetation on loess is generally of higher productivity. Continuous natural vegetation is rarely to be found here as agrarians have been cutting down the forests and breaking up the fields since the early postglacial times. In the semiarid climate, sand is less favorable for vegetation far from the water table. Productivity of herbaceous sand vegetation is particularly low on moving sand, where, for edaphic reasons, semidesert-like open grasslands occur as well. One can meet on sand, even today, larger patches of semi-natural vegetation. This was the reason for carrying out the experiments on sandy vegetation, particularly on the vegetation of calcareous rough sand in the Small and Great Hungarian Plains.

In the Hungarian plains, numerous sand landscapes isolated at present from one another by agricultural fields, settlements etc. are known to still bear more or less natural vegetation. In the course of a 4-year period, a number of sand landscapes were visited, where sites more or less characteristic of the given area, were selected. These sites were investigated using the same design and sampling methods. Studying the possible effect of the climate gradient, three sites (situated at the two opposite ends and at the middle of the gradient) were chosen for evaluation and comparison. For Site 1 a landscape in the Small Hungarian Plain was chosen, while the two other sites are situated in the Great Hungarian Plain (Fig. 1). (Distances: Site 1-Site 2: 128, Site 2–Site 3: 52, Site 1-Site 3: 148 kilometers.) In the landscapes, the place of the studied plots of 2 hectares was selected with the help of colored or black and white aerial photos. At each plot, a grid was created of 14 columns and 7 rows, altogether with 98 raster cells. In this way, one cell of the given grid covered 14 m × 14 m. Vegetation maps were created with the help of two different methods. First, coenological relevés of 1 m^2 quadrats were completed in each raster cell, along with 49 point measurements of soil quality parameters. In order to create a "traditional" map, the relevés were classified by the Zurich-Montpellier method, then a given cell – 14 m × 14 m – of the grid was qualified according to the relevé situated inside it. In this way vegetation maps – so-called raster vegetation maps (DIERSCHKE 1994) – were prepared. In

accordance with the second method, releveès were also classified by numerical methods (multivariate analysis), and the results of the classification were reallocated into the grid, and vegetation maps were also developed this way. The novelty in the methods described above lies in the use of vegetation maps prepared in a standard and repeatable way. It seems reasonable to compare the whole mosaic of the vegetation, not only the individual plant communities separately. In the comparisons, special attention was paid to the steppe plants.

RESULTS

The climate gradient

This was defined by the change in level of precipitation as one of the main factors that form the abiotic and water-limited sand vegetation. Data from the meteorological stations closest to the study areas were obtained. There were five categories, based on precipitation levels. Proportions of each category at the meteorological stations are shown in Figure 2. Years with high rainfall (701–800 mm) decrease from NW to SE. In parallel to this, dry years (300–400 mm and 401–500 mm) increase. The share of years characterized by moderate precipitation amounts (501–600 mm) shows a uniform, explicit growing tendency. It has to be empha-

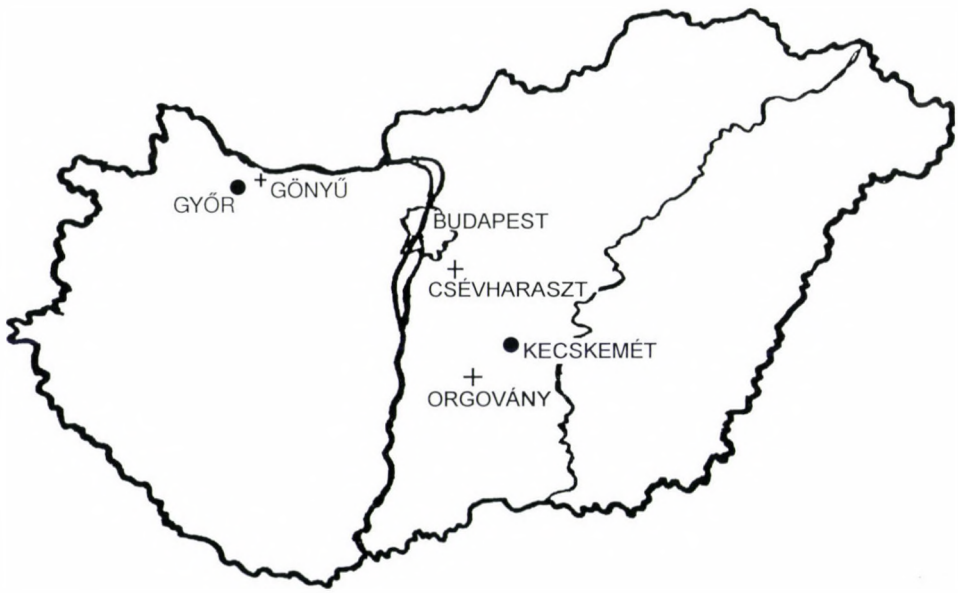

Fig. 1. The geographical position of the three sites. Site 1: Gönyű, Site 2: Csévharaszt, Site 3: Orgovány

sized that in case of years with low or moderate precipitation amounts, the warm summer period is the driest (cf. ZÓLYOMI *et al.* 1997, KUN 2000). According to the so-called semiaridity water deficit index (where the monthly amount of the precipitation and the monthly mean temperature above 0°C are taken into consideration), the number of semiarid years grows towards south-west (BORHIDI 1993).

Vegetation maps

Maps based on the traditional concept. Figure 3 presents the vegetation maps of the three sites based on classical concept. It has to be recalled that in this case, dominant and characteristic species were preferred for the identification of the communities. Regarding all the vegetation maps, 7 units representing herbaceous communities and 4 units representing scrubs (or forest) were distinguished.

Generally, perennial grasslands cover the areas. Their two contrasting groups are open semidesert-like perennial grasslands, and semiclosed-closed steppe grasslands. In the first group, the Pannonian endemic *Festuca vaginata* dominates. *Festucetum vaginatae* (1) is composed of perennial bunchgrasses such as *F. vaginata, Stipa borysthenica, Koeleria glauca* mixed with perennial herbs like *Euphorbia seguieriana, Alkanna tinctoria, Fumana procumbens* and has a sparse plant canopy covering 50–60 % of the soil surface. In the gaps, winter and spring annuals regularly occur. In some situations *Festuca vaginata* stands are mixed

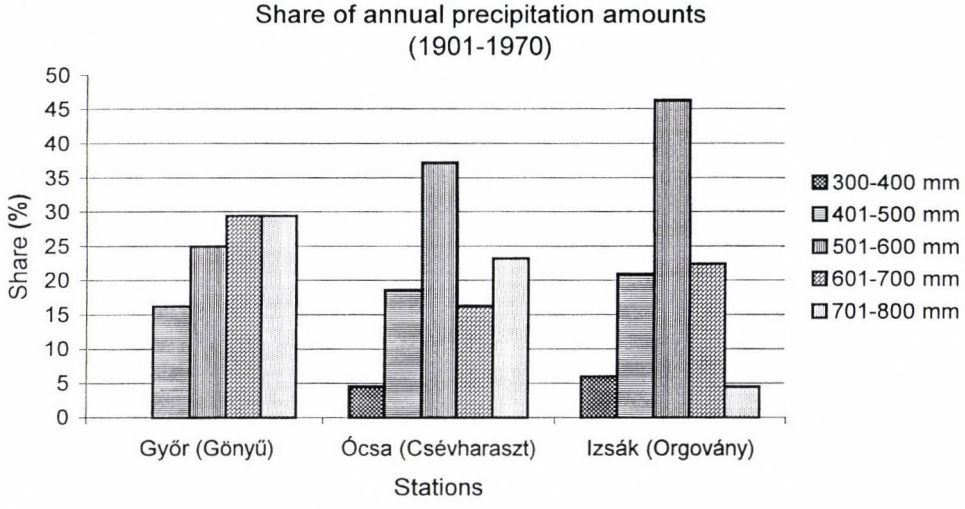

Fig. 2. Share of the categories of annual precipitation amounts (1901–1970) at the meteorological stations close to the study areas

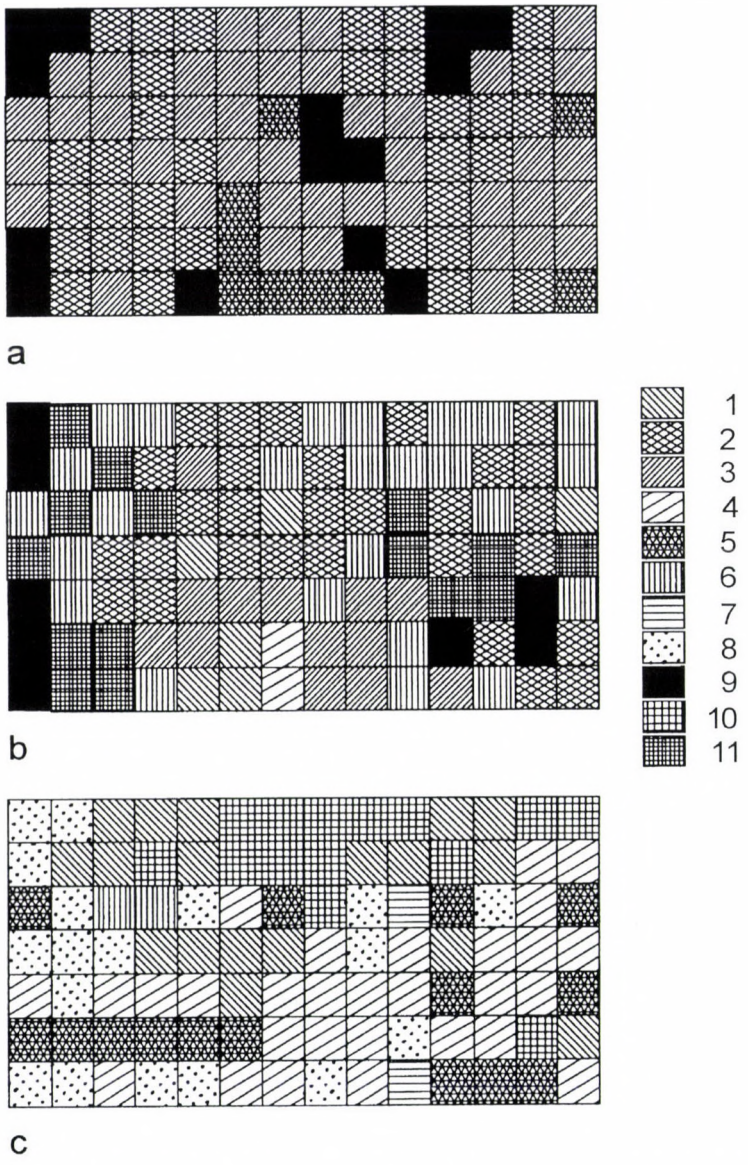

Fig. 3. The traditional vegetation maps of the three sites (a: site 1; b: site 2; c: site3). The vegetation units: 1 = Festucetum vaginatae (open perennial semidesert-like grassland); 2 = *Festuca vaginata* grassland with closed steppe elements; 3 = *Festucetum wagneri* (semi-closed steppe grassland); 4 = *Festucetum wagneri* grassland, species-poor; 5 = Meadow steppe (developed from wet meadow); 6 = *Poa angustifolia* steppe grassland (fringe community); 7 = *Salix rosmarinifolia–Holoschoenus romanus* wet meadow; 8 = Moss- and lichen-rich annual grassland; 9 = Forests (*Quercus robur, Populus alba, Robinia*); 10 = *Junipero-Populetum, Juniperus* scrub; 11 = *Crataegus monogyna–Ligustrum vulgare* scrub

with elements characteristic of steppe grasslands (2). In the group of the closed-semiclosed steppe grasslands four units occur. In most cases *Festuca wagneri* dominates, in the sward having coverage of 70(–80)%. The elements of the open grassland are depressed and their place is occupied by numerous steppe plants (e.g., *Phleum phleoides, Falcaria vulgaris, Eryngium campestre, Pseudolysimachion spicatum,* etc., (3). As in the case of *Festuca vaginata* grasslands, even with *Festuca wagneri* grasslands two types are developed (4: a unit poor in steppe plants). At the fringes of scrubs a loose sward of *Poa angustifolia* may develop (6). Finally, in interdune depressions in a state of drying up, a fourth unit called secondary meadow steppe was distinguished (5). For the further vegetation units see Fig. 3.

Considering the maps (Fig. 3) at Site 1 (Gönyű) it was observed that the steppe plants penetrate into the *Festuca vaginata*-dominated open perennial grassland as well. This community, together with *Festucetum wagneri* (rich in steppe elements) form large continuous patches. At Site 2 (Csévharaszt) influenced by *Festuca wagneri* steppe grasslands, shrubs and forests, the open perennial grassland allows some steppe plants in the majority of quadrats. As a difference, in comparison with Site 1 also *Poa angustifolia* dry grassland appears at the *Crataegus–Ligustrum* fringes. At Site 3 (Orgovány), steppe plants withdraw almost exclusively into the secondary meadow steppe. *Festuca vaginata* grassland does not contain such elements, the floristic composition of *Festucetum vaginatae* and *Festucetum wagneri* become very similar to each other. The extreme dry situation is indicated by the considerable extent of moss and lichen-rich annual grassland.

Maps based on multivariate analysis. There are other possibilities for visualizing the spatial vegetation structure of the three areas. First, the similarities between relevés can be calculated. Using these values, a clustering process may be applied and denoting and reallocating the relevés belonging to the same clusters, a new map can be constructed. Figure 4 depicts similarity maps based on species cover data. Here the similarity ratio (ROHLF 1963) was calculated using transformed cover values, and then the UPGMA (unweighted average linkage) clustering process (VAN DER MAAREL 1979) was applied. A given sign on the map indicates objects belonging to the same cluster. Figure 5 displays maps according to the presence-absence values, here the similarities were calculated by the Sørensen-formula (PODANI 1994), the further procedure is the same as in the former case.

Regarding the dominant-subdominant plant communities, similarity-vegetation maps of Site 1 and 2 resemble one another, while the separation of the third site from both sites is conspicuous (Fig. 4). Compared with the traditional vegetation map, the *Festuca vaginata* dominated grassland and *Festucetum wagneri* grassland separate more or less from one another at Site 1. At Site 2, the pattern of

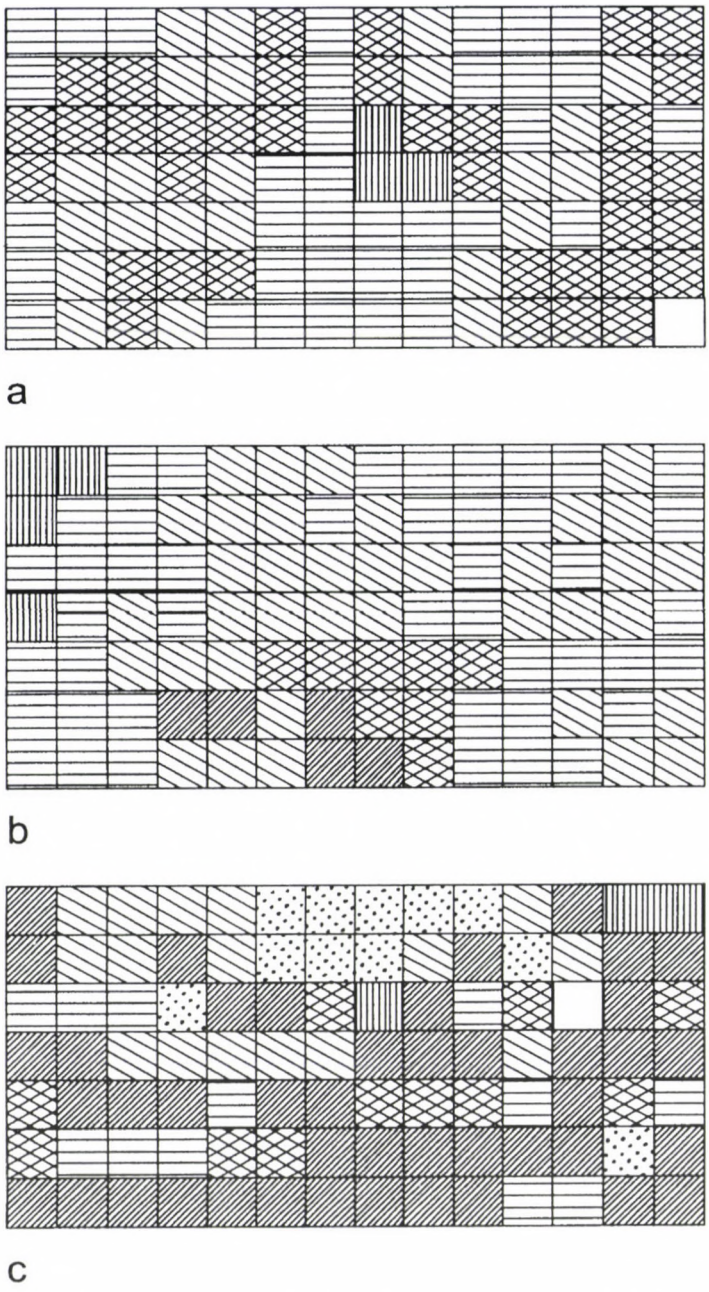

Fig. 4. Raster vegetation map. Similarities among relevés were calculated – based on cover data – by similarity ratio. a) Gönyű, b) Csévharaszt, c) Orgovány. For the details see the text

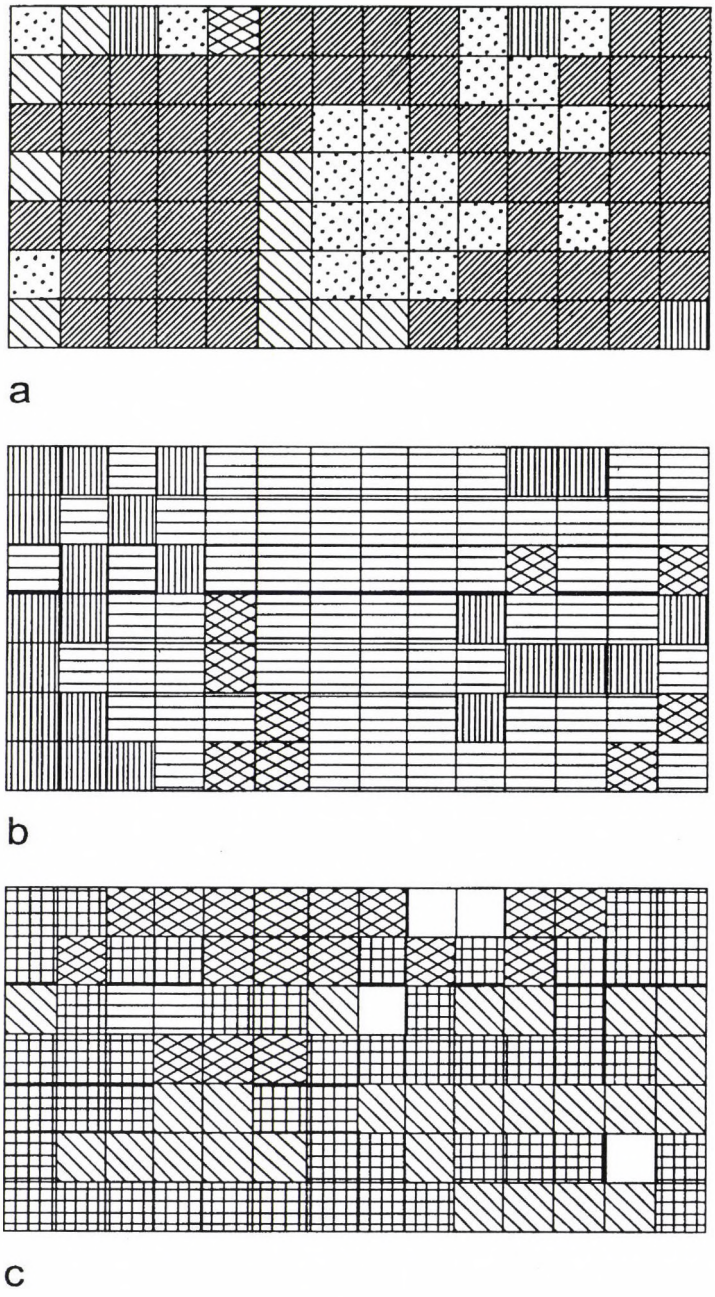

Fig. 5. Raster vegetation map. Similarities among relevés were calculated – based on presence-absence data – by the Sørensen formula. a) Gönyű, b) Csévharaszt, c) Orgovány

steppe-type *Festucetum vaginatae* can be identified, however, the shape of the patches of *Festucetum wagneri* is not outlined. Its quadrats break up into four groups. This community shows similarity in 7 quadrats with Site 1, while relation with Site 3 could be detected only in 3 quadrats. In Site 3, *Festucetum wagneri* barely resembles the steppe quadrats of the two other sites. This community merges with moss and lichen-rich annual grassland, sometimes with *Festucetum vaginatae.*

The contrast is even more obvious when the three maps are compared based on the calculation of similarities on presence-absence data (Fig. 5). Here – unlike in the former case – not even Site 1 and 2 resemble to each other. At Site 1 coincidence with the traditional vegetation map can only be found in an extreme situation: at the meadow steppe. The borders between open perennial grasslands and *Festucetum wagneri* become blurred owing to the steppe plants that penetrate into the former community. Similarly, at Site 2 systematic coincidence with the units of the traditional map is minimal. At Site 3 – in this species-poor landscape – the floristic difference between *Festucetum wagneri* and moss and lichen-rich annual grassland decreases considerably in some quadrats. This is indicated in the map where the two types merge into each other in some cases, a phenomenon that can be detected also at cover-based similarities.

Degree of steppe quality

To express the richness in steppe plants, a system was elaborated, where all species were evaluated and scored according to their differential affinity to dry grasslands including steppe communities in Hungarian plains (taking into consideration all substrates). The given scores are as follows: Sand steppe specialists: 10; Sand steppe generalists: 9; Sand steppe weeds: 7; Species of the open sand steppes: *(Festucetum wagneri)*: 5; Common species of the sand meadows and the sand steppes: 5; Common species of the sand steppe woodlands and the sand steppes: 5; Common species of the open sand grasslands and the sand steppes: 3; Common species of the sand steppe woodlands, the sand meadows and the sand steppes: 3. All other species have the score 0. Summing up the scores for each quadrat, maps of the degree of steppe character are created. According to Fig. 3, at Site 1 all quadrats bear steppe character, strong steppe quadrats dominating. At Site 2, quadrats with various degrees of steppe quality occur in similar proportions, but extremes are also present. At Site 3 strong steppe quadrats are rare and those in which steppe plants are lacking, occur in considerable numbers.

As mentioned above, a differentiation was made among the steppe plants. A group of species bound almost exclusively to the communities belonging to the so-

ciological group *Festucion rupicolae* were distinguished as specialists, while plants having lower affinity to this group were considered to be generalists. According to Fig. 3, Site 1 is the remarkable one among the investigated sites when only specialists are taken into consideration. It is a bit surprising that generalists do not dominate here, but at Site 2. At the same time, Site 3 is equally poor in both respects.

Table 1. Frequencies in the two groups of steppe plants. Note that the value of the possible (maximum) frequency is 98

	Site 1	Site 2	Site 3
SPECIALISTS			
Achillea pannonica	21	1	3
Asperula cynanchica	10	1	10
Bromus inermis	4	13	–
Chamaecytisus ratisbonensis	1	6	–
Helictotrichon pubescens	4	2	–
Hieracium echioides	7	9	–
Linaria angustissima	1	3	–
Stachys recta	4	1	–
Helianthemum ovatum	26	–	1
Anthyllis vulneraria ssp. *vulneraria*	6	–	–
Aster linosyris	66	–	–
Astragalus onobrychis	15	–	–
Campanula sibirica	1	–	–
Chamaecytisus austriacus	13	–	–
Dorycnium herbaceum	10	–	–
Fragaria viridis	1	–	–
Hieracium bauhinii	1	–	–
Jurinea mollis	18	–	–
Medicago falcata	4	–	–
Melampyrum barbatum	2	–	–
Oxytropis pilosa	1	–	–
Pulsatilla pratensis ssp. *nigricans*	1	–	–
Ranunculus polyanthemos	5	–	–
Sanguisorba minor	1	–	–
Scorzonera purpurea	10	–	–
Senecio jacobaea	1	–	–
Thesium linophyllon	2	–	–
Trifolium montanum	1	–	–
Agropyrum intermedium	–	4	–
Allium flavum	–	2	–
Senecio integrifolius	–	4	–
Turritis glabra	–	1	–
Veronica prostrata	–	3	–
Viola hirta	–	1	–
Number of species	28	14	3

Table 1 (continued)

	Site 1	Site 2	Site 3
GENERALISTS			
Eryngium campestre	17	24	19
Euphorbia cyparissias	26	25	12
Falcaria vulgaris	12	24	3
Galium verum	67	59	14
Phleum phleoides	55	48	2
Pimpinella saxifraga	11	10	4
Poa angustifolia	31	64	20
Seseli annuum	24	27	6
Thesium arvense	3	7	3
Dianthus giganteiformis ssp. *pontederae*	19	28	–
Hypericum perforatum	1	12	–
Knautia arvensis	6	4	–
Poa compressa	1	1	–
Taraxacum laevigatum	1	–	5
Tragopogon pratensis ssp. *orientalis*	7	–	2
Pseudolysimachion spicatum	–	46	8
Draba nemorosa	1	–	–
Gypsophila muralis	1	–	–
Petrorhagia saxifraga	1	–	–
Carex praecox	–	33	–
Cruciata pedemontana	–	3	–
Tragopogon dubius	–	1	–
Verbascum lychnitis	–	30	–
Number of species	18	18	12

For details, a comparison of the three sites was accomplished specifying all the steppe specialists and generalists (Table 1).

As many as 19 specialists have an exclusive affinity to Site 1. On the other hand, no species preferring Site 3 could be found. Interestingly and in contrast to specialists, numerous generalists occur with high frequency in all the three sites.

Abiotic factors

One may ask the question whether the climate alone is responsible for these trends? Does the substrate have an effect also? It can be believed that the physical parameters of the substrate show a systematic change in the given direction. Among them the granulation of the sand, more precisely the various ratios of the fine and rough particles may be responsible. As a hypothesis it may be assumed that the dominance of fine particles in the sand, that of the loess and clay fractions

Table 2. Averages, 95% confidence intervals (in parentheses) of the values of the physical fractions at the three sites. (Arcus sinus transformed values were used in the calculations and results retransformed into %)

	Site 1	Site 2	Site 3
Rough sand	45.48 (42.98–47.98)	51.88 (49.90–53.87)	40.67 (38.04–43.32)
Fine sand	45.64 (43.69–47.60)	43.50 (41.47–45.54)	54.33 (51.65–57.00)
Loess	1.58 (1.05–2.21)	0.73 (0.49–1.02)	1.03 (0.72–1.41)
Clay	5.54 (5.05–6.05)	3.07 (2.81–3.34)	2.80 (2.44–3.18)

favor the development of closed steppe grasslands and forests, while a high ratio of rough sand with its low water retention capacity support merely open grasslands.

For this reason physical fractions of the basic parent material were investigated at 49 points in each 2-hectare plot (see Table 2).

The data show that the gradient can not be explained purely on the basis of the quality of the basic parent material.

In spite of this, the investigation of the organic matter content shows different results (Table 3). This parameter, depending strictly on the biological production of the vegetation, is an integrated measure of the site quality in the arid areas. At Site 1, high values predominate, while at Site 2 low and high values as indicators of the site heterogeneity could be observed. At Site 3 slight quantities are characteristic, exceptions are the several quadrats on the place of former meadows.

CONCLUSION

Regarding the community level, a parallel study on the texture and structure of the open perennial grassland (KOVÁCS-LÁNG *et al.* 1999) was carried out along the same gradient. This research revealed that average species richness and canopy cover decreased significantly towards the dry end of the transect. The proportion of perennials in *Festucetum vaginatae* areas decreased as well, whereas proportion of annuals increased with increasing aridity. Classifying the species based on their geographic range, it was found that several species with European and Eurasian distribution occurred mainly or exclusively at the northern "wet end" of the

Table 3. Averages and 95% confidence intervals (in parentheses) of values of soil organic matter content at the three sites. (Arcus sinus transformed values were used in the calculations and retransformed into %)

	Site 1	Site 2	Site 3
Soil organic matter content	4.31 (3.90–4.73)	2.27 (2.00–2.57)	1.44 (1.18–1.73)

transect, while the share of species with continental or sub-Mediterranean distribution was smaller.

Exceeding the community level, the present paper examines the effect of the spatial climatic changes mainly at the level of landscape. Analyzing traditional vegetation maps of the three sites that are situated along the gradient, we showed that semidesert-like communities became dominant with the increasing aridity. Simultaneously, the closed grasslands were modified considerably as well. So *Festucetum wagneri* "lost" almost all of its steppe characteristics in the most arid landscape (Site 3) undergoing a transformation along the transect, which demonstrated its considerable plasticity in floristic composition. This – and similar phenomena – are the causes why the vegetation maps based on calculated similarities are different from those which where created on a traditional way.

The species pool of the landscapes – being isolated from one another – is different, which is an other reason why some communities show segregation (despite their common dominant species) according to the landscapes.

As an ultimate factor, soil organic matter content changes in relation to precipitation. So the question whether the effect of the macroclimate expresses itself in the flora and in the composition of the vegetation has been positively answered.

Attention has to be paid to another issue concerning the structure of the Pannonian forest steppe. At the beginning of this paper reference was made to previous results regarding the general decrease of forest plants from north to south in the Duna-Tisza Interfluve. In accordance with this finding, it was hypothesized that distributional maps of plants characteristic of closed steppe grasslands will yield point clouds that show a trend of increase in an opposite direction compared with that of the forest species. This expectation can be reasoned by the transitional character of this zone best recognizable in the wide Eastern-European space, where this zone (or biome) is influenced both by the belt of closed forests from the north and by the steppe belt from the south. However, data in Table 1 do not support this expectation.

Maybe the situation in the Carpathian Basin is not as clear as in Eastern Europe due to its closed space, where the position of the zones is somewhat concentric. For solving the contradiction and for correct interpretation of the structure of forest steppe, the preparation and the evaluation of further intersections are needed involving loess substrates as well.

*

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EUROPEAN COMMON COCKCHAFER (MELOLONTHA MELOLONTHA L.): PRELIMINARY RESULTS OF ATTRACTION TO GREEN LEAF ODOURS

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A synthetic mixture of typical compounds from green-leaf odours [(3*Z*)-3-hexenyl acetate : (3*Z*)-3-hexen-1-ol : benzaldehyde : (2*E*)-2-hexen-1-ol : 1-hexanol; 100:20:10:1:1] or freshly damaged oak leaves (*Quercus sessiliflora* SALISB.) were tested for field attraction using funnel traps in Hungary. Males of the European common cockchafer *Melolontha melolontha* L. (Coleoptera, Scarabaeidae, Melolonthinae) were significantly attracted to both baits, confirming recent findings of RUTHER *et al.* (2000) on the closely related *M. hippocastani* FABR. The phenomenon that volatiles from damaged leaves from host plants are attractive towards adult males seems to be widespread in the genus *Melolontha*. The present results may form a good basis for starting the development of a monitoring trap for *M. melolontha*.

Key words: *Melolontha melolontha*, Coleoptera, Scarabaeidae, Melolonthinae, field trapping, attractant, green-leaf odours

INTRODUCTION

In the Carpathian Basin the two most important pest scarabs from the genus *Melolontha* are the European common cockchafer (*Melolontha melolontha* L.) and the forest cockchafer (*M. hippocastani* FABR.) (ENDRŐDI 1956, HOMONNAY & HOMONNAYNÉ-CSEHI 1990). Recently, RUTHER *et al.* (2000) published novel data on the chemical communication of *M. hippocastani*. Baits of damaged leaves of both host (*Carpinus betulus* L. and *Quercus rubra* L.) and non-host (*Prunus serotina* EHRH.) tree species attracted *M. hippocastani* significantly better to traps in the field than intact leaves of the same species or unbaited traps. Also, a mixture of synthetic compounds, which mimicked the headspace of damaged *P. serotina* leaves performed significantly better than the unbaited traps (RUTHER *et al.* 2000).

The present tests were undertaken to study whether the same phenomenon occurs also in the closely related *M. melolontha*. In the experiments damaged oak leaves and a synthetic mixture of typical compounds from green-leaf odours were tested in funnel traps during the swarming flight of the common cockchafer in Hungary. In the present paper we report on captures of *M. melolontha*. Data on other chafers will be presented elsewhere.

MATERIALS AND METHODS

Test site

Trapping tests were performed at Telki (Pest county, Hungary), ca. 20 km from Budapest, at the edge of a mixed oak forest, where many cockchafers of Tribe V (SZELÉNYI 1950) could be seen swarming and feeding on the leaves. Tests were carried out between May 4–June 6, 2001. Sets of traps (one of each treatment in the given test) were put out in a line by the edge of the forest, at a height of ca. 2 m, on branches of forest trees. Traps within one set were ca. 10 m from each other; distances between sets ranged from 50–200 m. Traps were inspected on every second or third day, when captured beetles were counted, sexed and were removed from the traps.

Trap types

The VARb trap was the standard funnel trap used by the Budapest laboratory for catching scarab spp. (TÓTH *et al.* unpubl.). The trap consisted of a plastic funnel (top opening outer diameter: 13 cm, funnel hole diameter: 3 cm, height of funnel: 16 cm), under which a transparent plastic round catch container was attached by a rubber band. On top of the funnel a sheet of plastic (10×16 cm) was attached vertically reaching across the top opening of the funnel. The dispenser was suspended from the vertical plastic sheet, and the bait was hung in the middle of the funnel opening, at ca. 1 cm higher than the level of the upper edge of the funnel.

VARb3 was a modification of the VARb trap. The main difference between the two trap designs was that in case of the VARb3 trap the top funnel opening was enlarged by attaching transparent plastic sheets to the trap body, so that the inner diameter of the top funnel opening was ca. 20 cm.

The above two trap types were operated in parallel, since VARb was often used in several earlier experiments on other beetle pests (TÓTH *et al.* unpubl.), while VARb3 is a slightly modified design for capturing larger beetles.

Chemicals

The synthetic mixture of green leaf odours (GLmix) was a simplified version of the mixture described by RUTHER *et al.* (2000). It contained (3*Z*)-3-hexenyl acetate (100), (3*Z*)-3-hexen-1-ol (20), benzaldehyde (10), (2*E*)-2-hexen-1-ol (1) and 1-hexanol (1).

The compounds (2*E*)-2-hexen-1-ol, and (3*Z*)-3-hexenyl acetate were purchased commercially from Bedoukian Inc. (Danbury, USA), while (3*Z*)-3-hexen-1-ol, benzaldehyde and 1-hexanol from Sigma-Aldrich Kft. (Budapest, Hungary).

All compounds were >95% pure as stated by the suppliers.

Baits

The baits were made by administering 100 mg of the GLmix onto a 1 cm piece of dental roll (Celluron®, Paul Hartmann Ag. Heidenheim, Germany), which was placed into an airtight polythene bag made of 0.02 mm polyethylene foil. The dispensers were heat-sealed. and were attached to 8×1 cm plastic handler for easy handling when assembling the traps. Dispensers were wrapped singly in pieces of alufoil and were stored at –18°C until use.

For traps baited with damaged leaves of the natural host plant, oak leaves (*Quercus sessiliflora* SALISB.) were torn up by hand to 1–2 cm^2 pieces. After having removed the withered leaves, freshly prepared leaves (ca. 40 g) were regularly placed into the catch container of the traps when the traps were inspected.

Statistics

In statistical analyses, catches recorded at an inspection were regarded as replicates (results are given as means/trap/inspection). Capture data were transformed to (x+0.5)1/2 and differences between means were tested for significance by ANOVA followed by Games-Howell-test, or Student *t*-test, as appropriate. Statistical analyses were performed by the softwares StatView™ v.4.01 and SuperANOVA™ v1.11 (Abacus Concepts, Inc., Berkeley, USA)

RESULTS AND DISCUSSION

In the first tests, traps baited with the synthetic GLmix were consistently catching much more *M. melolontha* adults than the unbaited controls, in both tests using the VARb or VARb3 trap types (Fig. 1). All of the beetles in the traps were males.

In the second test, again larger numbers of beetles were recorded in the baited traps vs. unbaited, both when the bait was the synthetic GLmix, or artificially damaged oak leaves (Fig. 2). There was no significant difference between the catch of the two baited treatments, although numerically the catch in traps with damaged oak leaves was higher. In this test, as well, all the captured specimens were males.

The present preliminary results clearly suggest that odours from damaged leaves of the host plant exert a similar attraction towards male *M. melolontha* as it has recently been described for *M. hippocastani* (RUTHER *et al.* 2000). Consequently, this seems to be a general phenomenon in the chemical communication within the genus *Melolontha*.

Among leaf-feeding scarabs belonging to other subfamilies there have also been some examples described where plant odours emitted after

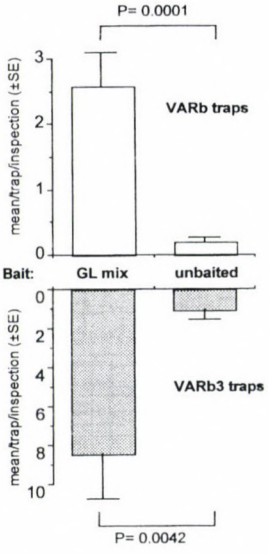

Fig. 1. Captures of male *M. melolontha* beetles in two types of funnel traps baited with GLmix or unbaited in Hungary. (VARb traps: May 7 – 18; a total of 88 beetles were captured in the test. VARb3 traps: May 14 – 18; a total of 114 beetles were captured in the test.) Significance: Student *t*-test

feeding damage acted as attractants. Adults of *Maladera matrida* ARGAMAN (Coleoptera, Scarabaeidae, Sericinae) have been shown to be attracted to injured host plants (HARARI *et al.* 1994). In the Japanese beetle (*Popillia japonica* NEWMAN) (Coleoptera, Scarabaeidae, Rutelinae), attraction of adults to damaged leaves of several host plant spp. has been reported (LOUGHRIN *et al.* 1995, 1996). Future research may show that the phenomenon is more widespread in scarabs as thought before.

In both cases of *M. matrida* and *P. japonica* adults of both sexes were reported to be attracted to leaf odours. In contrast to this, in the present tests only males of *M. melolontha* were captured. This confirms earlier results on *M. hippocastani* by RUTHER *et al.* (2000), who suggested the scenario that at first males orient towards damage-induced green leaf volatiles allowing location of feeding conspecifics on the trees, then they distinguish between non specific leaf damage and damage caused by females through orientation to a female-produced sex pheromone. *M. melolontha* may use a similar scenario. Unfortunately, in the present study we were not able to investigate this aspect of chemical communication in *M. melolontha* because unmated females were not available in sufficient numbers. Very recently, one component from the supposed female-produced sex pheromone

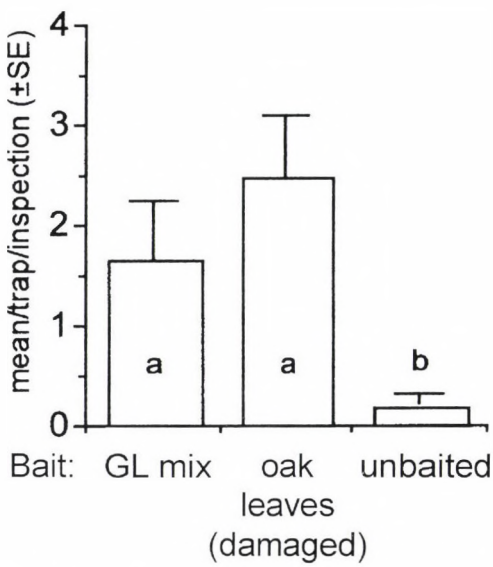

Fig. 2. Captures of male *M. melolontha* beetles in traps baited with GLmix, damaged oak leaves or unbaited in Hungary. (VARb traps; May 11 – 18; a total of 74 beetles were captured in the test.) Means with same letter are not significantly different at P=5% by ANOVA followed by Games Howell-test

has been identified as 1,4-benzoquinone in the forest cockchafer (RUTHER *et al.* 2001).

The numbers of *M. melolontha* caught by traps baited with natural oak leaves or synthetic plant compounds in this study were relatively low as judged by the number of swarming beetles at the test site. During the test period, hundreds of *M. melolontha* specimens were seen on each oak tree. Although low numbers caught suggest weak attraction, the present results may form a usable basis for further optimisation to develop a monitoring trap for *M. melolontha*.

*

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JERMYCOCCUS BOLIVIENSIS GENUS AND SPECIES NOVA (HOMOPTERA: COCCOIDEA, ORTHEZIIDAE)

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Jermycoccus genus nova and *Jermycoccus boliviensis* species nova is described from Bolivia. The new genus and species represent a special group, known only from Neotropical Region.

Key words: Homoptera, Coccoidea, Ortheziidae, *Jermycoccus*, Neotropical Region

INTRODUCTION

The family was analysed in detail by MORRISON (1925, 1952), KOZÁR and KONCZNÉ BENEDICTY (2001) and KOZÁR and MILLER (2000). This work is an extension of studies on *Ortheziola, Mixorthezia, Nipponorthezia* and the related genera, and adds to knowledge of the biogeography of ortheziids.

This study is the result of the analysis of samples collected in South America. The single insect was collected in Bolivia from a Berlese funnel and is deposited in the Collection of Coccoidea of the Hungarian Natural History Museum, Budapest, Hungary.

Jermycoccus KOZÁR et KONCZNÉ BENEDICTY **gen. n.**

Type species: *Jermycoccus boliviensis* KOZÁR et KONCZNÉ BENEDICTY, sp. n.

The new genus is similar to *Mixorthezia* in the presence of four-segmented antennae and the structure of the legs. However, the eyes stalks are not fused with the base of antenna, which sometimes is called the pseudobasal antennal segment (KOZÁR & MILLER, 2000). The dorsal marginal and median wax plate bands are absent. The dorsum is covered with small groups of wax spines, setae and four-locular pores.

Etymology: The genus is named in honour of Dr. TIBOR JERMY to mark his distinguished work in the Hungarian entomology.

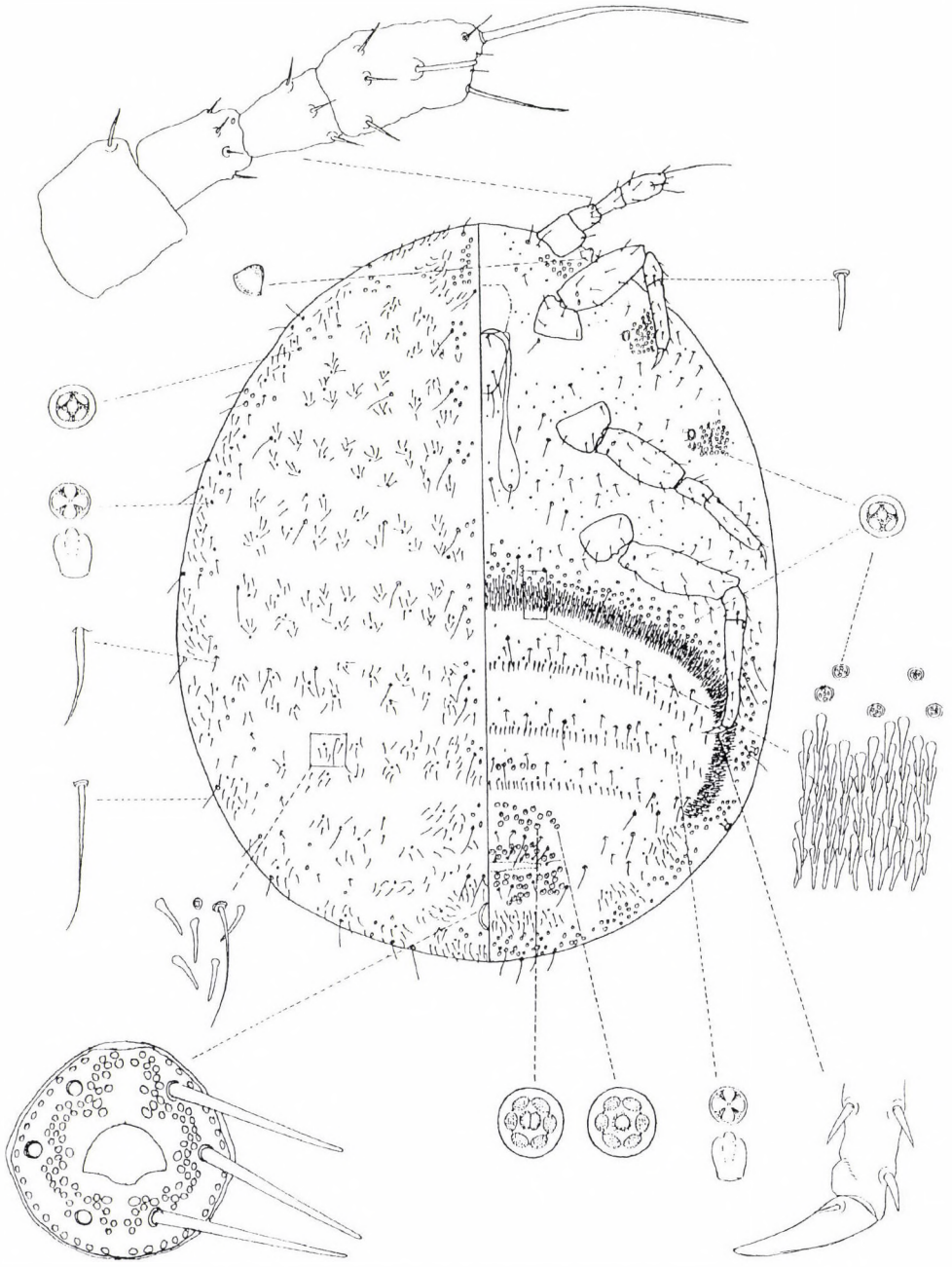

Fig. 1. *Jermycoccus boliviensis* gen. and sp. n., female

Jermycoccus boliviensis KOZÁR et KONCZNÉ BENEDICTY **sp. n.**
(Fig. 1)

Material examined: Holotype, female, No. B 13, on slide, Bolivia, between La Paz and P. Linares, 14–16 November, 1971, Leg. Dr. J. Balogh.

Description of adult female. Mounted specimen (Fig. 1) 1.24 mm long and 1.0 mm wide. Antenna four-segmented, with eyes situated far from pseudobasal antennal segment. Length of antennal segments: 1st – 51 μm, 2nd – 45 μm, 3rd – 38, and apical – 94 μm; 2nd and 3rd segments almost parallelsided. One sensory pore on 2nd segment. Apical seta of antenna 90 μm, subapical setae 43 μm. A strong flagellate sensory seta, 35 μm long, situated near to apical seta. Segments of antenna sparsely covered with thick setae.

Venter. Labium one-segmented. Stylet loop twice length of labium. Anterior legs: coxa 58 μm, trochanter-femur 154 μm, tibia 58, tarsus 122 μm, and claw 32 μm. Middle legs: coxa 62 μm, trochanter-femur 154 μm, tibia 64, tarsus 122 μm, and claw 32 μm. Posterior legs: coxa 72 μm, trochanter-femur 186 μm, tibia 70, tarsus 154 μm, and claw 36 μm long. Claw with strong spine; without denticle. Legs with rows of thick setae, and with one sensory pore on each tibia. Four-locular pores in a large group at opening of each thoracic spiracle and in a group at base of each antenna. Venter of thorax with scattered setae and four-locular pores. Venter of abdomen with three rows of wax plates on 3rd, 4th, and 5th segments, and large numbers of setae, with one row of 6-locular pores on 5th segment, and with a band 6-locular pores on 6th segment and around the vulva. Anterior edge of ovisac band with a band of four-locular pores. Only two pairs of abdominal spiracles visible.

Dorsum. Wax plates in a band around margin but absent on dorsal midline. Dorsum covered with small groups of wax plates each with 3–5 spines, a long seta and one four-locular pore. Midline of dorsum with a narrow band of bare cuticle, surrounded by scattered four-locular pores which occur in groups on head. Anal ring 58 μm wide and 60 μm long, with 6 strong setae, each 42 μm long. Anal ring with two inner rows of pores and one outer row. Multilocular pores absent from dorsum.

Etymology: The species is named after the country of collection.

CONCLUDING REMARKS

The ortheziid fauna of the Neotropical Region was studied comprehensively by KOZÁR and KONCZNÉ BENEDICTY (2001). According to characters used in a recent phylogenetic analysis (KOZÁR & MILLER 2000), the new genus belongs to the "*Mixorthezia*" group. However, this new genus and species described from Bolivia is different from all members of the "*Mixorthezia*" group (KONCZNÉ BENEDICTY & KOZÁR unpubl. data) in lacking wax plate bands on the margin and middle of the dorsum, and by having small groups of wax plates on the dorsum. Thus it is here separated as a new genus.

*

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JERMYIA GEN. N. AND SOME NEW OPPIID MITES FROM MADAGASCAR (ACARI: ORIBATIDA)

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This study deals with oppiid mites from Madagascar. Four new species (*Oxyoppiella zsuzsankae*, *Gressitoppia pocsi* and *Lanceoppia madagascarensis*) and a new genus (*Jermyia sensilla* gen. et sp. n.) are described. A list and a key to the oppiid species of Madagascar are appended together with some taxonomic notes on relationships. With 6 figures.

Key words: Acari, Oribatida, Oppiidae, new taxa, Madagascar

INTRODUCTION

I am continuously studying the oribatid species of Madagascar (Malagasy Republic) (e.g., MAHUNKA 1996) mostly on the basis of the material collected by Dr. B. HAUSER (Geneva, Switzerland) and Dr. T. PÓCS (Eger, Hungary). In my previous papers, I have described species belonging to different families. In the present publication I give the description of new species belonging to the family Oppiidae GRANDJEAN, 1951 which were collected by T. PÓCS.

Several species belonging to this family were described earlier from Madagascar (BALOGH 1960, 1962 and MAHUNKA 1994, 1996, 1997). In this paper I list the presently known oppiid species from this region and describe some of the newly collected species. The new taxa help a better understanding of the relationships existing among the species (see BALOGH 1983, SUBÍAS & BALOGH 1989, BALOGH & BALOGH 1992).

In the present paper I do not discuss the systematic position of the species either in the listing or in the identification key. Thus, for example, the genus *Fossoppia* MAHUNKA, 1994 may not belong to the family Oppiidae GRANDJEAN, 1951, or any other family for that matter. However, for the time being I do not think it wise to erect a new suprageneric taxon. Neither have I dealt with any synonyms among the suprageneric taxa. Thus, for example, without having examined the type species I shall not synonymize *Radamoppia* MAHUNKA, 1994 with the subgenus *Lanceoppia* (*Bicristoppia*) SUBÍAS, 1989, although it might well be necessary at some future date. In the listing the names are given in the combinations accepted as valid today.

LIST OF THE OPPIID SPECIES OF MADAGASCAR

Aethioppia spinipes (BALOGH, 1962)
Brachioppiella boraha MAHUNKA, 1994
Elaphroppia quadripilosa (BALOGH , 1960)
Fossoppia calcarata MAHUNKA, 1994
Fossoppia pirata MAHUNKA, 1994
Fusuloppia simplex (BALOGH, 1962)
Goyoppia sexpilosa (BALOGH, 1960)
Gressittoppia pocsi **sp. n.**
Jermyia sensilla **gen. et sp. n.**
Lanceoppia (Bicristoppia) kalalao MAHUNKA, 1997
Lanceoppia cucheana MAHUNKA, 1994
Lanceoppia madagascarensis **sp. n.**
Lasioelba lemuria MAHUNKA, 1997
Lemuroppia helleri MAHUNKA, 1994
Leptoppia benyovszkyi MAHUNKA, 1996
Leptoppia procera MAHUNKA, 1997
Oppiella nova (OUDEMANS, 1902)
Otoppia midas (BALOGH, 1962)
Oxyoppia pustulata MAHUNKA, 1997
Oxyoppiella zsuzsankae **sp. n.**
Pustuloppia madagassica MAHUNKA, 1994
Radamoppia ravenata MAHUNKA, 1994
Radamoppia vanga MAHUNKA, 1994
Ramusella aepyornis MAHUNKA, 1994
Sphagnoppia alata MAHUNKA, 1997
Striatoppia luisiae MAHUNKA, 1994
Striatoppia madagascarensis BALOGH, 1960
Trematoppia cristipes BALOGH, 1960

A KEY TO THE OPPIIDS OF MADAGASCAR

1 (4) Infracapitulum anarthric type, rutellum minute.

2 (3) Tibia of leg I with robust apophysis bearing solenidion φ1.
Nosybelba oppiana MAHUNKA, 1994

3 (2) Tibia of leg I without apophysis, solenidion φ1 arising on the surface of tibia I. (*Quadroppia* spp.)

4 (1) Infracapitulum diarthric type, rutellum normal.

5 (8) Spinae adnatae present. A pair of foramen-like structures in the sejugal region.

6 (7) Ten pairs of notogastral setae present. Surface of the genital plates with 5–6 striae *Fossoppia calcarata* MAHUNKA, 1994

7 (6) Thirteen pairs of notogastral setae present. Surface of the genital plates with 1–2 striae *Fossoppia pirata* MAHUNKA, 1994

8 (5) Spinae adnate absent. No foramen-like structure in the sejugal region.

9 (10) Tibia of leg I with apophysis bearing solenidion φ1. All femora with broad crest ventrally *Trematoppia cristipes* BALOGH, 1962

10 (9) Tibia of leg I without apophysis. No ventral crest on the femora.

11 (32) Lyrifissures *iad* in paraanal position.

12 (13) Four pairs of genital setae. Legs with modified, erect, spiniform setae *Aethioppia spinipes* (BALOGH, 1962)

13 (12) Five pairs of genital setae.

14 (23) Setae c_2 reduced or absent.

15 (18) Thirteen pairs of notogastral setae present (setae c_2 represented only by their alveoli).

16 (17) Setae ad_1 in postanal position. Only two pairs of very long setae present, all others very short *Lemuroppia helleri* MAHUNKA, 1994

17 (16) Setae ad_1 in paraanal position. Seven pairs of long and 5 pairs of very short setae present *Fusuloppia simplex* (BALOGH, 1962)

18 (15) Ten pairs of notogastral setae present (setae c_2 represented only by their alveoli).

19 (22) All notogastral setae nearly equal in length.

20 (21) Sensillus bacilliform, ciliate. Lamellar line present *Ramusella aepyornis* MAHUNKA, 1994

21 (20) Sensillus pectinate. Lamellar line absent
Sphagnoppia alata MAHUNKA, 1997

22 (19) Three pairs of notogastral setae much longer than the others. Sensillus smooth *Goyoppia sexpilosa* (BALOGH, 1960)

23 (14) Setae c_2 present.

24 (25) Prodorsum smooth, without any structure like a costula, lamellar line or crest *Lasiobelba lemuria* MAHUNKA, 1997

25 (24) Prodorsum with a costula or crest.

26 (29) Costulae long reaching to the rostral apex. Surface of notogaster and ventral plate ornamented by sculpture.

27 (28) Notogaster and ventral plate with polygonate design
Striatoppia luisiae MAHUNKA, 1994

28 (27) Notogaster and ventral plate with striae
Striatoppia madagascarensis BALOGH, 1960

29 (26) Costulae short, reaching to the insertion of the lamellar setae. Surface of notogaster and ventral plate smooth.

30 (31) All notogastral setae nearly equal in length
Oppiella nova (OUDEMANS, 1900)

31 (30) Two pairs of notogastral setae conspicuously long, all others minute
Elaphroppia quadripilosa (BALOGH, 1960)

32 (11) Lyrifissures *iad* in apoanal position.

33 (34) Lyrifissures *iad* in direct apoanal position. Surface of the body with sculpture consisting of granules and striae
Oxyoppiella zsuzsankae sp. n.

34 (33) Lyrifissures *iad* in inverse apoanal position. Surface of the body without sculpture.

35 (40) Four pairs of genital setae present.

36 (37) Setae c_2 absent. Acetabula of leg IV normal **Gressittoppia pocsi** sp. n.

37 (36) Setae c_2 present. Acetabula of leg IV removed posteriorly, far from the acetabula III.

38 (39) Setae ad_1 in paraanal position. Great differences exist between the notogastral setae **Jermyia sensilla** gen. n. et sp. n.

39 (38) Setae ad_1 in postanal position. Notogastral setae equal in length *Leptoppia benyovszkyi* MAHUNKA, 1996

40 (35) More than four pairs of genital setae present.

41 (46) Five pairs of genital setae present.

42 (45) One pair of interbothridial crests and two pairs of sigilla present. Epimera III and IV much larger than epimera I and II.

43 (44) Rostral apex tripartite. Notogastral setae conspicuously short, much shorter than the lamellar setae *Leptoppia procera* MAHUNKA, 1997

44 (43) Rostral apex rounded. Notogastral setae normal in length, they are longer than the lamellar setae *Brachioppiella boraha* MAHUNKA, 1994

45 (42) One unpaired interbothridial basal crest and three pairs of sigilla present. Epimera III and IV normal, not larger than epimera I and II *Pustuloppia madagassica* MAHUNKA, 1994

46 (41) Six pairs of genital setae present.

47 (54) One pair of tubercles or crests present in the interbothridial region.

48 (49) Notogastral surface with tubercles. Notogastral setae very long *Radamoppia vanga* MAHUNKA, 1994

49 (48) Notogastral surface smooth.

50 (51) Setae *la* and *lm* arising in one longitudinal row *Radamoppia ravenala* MAHUNKA, 1994

51 (50) Setae *la* and *lm* arising in one transversal row.

52 (53) A pair of triangular tubercles present in the sejugal region. Interlamellar and lamellar setae normal in length *Lanceoppia (Bicristoppia) kalalo* MAHUNKA, 1997

53 (52) No triangular tubercles in the sejugal region. Prodorsal and notogastral setae – except the rostral ones – minute *Lanceoppia cucheana* MAHUNKA, 1994

54 (47) No tubercles or crests in the interbothridial region.

55 (56) Pedotecta I conspicuously long and sharply pointed anteriorly. Notogastral setae minute *Otoppia midas* BALOGH, 1962

56 (55) Pedotecta I normal. Notogastral setae well-developed **Lanceoppia madagascarensis** sp. n.

DESCRIPTION OF THE NEW TAXA

Jermyia gen. n.

Diagnosis: Family Oppiidae GRANDJEAN, 1951. Rostrum roundish, undivided. Prodorsal surface without distinct costulae, a fine lamellar line and three pairs of interbothridial sigilla present. Sensillus fusiform, with long branches. Notogaster without crista, ten pairs of setae, c_2 short. Exobothridial surface weakly sclerotised, lightly covered by granules. Position of the acetabula of legs characteristic, acetabula IV removed posteriorly, far from acetabula III. Discidium long, reaching to acetabula. Epimera I and II narrow, epimera III and IV very large, their posterior borders directed posteriorly to acetabula IV. Four pairs of genital setae present, setae ad_1 and ad_2 in paraanal, ad_3 in preanal, lyrifissures *iad* in inverse apoanal position.

Type species: *Jermyia sensilla* sp. n.

Remarks: The new genus is undoubtedly related to the *Brachioppia – Brachioppiella* group and is nearest to *Leptoppia* MAHUNKA, 1997. In the case of the known genera and subgenera – excepting the genus *Leptoppia* – the position of the acetabula, and in connection with it the structure of the podosoma and the sternocoxal region, is normal. In the case of the new species as a consequence of the more posterior position of leg IV this situation is changed as described in the diagnosis. Among the other related taxa only the subgenus *Brachioppiella (Gressittoppia)* BALOGH, 1987 and the genus *Brassiella* BALOGH, 1987 (see SUBÍAS & BALOGH 1989) have four pairs of genital setae. However, the epimeral region of both latter taxa is normal and setae ad_1 is located in a posterior position. This difference from the known related taxa suggests that a separation on the generic level is necessary.

Etymology: I dedicate the new species to my dear friend Prof. Dr. TIBOR JERMY upon his 85th birthday. He is the doyen of ecology and plant protection zoology in Hungary, whose advice and help not only for me but for many a Hungarian taxonomist and ecologist have gone a long way in furthering our science as a whole.

Jermyia sensilla sp. n.
(Figs 1–4)

Measurements. – Length of body: 173–181 μm, width of body: 135 μm.

Prodorsum: Rostrum roundish. Prodorsal surface with a pair of short lamellar lines located laterally, comparatively far from the lamellar setae and overlapping over their insertion points (Fig. 1). Three pairs of interlamellar and some lateral sigilla present. Bothridia relatively small, nearly oval with large posterior lobes. Rostral setae arising on the prodorsal surface, far from each other. All four pairs of prodorsal setae – excepting setae *in* – setiform, their ratio: *ro* ≅ *in* > *ex* > *le*. Setae *ro* conspicuously ciliate, setae *in* roughened. Sensillus (Figs 1, 3) with an asymmetrically fusiform head having 6 branches unilaterally. A pair of small tubercles in the sejugal region, behind the bothridia.

Notogaster: Conspicuously elongated. Median part of the dorsosejugal suture only slightly arched (Fig. 1). Ten pairs of notogastral setae present, setae c_2 much shorter than the others, directed laterally. All others long, finely ciliated, four inner setae (*la, lm,* h_2, h_3) arising in a conspicuous longitudinal row.

Lateral part of podosoma: Position of the acetabula of the legs are characteristic, acetabula IV located far away posteriorly from acetabula III; distance of acetabula between III and IV four times longer than the same between acetabula II and III (Fig. 3). Acetabula III and IV surmount acetabula I and II. Exobothridial region somewhat sclerotised and the field between acetabula II and III slightly granulated. Pedotecta I small, pedotecta II-III reduced, discidium very long, flat, its lateral margin sinuous, reaching to the acetabula IV.

Ventral parts of the body (Fig. 2): except the anterior part of the sternal apodeme and borders all epimeral borders and apodema are well-developed, but all narrow. Epimera III and IV very large, apodema IV directed posteriorly to the acetabula IV, straight, arched only near acetabula IV (Fig. 2). Inner part of epimeral surface with a polygonate pattern. Setae *1c* arising on pedotecta I. Setae *4c* arising on the anterolateral corner of discidium. Epimeral setae of normal size, setae *1c, 3c, 4b* and *4c* ciliate, all others nearly smooth. Epimeral setal formula: 3–1–3–3.

Genital opening much smaller than the anal one. On the genital plates an anteromedian crest, directed inwards, observable. Anogenital setal formula: 4–1–2–3. Position of the aggenital setae normal, adanal setae characteristic for this genus: two pairs (ad_1 and ad_2) in paraanal, ad_3 in preanal position. Lyrifissures *iad* also characteristic (inverse apoanal) for the genus.

Infracapitulum, chelicerae and palps are of the normal type.

Legs: Length of all joints normal, tibiae of legs II and III dilated, shape of leg I is shown in Fig. 4. Femur of leg I with short crest.

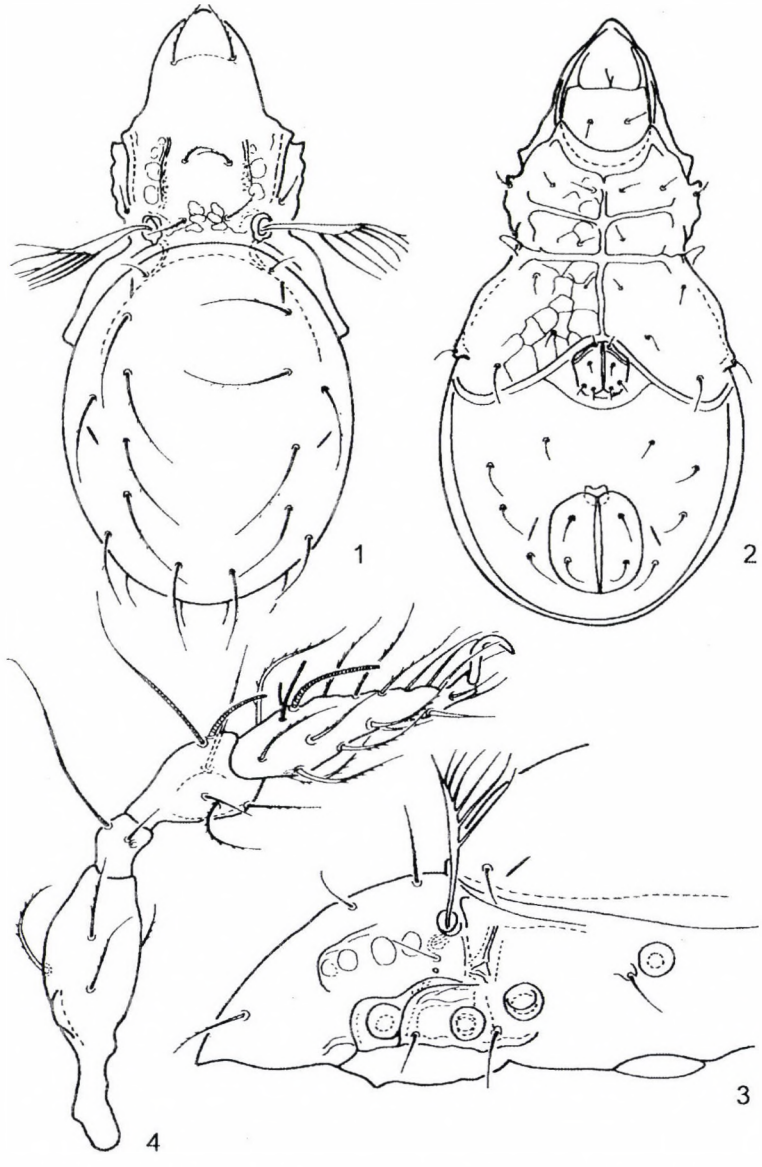
Legs setal formulae:

I: 1–5–2+1–4+2–20+2–1.
IV: 1–2–2–3+1–10–1.

Material examined: Holotype – Malagasy Republic, Toamasina Province. Peat forest and woodland often with thick *Sphagnum* layer on coastal white sand, with shallow lakes, between Ampangalanas Canal and the ocean. 5 km N of Andovoranto, between Andombo and Andovoa, at 10 m alt. 24. Aug. 1998. Leg. T. PÓCS, No. 9887. 1 paratype from the same sample. Holotype (1653-HO–01) and paratype (1653-PO–01) deposited in the Hungarian Natural History Museum, Budapest, with identification numbers of the specimens in the Collection of Arachnida.

Remarks: The new species is readily characterised by the long and conspicuously ciliate notogastral setae.

Etymology: The species is named after the characteristic form of its sensillus.



Figs 1–4. *Jermyia sensilla* gen. et sp. n. – 1 = body in dorsal view, 2 = body in ventral view, 3 = podosoma in lateral view, 4 = leg I

Gressittoppia pocsi sp. n.
(Figs 5–9)

Measurements. – Length of body: 248–270 μm, width of body: 124–138 μm.

Prodorsum: Rostrum widely rounded. Prodorsal surface with a pair of lamellar "elevation" covered by small granules (neither clear lamellar lines nor costulae visible, but a weak transcostula present). The elevations are located laterally, comparatively far from the lamellar setae and reaching over their insertion points (Fig. 5). Three pairs of interlamellar and some well-developed lateral sigilla present, a pair of weak interbothridial apophyses also observable. Bothridium small, cup-shaped, without posterior lobe. Rostral setae arising on the lateral margin of prodorsum, conspicuously far from each other, and longest of all the prodorsal setae. Lamellar setae shorter, bent inwards, interlamellar ones shortest of all and smooth. Sensillus long, also bent inwards (Fig. 6), asymmetrically fusiform, pectinate. Its branches (mostly 9) long.

Notogaster: Conspicuously elongated. Median part of the dorsosejugal suture convex (Fig. 5). Nine pairs of notogastral setae present, setae c_2 absent, represented only by their alveoli. All others nearly equal in length, comparatively thick and well ciliated. Setae *la* stands before *lm*.

Lateral part of podosoma (Fig. 9): Position of the acetabula of legs are characteristic, acetabula III and IV located over acetabula I and II. Exobothridial region somewhat sclerotised and a field between acetabula II and III slightly granulated. Pedotecta I small, pedotecta II-III reduced, discidium normal, its margin sinuous in ventral view.

Ventral parts of the body (Fig. 7): All epimeral borders and apodemes well developed, and broad. Foveola-like structures are in the surface of the epimeral borders: an unpaired one behind the mental tectum, and one pair each on *bo. 2.* and *bo. sej.* Setae *1c* arising far laterally on pedotecta I. Setae *4c* arising at the basis of discidium. Epimeral setae of normal size, long and thin, setae *1c, 3b, 3c, 4b* and *4c* well ciliate, all others roughened only. Epimeral setal formula: 3–1–3–3. Genital opening much smaller than the anal one. Anogenital setal formula: 4–1–2–3. Position of the aggenital setae normal, adanal setae typical for this genus: ad_1 in postanal, ad_2 in paraanal, ad_3 in preanal position. Lyrifissures *iad* also typical (inverse apoanal) for the genus. All setae in this region simple, smooth.

Infracapitulum, chelicera and palps are of the normal type.

Legs: Length and shape of all segments normal. Leg setal formulae:

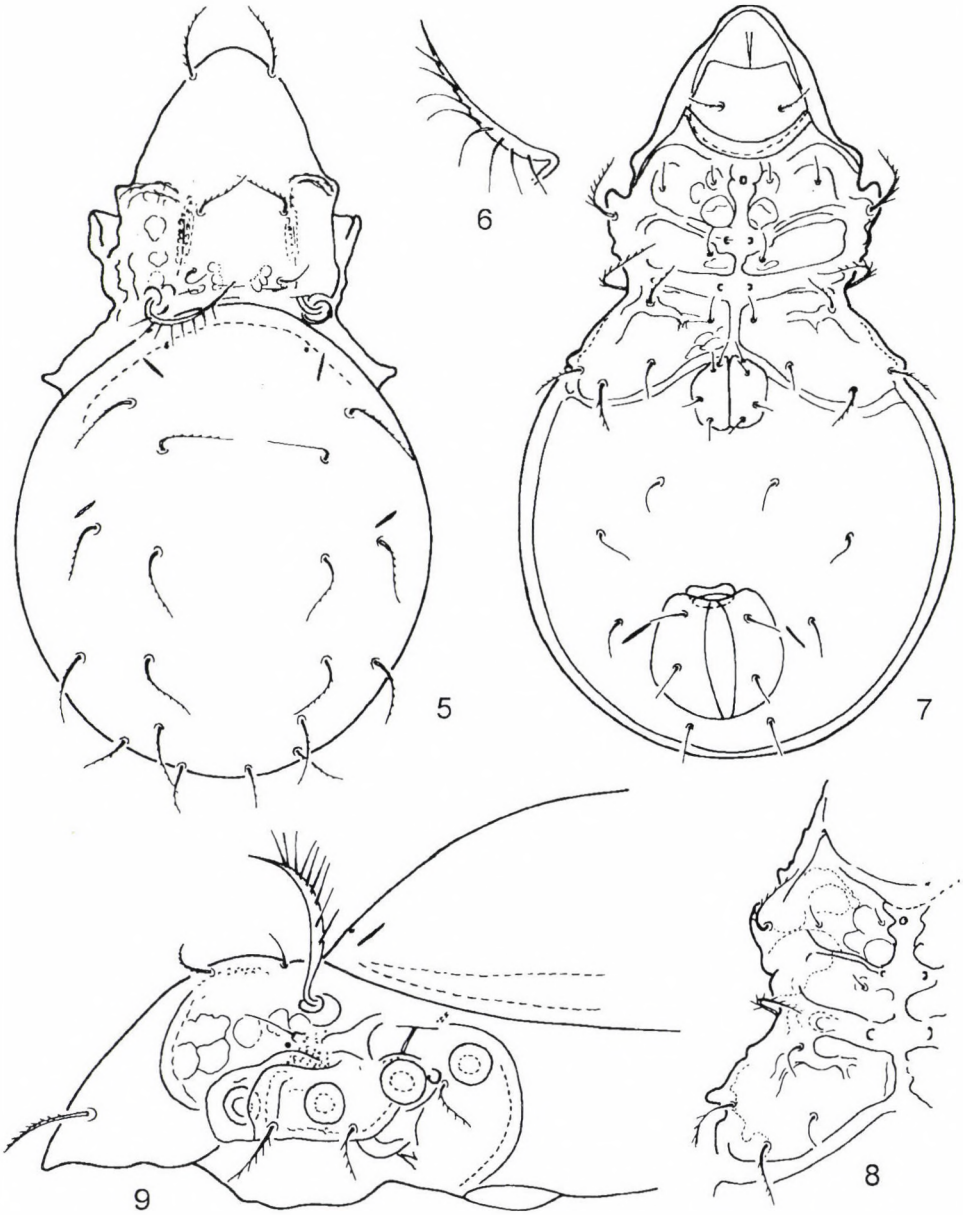
I: 1–5–2+1–4+2–20+2–1.

IV: 1–2–2–3+1–10–1.

Material examined: Holotype: Malagasy Republic, Toamasina Province. Peat forest and woodland often with thick *Sphagnum* layer on coastal white sand, with shallow lakes, between Ampangalanas Canal and the ocean. 5 km N of Andovoranto, between Andombo and Andovoa, at 10 m alt. 24. Aug. 1998. Leg. T. PÓCS, No. 9887. 3 paratypes from the same sample. Holotype (1654-HO–01) and 2 paratype (1654-PO–01) deposited in the Hungarian Natural History Museum, Budapest, with identification numbers of the specimens in the Collection of Arachnida, 1 paratype in the Muséum d'Histoire naturelle, Geneva.

Remarks: On the basis of the form of costulae, the new species stands nearest to the type species of the genus *Gressittoppia* BALOGH, 1983 (*Brachioppia moresoensis* KOK, 1967). The new species is distinguished from it by the very long epimeral setae, especially setae *1c* and *3c* and the much longer sensillar head.

Etymology: I dedicate the new species to my friend, Prof. Dr. T. PÓCS (Eger, Hungary), the renowned bryologist and the collector of this material.



Figs 5–9. *Gressittoppia pocsi* sp. n. – 5 = body in dorsal view, 6 = sensillus, 7 = ventral view, 8 = anterior part of the epimeral region, 9 = podosoma in lateral view

Lanceoppia madagascarensis sp. n.
(Figs 10–12)

Measurements. – Length of body: 356–389 μm, width of body: 210–233 μm.

Prodorsum: Rostrum elongated, a small nasiform part separated from the prodorsum. Prodorsal surface with a pair of weak lamellar elevations, true costulae absent. A conspicuous transversal lath before the lamellar setae is also present. Two pairs of interlamellar and some lateral sigilla conspicuous (Fig. 10). Rostral setae longer than the remaining prodorsal setae, arising laterally, on the surface of the prodorsum, and curving inwards. Lamellar setae short, fine, setiform; interlamellar ones straight, directed posteriorly, slightly erect. Exobothridial setae simple, small. Bothridia relatively small, nearly oval and with posterior lobes. Sensillus (Fig. 12) long, its head fusiform, elongate, bearing some spicules. A pair of tubercles in the sejugal region, behind the bothridia.

Notogaster: Conspicuously elongated. Median part of the dorsosejugal suture convex, roundish. Nine pairs of notogastral setae present, setae c_2 represented only by their alveoli. All others setiform, slightly ciliated. Setae *p* much shorter than the anterior pairs. Setae *la* arising at the same level as *lm*.

Lateral part of podosoma: Acetabula I–IV in normal position, lying on the same level (Fig. 12). Exobothridial region well sclerotised, their lateral part and a field between acetabula II and III well granulated. Pedotecta I small, pedotecta II-III reduced, discidium long, with a small, sharp posterolateral corner.

Ventral parts of the body: All apodemes and epimeral borders well developed, epimeres well framed. Along the sternal apodeme a well-developed minitectum present (Fig. 11), thus the borders of the epimeral fields appear double in outline. Epimeral setae long and thin, simple, all setae nearly smooth. Setae *1c* arising far laterally on the surface on pedotecta I. Epimeral setal formula: 3–1–3–3. Genital opening much smaller than the anal one. Anogenital setal formula: 6–1–2–3. Position of the aggenital setae normal, posterior pair of adanal setae located posteriorly. All setae in the anogenital region smooth. Lyrifissures *iad* in inverse apoanal position.

Infracapitulum, chelicerae and palps are of the normal type.

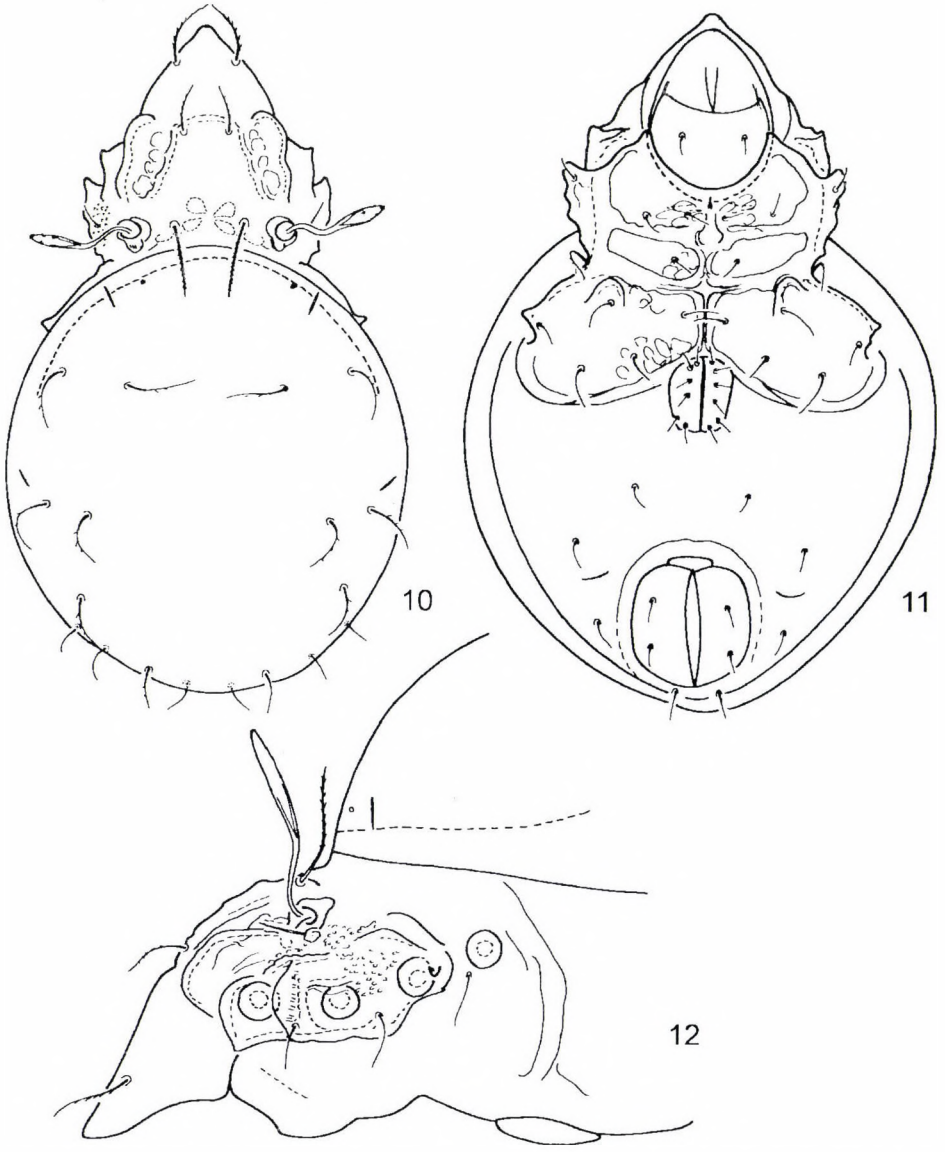
Legs: All conspicuously long, their segments elongated.

Material examined: Holotype: Malagasy Republic, Toamasina Province, Maroizaha forest. Mossy montane rainforest with bamboo (*Nastus* sp.) undergrowth on the summit ridge of Mt. Maromiziha, south of the Andasibe Nat. Park and Antananarive Tomasina road, 2 km W of Anevoka village, at 1080–1214 m alt. 26 August, 1998. Leg. T. PÓCS, No. 9890. 5 paratypes from the same sample. Holotype (1655-HO-01) and 4 paratypes (1655-PO-01) deposited in the Hungarian Natural History Museum, Budapest, with identification numbers of the specimens in the Collection of Arachnida,1 paratype in the Muséum d'Histoire naturelle, Geneva.

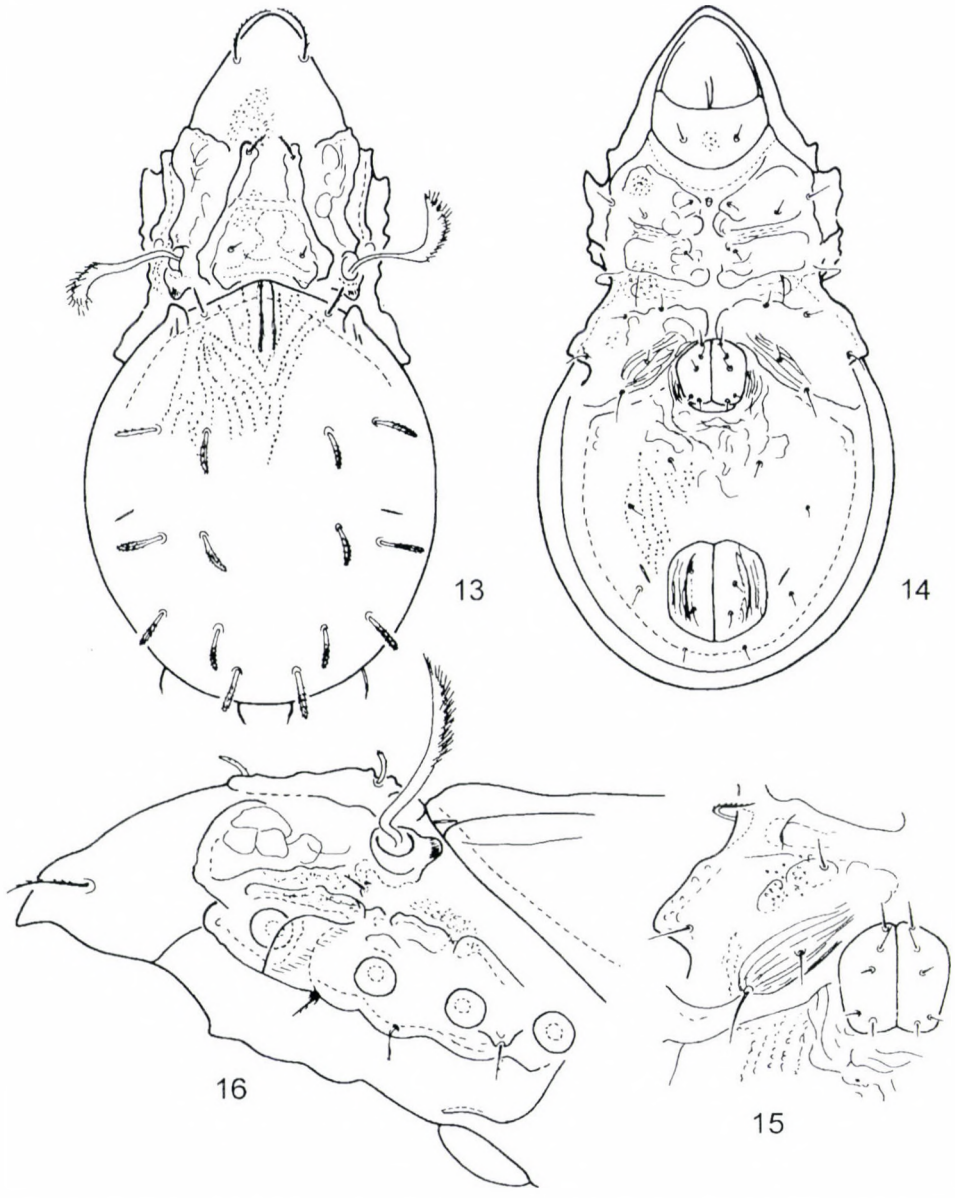
Remarks: The new species is readily characterised by the 4 pairs of interbothridial sigilla, the long, backward directed, erect interlamellar setae and the comparatively long and well ciliate notogastral setae. Most of the heretofore described species have either short interlamellar setae e.g., *Lanceoppia woodringi* HAMMER, 1968, or in their interbothridial region the sigilla are absent e.g. *Lance-*

oppia tortile MAHUNKA, 1989. This combination of features is not known in the other species.

Etymology: The new species is named after its locality.



Figs 10–12. *Lanceoppia madagascarensis* sp. n. – 10 = dorsal view, 11 = ventral view, 12 = podosoma in lateral view



Figs 13–16. *Oxyoppiella zsuzsankae* sp. n. – 13 = dorsal view, 14= ventral view, 15 = posterior part of the epimeral region and genital plates, 16 = podosoma in lateral view

Oxyoppiella zsuzsankae sp. n.
(Figs 13–16)

Measurements. – Length of body: 196–218 μm, width of body: 103–115 μm.

Prodorsum: Rostrum roundish, undivided. Prodorsal surface densely covered by granules. A pair of distinct costulae, a weaker transcostula and a pair of lateral costulae present (Fig. 13). Interbothridial region with one pair of interbothridial tubercles, interbothridial sigilla absent, in this region a pair of indistinct fields visible. Rostral seta long setiform, lamellar and interlamellar setae short, bacilliform, exobothridial ones simple, spiniform. Bothridium with a large posterior lobe, standing opposite to the humeral apophysis of the notogaster. Sensillus long with fusiform head, scopulate.

Notogaster: Median part of the dorsosejugal region convex and penetrating into the interbothridial region (Fig. 13). A pair of large humeral apophyses, a pair of short, weak cristae and an anteromedian, unpaired lath present. Notogastral surface ornamented, and/or covered by granules, mostly arranged in longitudinal rows. Ten pairs of dilated setae, setae c_2 and setae *p* much shorter and finer than the others. Setae *lm* and *la* arising at the same level.

Lateral part of podosoma: Acetabula I–IV in normal position, lying on the same level (Fig. 16) exobothridial and acetabular regions well sclerotised, distinctly granulated. Exobothridial seta arising on a small tubercle. Pedotecta I small, pedotecta II–III reduced, discidium short with protuberances.

Ventral parts of the body (Fig. 14): Surface of mentum and the epimeral surface irregularly but distinctly granulate. All apodemes well sclerotised, epimeral borders also conspicuous. An unpaired foramen-like structure and a pair of tubercles observable on epimera III and bearing setae *3b*. Setae *1c* located laterally, near to the margin of pedotecta I. Epimeral borders *bo. sej.* with a pair of longitudinal crests laterally. Posteromedian surface of epimera IV striate (Fig. 15). Form of the epimeral setae normal, epimeral setal formula: 3–1–3–3. All setae nearly smooth. Surface of the ventral plate striated and covered by granules like the notogaster. Genital plate smooth, anal plate striated carrying a longitudinal median lath. Anogenital setal formula 5–1–2–3. Setae ad_1 in postanal, ad_3 in preanal, lyrifissures *iad* in direct apoanal position. All adanal setae slightly dilated.

Infracapitulum, chelicera and palps are of the normal type.

Legs: Solenidion φ1 arising on a small apophysis.

Material examined: Holotype: Malagasy Republic, Toamasina Province. Peat forest and woodland often with thick *Sphagnum* layer on coastal white sand, with shallow lakes, between Ampangalanas Canal and the ocean. 5 km N of Andovoranto, between Andombo and Andovoa, at 10 m alt. 24. Aug. 1998. Leg. T. Pócs, No. 9887. 5 paratypes from the same sample. Holotype (1653-HO-01) and 4 paratypes (1653-PO-01) deposited in the Hungarian Natural History Museum, Budapest, with identification numbers of the specimens in the Collection of Arachnida, 1 paratype in the in the Muséum d'Histoire naturelle, Geneva.

Remarks: The new species is readily distinguishable from all related taxa by the unique sculpture of the notogaster, which resembles the sculpture of some *Striatoppia* BALOGH, 1958 species.

Etymology: The new species is dedicated to my assistant for her valuable help in my studies.

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THE RELIABILITY THEORETICAL ASPECTS OF THE BIOLOGICAL CONTINUITY PRINCIPLES

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Continuity requirements ensure the unbroken dynamics of evolution. Continuity principles describe the conditions for the origin, maintenance and transitions of the organizational units and their networks. It can be shown that the empirical foundations of the continuity principles are based on the reliability theoretical aspects of the living entities.

Key words: reliability, evolution, continuity, organization

THE PROBLEMS

Evolutionary processes can be described in terms of heredity, reproduction and variation. A main problem in ecology and evolutionary biology is that this simplified evolutionary picture does not tell us the sufficient criteria of a dynamically satisfactory description of evolution (see LEWONTIN 1974 for details). A second problem is the object of this paper. Specifically, we shall analyse here the main conditions that keep evolution in motion. We follow FISHER (1930), whose first statement in his classic book, *The genetical theory of natural selection* is that "Natural selection is not evolution."

To anticipate an answer to the problems raised above, there exist a number of conditions or requirements, which must be satisfied for keeping evolution in motion. Briefly, we shall refer to the description of these conditions as continuity principles. We intend to point out the connections of the continuity principles and the reliability of biological objects.

THE CONCEPT OF A CONTINUITY PRINCIPLE

The structure of a continuity principle

The structure of a continuity principle is the following type of statement: 'If a specific set of condition is satisfied, then the evolutionary continuity by descent with modifications is satisfied'. Two classical types of these continuity principles are MENDEL's laws and WEISMANN continuity of germ plasm doctrine. Both of these concern with the evolutionary continuity of heredity. These principles ex-

press regularities of hereditary transmission of genetic properties occurring in the germ line and the non-heritable, mortal character of the soma. In other words, these statements express the evolutionary behaviour of the separated soma and germ in genetic terms. It can be shown, however, that these hereditary principles do not exhaust completely even the concept of genetic continuity [see CAVALIER-SMITH's (1991, 2001) discussion of the membrane inheritance or the concept of dual inheritance (JABLONKA & LAMB 1995, MOLNÁR 1990)].

The principles of heredity refer to rules of the transmission of genetic information. The term 'principle' is associated with other important genetic, developmental and evolutionary concepts, like rule and constraint. The principal importance of the continuity principles is that they describe the couplings and the separations of organizational levels or units in organisms and their groups, moreover the transitions between organizational levels or units. Therefore, the dynamical coexistence of the organizational levels or their parts obey continuity principles. For instance, the origins of cells by symbiosis and autogenesis was generated by fusion and separation of organizational levels, as explained clearly by CAVALIER-SMITH (1987), in terms of symbiosis between membranes, catalysts and genes. Symbiosis is an example for a continuity principle. The generation of the evolutionary novelty by symbiosis, however, has limits. There are other related principles, such as the 'mix-match' principle.

The aim of this paper is to summarize the existing knowledge about continuity principles and to make some steps towards the explorations of their nature, relations, relevance and further methodical explorations. The area of continuity principles is capable of generating efficient integration in evolutionary biology, creating more consistency and awareness in evolutionary practice and theory. A typical structure of a continuity principle can be described in the following form:

*i*th unit of organization — transmission → *i*th or *j*th unit of organization.

In other words, a continuity principle describes the origin, maintenance and the transmission of various units of biological organization under internal and external living conditions. As we shall see later, the theoretical basis of such problems can suitably be treated by the tools and the concepts of the theory of reliability, where the concept of continuity is of central importance. The reason is simple. In general, reliability is the precondition of the successful operation of a system, an organizational unit or their networks.

A classification of the continuity principles

As a first step, it is plausible to separate continuity principles into three classes, as genetic, developmental and ecological continuity principles. Then, later on, it would be useful to look at their combinations.

Continuity of genetic systems. We can mention several genetic continuity principles, such as the operation of autocatalytic systems, the complementarity of base pairing according to the CHARGAFF's rules, MENDEL's rules, WEISMANN's continuity of germ and the germ-soma separation, and finally the membrane inheritance without genes.

Continuity in phenotypes and development. The phenomenon of phenotypic or developmental continuity can be observed both in unicellular and multicellular organisms. In ciliates, the surface or cortical structures are perpetuating, apparently without detectable genetic control, from generation to generation (see JABLONKA & LAMB 1995 for an overview). This means that there exists at least one case, where the unbroken chain of the propagating developing structures and their transformations can be transmitted between generations by seemingly purely developmental mechanisms. The cortical inheritance is a clear case of Lamarckian inheritance of acquired characters. JABLONKA & LAMB (1995) argue that the clonal propagation of cortical structures in ciliates affects the symmetry, pattern and form of these organisms.

An important phenomenon in the development of multicellular organisms is the embryonic induction. This is an interaction between two cell populations. The inducing cells transform the qualitative properties of the induced, competent cells. A major element of the multicellular development consists of a network or cascade of inductive effects. An essential requirement of the inductive chains is their continuous, unbroken propagation. When the inductive chain is broken, the development stops. This important requirement is expressed as a continuity principle of multicellular development (HORDER 1983). As HORDER (1983, p. 339.) says: 'This proposal satisfies an essential requirement which should be met by any hypothetical evolutionary sequence; a continuous sequence of morphogenetic events in an embryo is a repetition of a continuous sequence of morphological steps built up through the preceding evolving series of embryos, each stage of which must have been functionally advantageous in the transitional organism. This will be referred to as the continuity principle.' HORDER considered the evolution of the eyes in vertebrates. He showed that the specific components of the vertebrate eyes were acquired in a gradual way. Firstly, the photoreceptive element evolved. Secondly, these elements localized under the surface of the body. Thirdly, this system was complemented by the lens and the cornea, constituting the image projecting elements, seemingly step-by-step.

Because of the 'functional advantage' of the developmental stages, the continuity requirement is neither tautological, nor easy to explore. In the light of a more explicitly dynamical view of the developmental sequence concept (e.g., ALBERCH 1985) discontinuous developmental dynamics or bifurcations of developmental programs and developmental continuities can be easily reconcilable, if the underlying developmental control parameters vary continuously. In such cases, developmental outcomes can show discontinuities, as in the case of generation of skin organs (OSTER & ALBERCH 1982). Therefore, continuity and discontinuity are not necessarily mutually exclusive views in the phenotypic organization and its evolution.

A set of discontinuous biological shapes [e.g., self-reproducing primeval cells, gastrula, spatially periodical structures, obcell (primeval cell) membrane (cf. CAVALIER-SMITH 1987)] can be generated on the basis of a variation principle (CIANCHO *et al.* 1996). The essence of this 'curvature' model is the minimization of the curvature energy, generating various anisotropic bilayers. There are at least three evolutionary implications of this model. First, the organisms and their parts can be regarded as an infolding of dynamically interacting shell/membrane systems. Secondly, not only genes, but also generative mechanisms can exhibit evolutionary conservation or continuity with manifold, apheliotropic effects, as in the case of the origins of blastulae and gastrulae (WOLPERT 1990). The real number of the germ layers (endo-meso-ectoderm) seems to be an unsolved problem in the light of the hierarchical shell/membrane infolding picture of the organisms. Finally, the simplest forms of the self-reproduction originated from morphogenetic processes.

Ecological continuity

We are aware of only two important aspects of the continuity of ecological systems. The first is concerned with the connection of adaptation and population demography. The second is about the matching between phenotypic and environmental patterns.

LEWONTIN (1978) realized the evolutionary importance of two characteristics of the selection, existing between character states and reproductive fitness. These characteristics are continuity and quasi-independence. 'Continuity means that small changes in a characteristic must result in only small changes in ecological relations; a very slight change in fish shape cannot cause a dramatic change in sexual recognition or make the organism suddenly attractive to new predators. Quasi-independence means that there is a great variety of alternative paths by which a given characteristic may change, so that some of them will allow selection

to act on the characteristics of the organism in a countervailing fashion; pleiotropic and allometric relations must be changeable. Continuity and quasi-independence are the most fundamental characteristics of the evolutionary process. Without them organisms as we know them could not exist because adaptive evolution would have been impossible.' (p. 169). We can only agree. LEWONTIN expressed in a transitive way that reliability belongs to the most fundamental evolutionary organizational principles, on which continuity and quasi-independence are based. It is fair to say that some aspects of LEWONTINS' principles were formulated in a vaguer style by RONALD FISHER in 1930 (see MOLNÁR 1995).

The other important aspect of the continuity of ecological relations is connected to the dynamical phenotype-environmental pattern matchings and its recognitions (DETHIER 1986, JERMY *et al.* 1990, JERMY 1993, MOLNÁR 1990, SCHOONHOVEN *et al.* 1998, CHAPMAN 1999). Reaction norms may also change continuously or show various bifurcations.

Combinations of genetic, phenotypic and ecological continuity

The complex combinations of genetic, developmental and ecological continuity can be simplified first using pairwise connections: 1. genetic-phenotypic, 2. genetic-ecological, and 3. phenotypic-ecological relations of continuity.

A useful way of analysing genetic and developmental connections is the embedding of locally acting specific genetic elements or systems into typical or generic, globally and/or locally acting physicochemical pattern and form generating mechanisms (MITTENTHAL 1989, NEWMAN & COMPER 1990, MOLNÁR 1986). The essential continuity requirement for the existence of coupled genetic-generic effect combinations is to fulfil or obey a matching principle (MITTENTHAL 1989, MOLNÁR 1986). This matching principle claims that short-range and long-range genetic and generic physicochemical mechanisms and their effects should meet. This principle implies that the continuity of development and evolution depend on the interactions between genes and the physicochemical mechanisms of developmental dynamics, generating ecologically relevant or competent phenotypes. Our view differs from the rest. The (often dually heritable) genetic-generic effect combinations operate within the internal and external ecology of organisms (cf. BUSS 1987), consisting of dynamical coexistence of competitive and cooperative selective factors (such as cell death, cell and cell lineage competitions and/or cooperations). To put more simply, our suggestion is that generic-genetic effect pairs or combinations and dynamically coexisting cooperative and competitive organism parts (multilevel parasitism, predation, mutualism, etc.) reciprocally drive

each other through a set of mediators during development, in its evolution, and in life cycle evolution, and in their coevolution.

A RELIABILITY THEORETICAL BASIS OF CONTINUITY PRINCIPLES

The argument for creating a reliability theoretical basis of the biological continuity principles

As mentioned previously, reliability can play a fundamental role in the generation of continuous operations in biological entities. Here we outline the elements of this conviction. A technique for incorporating reliability theoretical foundations into continuity principles is to connect the essential reliability shaping factors with the following scheme:

*i*th unit of organization — transmission → *i*th or *j*th unit of organization.

For this reason, we determine specific connections between reliability modifying factors with organizational units or their networks, such as genes, genomes, phenotypes, and ecological or social structures. The two fundamental classes of reliability determining factors are (1) error production and error reduction, and (2) generation of so called composite structures, the couplings of which can be series, parallel or their combined designs. Such a work is in progress, extending the status quo described in this paper. First, let us summarize briefly the elements of reliability theory.

The concepts of reliability

In this part of the paper, we show that a convenient way to treat the biological continuity principles is the theory of reliability.

The "reliability" of a system has several meanings. We present two of them in terms of measures of reliability. The reliability of a system is the probability of successful operations during given time, in a given environment (reviewed in ALEXANDER 1981, BARLOW & PROCHAIN 1965, MOLNÁR 1995). Reliability can also be expressed (ALEXANDER 1981) in terms of safety factors (SF) (SF = Capacity/Demand).

It is sometimes assumed (DAWKINS 1995) that safety factors are evenly distributed in an organism, because natural selection fine-tunes the costly safety factors. However, data show that vital organs can loose components or capacity in a variable manner; safety is unevenly distributed within a given range (ALEXANDER 1981, DIAMOND 1994, WEISS *et al.* 1998, NIKLAS & SPECK 2001), and the safety

factors can numerically differ among the parts of an organism, ranging from one to eight in the case of bones and tendons (ALEXANDER 1981) or between one and 2.7 in metabolic systems (WEISS *et al.* 1998), depending on loads. Highly unpredictable loads imply high, more predictable loads imply low safety factor (ALEXANDER 1981). (Un)Predictability can characterize the environment, which influences reliability.

The exact measurement of reliability in organisms is a difficult problem. Therefore, we discuss organismic reliability in terms of reliability decreasing errors, typical or generic reliability enhancing factors (REFs) and their effects. A reliability enhancing factor, or more simply a reliability enhancer, is a determinant that ensures the propagation of information, matter and energy within and between organisms. Alternatively, to put more generally, within and among organizational units, such as selective or evolutionary units, as we shall see later. These REFs include redundancies, repair mechanisms, storage materials and mechanisms, feedbacks, activators, inhibitors, replacements and combinations of series or parallel structures. There exists proof for direct or indirect relationship between reliability and its enhancers in the engineering and in the biological literature (ALEXANDER 1981, BARLOW & PROSCHAN 1965, MOLNÁR & VÖRÖS 1994, MOLNÁR 1995, NOWAK *et al.* 1997, JORDÁN & MOLNÁR 1999, JORDÁN *et al.* 1999), except for the case of selective processes. It is intuitively clear, however, that by removing erroneous parts from organisms by internal selective processes, the number of errors or the error rate can be decreased (see later), and consequently, the reliability can indirectly be increased. The same is true for the effects of other reliability enhancers as well, when reliability enhancers act after the formation of errors, as in the case of repair, feedback or replacement. Redundancy, storage and certain combinations of parallel and series structures tend to prevent error formation. A further confirmation of the connection between reliability enhancers and reliability would be the removal of reliability enhancers from organisms, and to evaluate their effects on reliability. There will be further concrete examples showing the action of reliability enhancers later in this paper. Error (or failure) is a factor, that inhibits or blocks the propagation of matter, energy and information, or capable of causing various other defects.

We now introduce a classification of various reliability enhancers, which helps to put all these factors in perspective. In the next three parts of this paper the reliability increasing and decreasing components will be outlined: first, the noise and/or errors, secondly, the reliability increasing factors, thirdly the composite structures.

The meaning, variation and classification of biological errors

The genesis of genomes and phenotypes include dynamic molecular, cellular, organismal, populational or higher phenomena. These events constitute patterns (ordered inhomogeneity) with characteristic shape, or more simply, with morphogenesis. Morphogenesis is the birth of biological forms. The major genotypic, phenotypic or ecological systems change in evolution. In addition, these systems have been associated with balanced changes between several error increasing and error reducing factors. We are aware that errors represent a fraction of the variation. Variation, however, is necessary for evolution, but errors are not. By error (or more generally speaking, by failure) we shall mean such effects, which decrease the reliability of the units of selection.

The variation of failures is associated with patterns, rates and with dynamic, evolving genotypic, phenotypic or ecological structures, functions, processes, evolving modes of heredity, variation generation, reproduction, evolutionary lineages or else.

An elementary classification of the diversity of failures can be organized according to the following properties of failures. A. According to their appearance, failures can behave continuously (i.e., accumulative), sudden (catastrophic, lethal, sublethal). B. According to connectivity or distance of interaction, failures can be classified as independent or local, moderately or highly connective, dependent, global failure groups, with varying interaction strength. C. According to spatial, temporal or spatiotemporal behaviour, failures can be classified as temporary, repetitive or constant failures. Certain failures can cause other failures, propagating in series, parallel or in combined ways. D. According to failure localisation in composite structures, we can make distinctions between failures emerging in series, parallel systems or in their combinations, e.g., in bridge structures. E. According to origins, failures can be dependent upon genotypic, phenotypic or environmental factors, or they can reflect their independencies on them or on their combinations.

Error production and error propagation in evolution

We do not know the quantitative measure of error rates in the separate or the joint evolution of heredity, variation and of reproduction. What we do know, however, is the fact that these evolutionary properties are prone to failures. Traditionally, studies on the evolution of error patterns or error rates focus on the heritable mutations. We would like to know, however, not only the failures of hereditary information, but the sources, patterns and rates of failures in the generation of genotypic, phenotypic or environmental variation, and the failures observed in the various modes of evolution of reproduction or the failures of the invasion of

genotypic or phenotypic variants. Now we will refer to some representative investigations studying the evolutionary patterns and rates of heritable, variation generating or reproductive failures and their possible evolutionary interactions.

Mutations do not constitute unambiguous error sources, because a subset of mutations has evolutionary advantage. EIGEN (1971), DRAKE *et al.* (1998), NINIO (1997) have described quantitative measures of mutation rates and their evolution.

We have a very rich evolutionary literature on the origins of erroneous genetic and phenotypic variation. Some of them include GOLDSCHMIDT's (1940) book on the hopeful monsters capable of spreading under favourable conditions. GRUNEBERG (1963) wrote a whole book on the pathology of development. As for the erroneous genetic variants, a number of monographs have published largely inconclusive information about the real distribution on the various patterns and rates of genetic errors.

What can we say briefly about the evolutionary interaction of the heritable variation generating and spreading of the successful variants? Perhaps the best example is the concept of ESS (MAYNARD SMITH & PARKER 1973), which defines the condition of the spread of a potential, new variant, and its failure to spread. Accordingly, evolutionary game theory cannot explain the origins of novel variants; it just assumes their existence in its strategical reasonings. The views of the origins of variants, however, cannot take into account the generative mechanisms of the variation generation. Finally, it is safe to say that there must be an equilibrium in the production of successful and in the erroneous variants in preventing or avoiding extinction.

Classification of genotypic, phenotypic and ecological reliability enhancing factors

In many cases, we cannot determine the level of the exact quantitative value of reliability, neither safety factors, nor transition probabilities. In such cases, we can still qualitatively detect if a factor decreases or increases the value of reliability.

We propose (MOLNÁR & VÖRÖS 1994, MOLNÁR 1995, MOLNÁR unpubl.) that all reliability-enhancing factors fall into the following categories, which are illuminated in each case by typical examples.

1. Repair. Examples include: Recombinational repair during which elimination of genetic errors can take place (EISEN & HANAWALT 1999, AARAVIND *et al.* 1999). Cellular detoxification of poisons. Wound-healing and regeneration (KIRKWOOD 1981).

2. Replacement. The replacement of lost cells and tissues in the epithelium of the intestine by means of stem cells or the replacements of immune or sperm cells.

3. Feedback. Feedback regulation is well known in the neural or hormonal control. According to MEINHARDT (1995), the reliability of development is mainly based on autocatalytic self-activation, cross reactions and feedback of gene products. But as WOLPERT (1994) realized, embryonic development cannot be stabilised by negative feedback alone, because embryos would get into "frozen" or stabilised states instead of going through their successive developmental pathways. Self-stabilising genetic, cellular and other redundancies seen in intracellular and intercellular processes can contribute to the stabilisation of developmental pathways (see MOLNÁR & VÖRÖS 1994, MOLNÁR 1995, NOWAK *et al.* 1997, TAUTZ 1992, THOMAS 1993, WOLPERT 1992).

4. Storage. Good examples for variation of storage are plant storage proteins (SHEWRY 1995), especially starch, which is controlled by a single gene, and the yolk in animal eggs (BERRIL 1948). The role of storages can be important in fluctuating environments in averaging fluctuating resource density, for instance. The evolutionary success of the *Volvox* can in part be regarded as the success of large extracellular matrix, which is capable of buffering uneven resource level (BELL & KOUFOPANOU 1991, KIRK 1998). Storages represent excess or reserve materials that can be mobilized.

5. Redundancy. Genetic information can contain variable amount of genetic redundancy (OHNO 1970, ANDERSON & ROTH 1977, TAUTZ, 1992, THOMAS, 1993, BROOKFIELD 1997, NÁDORI *et al.* 1996, NOWAK *et al.* 1997).

6. Combination of series and parallel structures. A representative example is the bridge structure, which is a parallel organized structure which contains one or more crosslinks (BARLOW & PROSCHAN 1965, JORDÁN & MOLNÁR 1999, MOLNÁR unpubl.). Bridge structures are ubiquitous in nature; they can be observed in molecular networks, such as gene regulatory networks, signal transduction pathways, cellular networks, such as cytoplasmic bridge structures of *Volvox*, anatomical networks, such as venation or blood vessel patterns, or even in ecological networks, such as food webs (BARLOW & PROSCHAN 1965, BELL & KOUFOPANOU 1991, INGBER 1993, JORDÁN & MOLNÁR 1999, JORDÁN *et al.* 1999, KIRK 1998, MOLNÁR & JORDÁN unpubl. results).

As we have demonstrated elsewhere by using graph theoretical models of specific molecular, cellular, supracellular and ecological networks, these models possess predictive features in the reliability theoretical analysis and synthesis of biologically important networks (MOLNÁR & JORDÁN, unpubl. results). The relevance of these models is the quantitative prediction and demonstration of the existence of certain preferred biological structures.

7. Activation and inhibition. These actions are well known in the operation of the nervous systems.

8. Multilevel selection. The various sources of multilevel selection (LEWONTIN 1970) can also be regarded as reliability enhancing factor, because their function is the reduction of genetic, phenotypic or developmental errors. Spontaneous abortion in human pregnancy belongs to this category.

Balance between the error formation and the error reduction in the main stages of evolution

We propose a hypothesis for describing alterations in reliability enhancers in evolution. The core of this hypothesis is that it is likely that there exists a balance between errors and their controls. The origin of genotypic or phenotypic variability seems to involve coevolution between novel error possibilities and their novel controls.

The assumption that there exists a balance between the level of errors (or more correctly error rates) and the rates of generating reliability enhancing factors in evolution requires a justification. The errors are unavoidable factors in organisms. When the error level is high, the continuity of the biological processes can break down. This phenomenon can be observed in aging (KIRKWOOD 1981), in developmental defects caused by lethal factors, and in the dynamic of the heart caused by failures, for instance.

The most clearly known example of the control of error rate by reliability enhancing factors is the origin and maintenance of the error level in DNA molecules (DRAKE *et al.* 1998, NINIO 1991, REANNEY 1987, REANNEY *et al.* 1983). The evolution of mutation rate of DNA can be taken as an example for demonstrating the evolutionarily changing balance between error formation and error reduction. It is assumed, (REANNEY 1987) that in an initial stage of DNA evolution, the error rate was high, 10^{-2}/nucleotide/generation. Later, antimutator and repair or proofreading genes and catalysts, furthermore suppressors were capable of reducing the error rate to 10^{-9}/nucleotide/generation, in DNA molecules. So the errors cannot be eliminated, but their occurrence can be reduced to a certain level (DRAKE *et al.* 1998, NINIO 1997, REANNEY 1987). Similar events can be observed in protein synthesis. We propose that the principle of balanced error producing and error reducing processes occurring at genetic level can be extended to phenotypic organizational levels as well. Important initial steps towards such a direction have been made at molecular level, for instance (NINIO 1991, 1997, DRAKE *et al.* 1998).

We do not know exactly the level of balance of error producing and error reducing factors above the molecular level. We do know, however, that novel, variable errors must have come into existence at different organizational levels, such as damage of membrane or cytoskeletal elements in cells, and errors in cell divi-

sion, cell assembly or cell replacement, and so on. All these phenomena have been convincingly demonstrated by the huge databases of the pathological molecular, cellular and developmental processes. As we have seen, the error reducing reliability enhancers changed through the main steps of evolution in concert with the appearance of novel sources of errors. Since the maintenance of reliability enhancing factors is costly, their levels must be constrained within maintainable ranges (ALEXANDER 1981, DIAMOND & HAMMOND 1992, MOLNÁR & VÖRÖS, 1994, NÁDORI *et al.* 1996). If the level of reliability enhancers were low, saving energetic or other cost of their maintenance, biological processes would be more vulnerable or would break down. We need a quantitative theory for describing the balance of errors and their controls at phenotypic level. But even some trivial questions still were missing at the beginning of a more systematic analysis of the role of reliability in morphogenesis, development and evolution (MOLNÁR & VÖRÖS 1994, MOLNÁR 1995).

It is likely that reliability enhancers possess multifunctional properties, i.e., that they have been involved in several functions, in parallel or sequentially. It seems plausible to consider the origins of reliability enhancing factors as evolutionary novelties, which reappeared at the birth of novel organisational levels. This view raises an important problem. Reliability enhancing factors show specificity sometimes, as in the case of recombinational repair, and multifunctionality in many other cases. It seems that the degree of their specificity might tell us whether the REFs have specialized for error correction or not. We need not know exactly all the possible functions of structures or mechanisms to recognize cases when a structure or a mechanism plays a role – among other roles – in error correction.

The concept, the variation and the behaviour of the composite structures in evolution

A composite structure consists of more than one serially or parallel coupled elements. Composite structures consisting of more than two components have high relevance of their topologic coupling from reliability theoretical point of view. The various patterns and processes in the living world can be represented by composite structures.

Reliability of composite systems change according to their architecture. We propose the following view in this paper: The characteristic patterns and processes in life cycles or evolution can be regarded as composite structures with their respective reliability. Hence, the principal processes of evolution, such as microevolution, macroevolution, speciation, body plan evolution, coevolution are considered to be various composite structures. A reinterpretation of the patterns and

processes in nature may lead us to a novel grandeur of the history of life. The continuity of living patterns and processes can be discussed in terms of evolutionary genomics and phenomics.

Now let us discuss the concept, the variation and the behaviour of the k-out-of-n structures in evolution, as a special class of the composite structures. Imagine a system consisting of n components of subsystems. A system with k-out-of-n structure works, if at least k elements work, and $k \leq n$.

In this part of this paper, we describe an hypothesis for the evolutionary origins of genomes (NÁDORI *et al.* 1996). A basic character of the genetic systems is that their composition allows the loss of certain genes. We propose that this property or the dispensability of a specific set of elements corresponds to the k-out-of-n-like structure class of the reliability theory (BARLOW & PROSCHAN 1965). Knockout experiments or gene targeting show (TAUTZ 1992) that a number of genetic elements can be lost or inactivated without visible phenotypic effects. The case of the regulation of the Krüppel gene by four other genes in *Drosophila*, and its intact function when its 1, 2 and 3 regulators were knocked-out (TAUTZ 1992), is a nice illustration of a k-out-of-n-like behaviour. The minimal genome concept (the fact, that nearly 256 genes or even less operate in a given bacterial cell, living on optimal resource without competition) reviewed by KOONIN (2000) also provides a good example for the operation of minimal genetic systems reduced to indispensable genes. Since there exist many similar examples for the genetic phenomenon at different phylogenetic positions, we think that this is an evolutionarily conserved property. We assume that the evolutionary origins of the genomes may have emerged from coupled islands of k-out-of-n-like genetic elements. The result of this effect is the existence of genetic systems with multiple channels. The mechanisms of the coupling of genetic elements may have been the same, as in the case of the scenario. This is a clear case of the nontrivial, but probably widespread, unavoidable recapitulation. (Recapitulation is the repetition of evolutionary events in development.) We also remark that several constraints may act on the value of k.

Our approach can be applied to the treatment of other phenomena as well, occurring at different organizational levels. The potential role of k-out-of-n structures has been discussed by MOLNÁR (1995) at different organizational levels, as in the case of cell lineages, replacements of stem cells or other organismic devices (see DIAMOND 1994, for further examples of the reducibility of various phenotypic structures, the loss of which until a threshold level is still compatible with survival and reproduction).

OSTER & WILSON (1978) have applied this idea for describing the k-out-of-n behaviour in the organization of behavioural sequences in animal societies. OSTER

& WILSON (1978) described the evolutionary transition from a solitary to a colonial animal in terms of a reliability theoretical model. They regarded the steeper reliability relation between the component animals and the social group as a key selective advantage in the transition.

The evolutionary effects of reliability enhancing factors

An obvious way to point out these effects is to show their potential fitness consequences. We do not understand clearly the control (or proximate or ultimate causes) of the quantitative aspects of REFs. The simplest form of the problem is the following: If a high level of overdetermination or reliability enhancing factors is useful, why do not exist more of them? More explicitly, if two kidneys are better than one, why not have three (DIAMOND 1994). The simplest explanation is that reliability enhancers require cost and limited, organised packing (see ALEXANDER 1981, and DIAMOND 1994 for cost consideration in the maintenance of reliability).

In this regard, the same hypothesis connects the various data sets. As we have seen above, this requirement is satisfied. We are, however, aware of the incompleteness of our data, but the multiplication of the various data would not affect the essence of our two central organizing principles. A second type of evolutionary hypothesis testing is to ask whether the traits in question can propagate or invade efficiently under certain conditions. The tool of studying of this second strategic or ecological aspect of reliability enhancers can in principle be determined in terms of their fitness consequences. We describe first two direct and then one indirect relationships connecting reliability enhancing factors and fitness.

1. The influential paper of ALEXANDER (1981) describes the fitness cost of safety.

2. We have developed a mathematical method for the treatment of the joint actions of reliability determinants on fitness elsewhere (MOLNÁR & VÖRÖS 1994, and MOLNÁR & VÖRÖS unpubl. results, for a novel view of the evolution of aging). We have pointed out in a model that the coupling between various REF combinations and selection can describe the evolution of aging and longevity. (Description of aging is a prototype of the description of deterioration or its control in biological systems.) Unfortunately, our approach has not yet been applied for describing phenotypic properties under the effects of changing reliability enhancers.

3. An important possible step in connecting reliability to its ecological consequences has been put forward by VERMEIJ in his hypothesis of escalation (VERMEIJ 1994). Briefly, VERMEIJ's central thesis is that the main devices of the competition for various resources between enemies (predators, competitors and dangerous preys) are defensive or offensive means, which can be escalated in arms

races by positive feedback. For illustrating the similarity between VERMEIJ's view and ours, it is useful to quote him: "Individuals often fail to acquire or retain resources during encounters with other individuals. Insofar as failure reduces the probability of survival or opportunities for reproduction, there is room for adaptive improvement. The potential for improvement can be roughly gauged by the frequency and cost of failure." (VERMEIJ 1994, p. 221.) The main difference between VERMEIJ's and our views is that we think that various combinations of reliability enhancing factors can be an underlying basis for escalating defences and offensive weaponry. Furthermore, we study the connections of reliability enhancers in the context of the major morphogenetic transitions, and so neglect the fascinating topic of defences and offences. Finally, we think that the escalation of defences and offences were preceded by an escalation of several reliability enhancers.

The acquisition of reliability decreasing and increasing factors in the main steps of evolution

In this part of the paper, we present a pattern of evolution: an association between error possibilities in the novel ways of genotypic, phenotypic, ecological or social systems and error control exerted by REFs. In a very popular sense, our approach reflects the fight between good and evil forces. This mythical sense is being projected into the structure and the operation of biological objects. The outline of this evolutionary scenario is shown in Table 1, which presents the successive evolutionary origins of different types of REFs. These REFs might have played potential error reducing or other roles in the major stages of evolution.

CONCLUSIONS

In this paper, we have briefly outlined reliability theoretical foundations of the biological continuity principles. Finally, we summarize the main points of the paper.

1. As WOLPERT remarked, "Selection on developmental processes acts primarily on reliability and this requires consideration of buffering and redundancy in developmental processes." (WOLPERT 1992). If so, the various evolutionary views should be compatible with the reliability theoretical approach to evolving hereditary systems, phenotypes and ecological or social design generating processes.

2. The various reliability enhancers can be regarded as evolutionary novelties, which could have reappeared at various evolutionary stages in evolutionarily changing ways. Accordingly, evolution repetitively invented similar construc-

tional devices at various organizational levels in an iterated way. Using this evolutionary "trick", natural selection is capable of preserving the successful units of organization more efficiently.

3. Reliability enhancers often have dual or even multiple functions (MOLNÁR & VÖRÖS 1994, MOLNÁR 1995). Dual function means that reliability enhancers are capable of conserving genetic, phenotypic, cellular, developmental, ecological

Table 1. Associations between the main steps of evolution and their acquired reliability enhancing factors, such as repair, replacement, storage, redundancy, feedback, series and parallel structures. T1–4 indicates the main steps between evolutionary stages. References are in part given in the text or can be obtained from the author.

1. PROTOCELLS
unknown reliability enhancing factors
T1
↓
2. PROKARYOTES
holoenzyme (autolysine+ transpeptidase) redundancy in wall stress regulation,
repair, genetic redundancy, *k*-out-of-*n* behaviour of bacterial colonies
(every clone behaves in *k*-out-of-*n* manner, D. KAISER, pers. comm.),
feedback in metabolic networks, partial redundancy in autocatalytic cycle.
T2
↓
3. PROTOZOA
self-regulating local and global positional information,
repair, genetic redundancy, bridge structures in cytoskeleton,
redundancy in signal transduction,
feedback in metabolic network, partial redundancy in autocatalytic cycle.
T3
↓
4. MULTICELLULAR ORGANISMS (ANIMALS, FUNGI, PLANTS, CHROMISTA)
k-out-of-*n*-like behaviour in cell populations,
bridge structures in molecular and cellular networks *Volvox*,
crosslinks between ECM molecules enhancing mechanical reliability,
cell replacement, e.g. stem cell activity,
storages, such as Volvox ECM, (better starvation tolerance in fluctuating
environment) ontogenetic buffer mechanisms,
elastic energy storage in tendons for animal movement,
feedback in embryonic induction or in neuroendocrine control,
multiple assurance in intercellular signal propagation, e.g. in induction,
genetic, cellular or modular redundancy.
T4
↓
5. PHENOTYPIC PATTERNS OF ANIMAL COLONIES
feedback in caste determination, storages, such as pollen or honeycomb,
redundancy in the number of colony members.

or social characters, as the buffering role of the redundant genes indicates in the case of canalisation. At the same time, these factors are capable of generating novel genetic, morphogenetic, ecological and evolutionary possibilities, as in the case of heterochrony (MOLNÁR & VÖRÖS 1994, MOLNÁR 1995). Because of their dual or multiple effects, reliability enhancers constitute a specific set of factors governing evolvability (GERHART & KIRSCHNER 1997, WAGNER & ALTENBERG 1996) since reliability enhancers are capable of generating and preserving evolutionary potentials.

4. What problem does all this create for evolutionary theory? First, it seems reasonable to think that error formation and error control play a fundamental role in the "struggle for existence", which should be explored more explicitly. According to DARWIN, the term "struggle for existence" refers to two notions: "dependency of one being on another" and to "success in leaving progeny" (DARWIN 1859). Reliability of the organisms affects both properties. The view presented here overlaps with and complements DARWIN's evolutionary vision by emphasizing an important class of internal factors of evolution and their potential connections with ecologically important defensive and offensive characters (VERMEIJ 1994). Second, the relationships between the view of evolution presented in this paper and other evolutionary scenarios, such as the conflict-based view of evolution, should be formulated more exactly, because they describe different aspects of the evolving biological organization. For example, parent-offspring conflict, genetic conflicts, sexual selection or predator-prey arms races represent typical conflicts driving evolution. Third, reliability-related errors and error controls reflect mainly self-organisation within and among organisms resulting in both chance and ordered evolutionary consequences, in many cases even before the action of natural selection. Finally, errors or failures represent a fundamental aspect of historical contingency (cf. GOULD 1989, CONWAY MORRIS 1998, LAWTON 1999). Therefore, any fundamental view of the evolutionary history of biological processes should contain a description of errors and the safety techniques of the organisms, or more generally, the various units of biological organization and of their networks.

*

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DIPTEROUS GUILDS OF SMALL-SIZED FEEDING SOURCES IN FORESTS OF HUNGARY

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Insect guilds (of Diptera and Coleoptera) on "very small-sized feeding sources" (droppings of forest animals, dead snails, tinder fungi, decaying fungi, sap of deciduous woods, *Vespa* nests, etc.) in low mountain forests in Hungary were studied from 1995 to 1998 (504 positive samples for flies, more than 20500 dipterous individuals). A small but significant fraction (about 20%) of these sources is not exploited by flies at all. The high species diversity of those that are colonized represents a majority of forest Diptera diversity in Hungary (with numerous species and genera new to Hungary and even new to science). The quality, size, persistency and place of renewal of the sources, the potential size of each dipterous population, the flies' ability to find new sources and composition of the local fauna are all important factors in determining the actual frequencies of species found on extant sources.

Although the primary texture of the forest community structure is formed by the more abundant forest species populations, those species in guilds on small-sized food sources put a colourful pattern on that texture. They are mostly rare and are probably insignificant for the main energy flow processes, but knowledge of their presence and life histories would seem to be indispensable for a complete understanding of ecosystem structures and diversity maintenance. Biomonitoring of these species, however, is a challenge because of their poorly understood ecology and fluctuating abundance. The relationships of rarity and the species colonizing these sources are discussed and the development of raritology (study of rare species) as an individual branch of ecology is predicted.

Key words: small-sized feeding sources, Diptera, species composition, diversity, raritology, Hungary

INTRODUCTION

The insect guilds found in small-sized food sources have attracted very little attention in ecology, particularly so for those sources consisting of dead organic matter. In ecology textbooks, even in the best ones, only a small portion is devoted to animals developing in droppings, carrion, etc. (cf. KREBS 1985, PRICE 1984, THOMPSON 1984). Even SZELÉNYI (1953) left them out of consideration. The most comprehensive analysis was found in BALOGH's (1953) book which, although qualitative, summarised the important literature of the time and assigned these guilds their proper importance by including them as a category in forest ecosystems. (Note that I use the term "guilds" in the sense of HAWKINS and MACMAHON (1989) rather than in its original meaning (ROOT 1967)).

Despite their importance to the understanding of the diversity of many ecosystems, comparatively few papers have dealt with insects from small-sized food sources. This is probably because: (a) Their role in the material and energy turnover of the communities is negligible; (b) Their study is difficult from a methodological point of view, and the classical methods and considerations are not usable for their study without modification (cf. SOUTHWOOD 1978); and (c) The results of previous studies reported that the species composition and frequencies of these insect populations appeared to be highly variable, almost accidental; hence entomologists – like any other natural scientists tuned to look for invariance – did not find pleasure in their long-term study. Most of the studies resulted in the publication of a list of the collected species and usually not much more.

In view of these problems, we developed new collection techniques to more effectively obtain critical data on composition and frequencies of species that comprise the guilds on small-sized food sources. We used regular sampling and simple but reliable methods (i.e., counting rather than making estimations on abundance of flies on the small-sized sources in natural conditions). With the voluminous data thus obtained we hope to answer the following questions: (a) How repeatable is the species composition of the guilds on a given type of small-sized source? (b) Based on the abundance of the dominant and subdominant species we found, may we attribute any structural characteristics (i.e., less than a true structure) to those assemblies/assemblages (there is no reason to call them communities)? (c) Is there enough commonality in the organisation of the guilds of the various small-sized sources to give them a unifying name?

Our goal for this research is to be able to estimate the contribution of these guilds to the species richness of the forest ecosystems. In additon, we also hope to increase the scientific community's awareness of the forms of rarity among insects.

MATERIAL AND METHODS

The sampling sites were selected in low mountain forests in Hungary:

1) Börzsöny Mts (central North Hungary): Verőce-Magyarkút: Keskenybükki-patak valley and the Les-völgyi-patak valley; forests along the road from Diósjenő to Kemence; two forested brook valleys (Vasfazék valley and Szénpatak valley) accessible from Királyrét;

2) Visegrádi Mts (central North Hungary): Apátkúti valley near Visegrád, on the other side of Danube;

3) Vértes Mts (NW Hungary, Transdanubia): Fáni valley.

Supplementary collections were made also in other parts of Hungary (Kőszegi Mts, Bükk Mts, Zempléni Mts).

Insects were collected on or near various small organic sources as listed in Table 1. Techniques were developed to determine the abundance of each species on a given source sample by

counting and not by estimation. Therefore isolators were used to capture flies and other insects actually present on these sources. The isolators are large aluminium funnels used in wine cellars and a glass aspirator used to catch mosquitoes bound with sections of bike tires (see PAPP 1985). Using a strong aspirator, I captured the smallest flies which might crawl out from under the rim of the funnel.

We constructed special traps (in a way similar to some pitfall-traps) to collect all the flies including phorids on dead snails; we then reared them to adulthood to determine the quantities and species from each source.

A new type of soil bait trap was constructed to collect adult Diptera on dead *Helix* snails (PAPP & TÓTHMÉRÉSZ in prep.). These special traps were necessary because of the special properties of the Phoridae species (the photo-eclector type traps we used at first were ineffective, since the phorids – unlike other Diptera – do quite well in complete darkness).

Some kinds of substrates were collected and taken into the laboratory where Diptera adults were reared from them. This way one can collect data on the actual quantity of the individuals and species composition developing in small-sized feeding sources such as dead *Helix* snails exposed for 48 hours and *Vespa crabro* nests (PAPP 2000). Rearing was done largely by MIHÁLYI's (1967) method.

Where the distance of the sampling points were reliably measurable, we used a Data Disto device to obtain distance data, and a map was drawn by the aid of the "Profly" software.

To find small-sized sources in a native forest is mostly a matter of good luck. One can find a good piece of tinder fungi comparatively easily, whereas one may seek all the day in vain for deer dung.

In the past we have collected extensive data on flies from wild fruits (PAPP 1992, apple bait collections) and human faeces in the same forest brook valleys (PAPP 1993), as well as on flies developing in fruiting bodies of mushrooms (ÁGNES DELY-DRASKOVITS reared 50 thousand adult Diptera of 128 species in 24 families; see DELY-DRASKOVITS 1976), but these data were not included in this project.

Statistical analysis of species richness data was done using the non-parametric analysis (Chao2 and Jack1, the first order jackknife method). The structure of our other data does not allow us to use more sophisticated methods formerly used (IZSÁK & PAPP 1994, PAPP *et al.* 1997, PAPP & IZSÁK 1999).

RESULTS

Ecological results

From April 1995 to November 1998 insects (flies and beetles) were collected on more than 500 small source samples; more than twenty thousand adult flies were captured or reared. Number of species, individuals and samples collected from 1995 to 1998 are summarised in Table 1. A separate paper was published about the flies reared from *Vespa crabro* nests (PAPP 2000).

Table 2 shows a part of our results obtained in a creek valley of the Börzsöny Mts where we applied special traps to collect flies on dead snails (*Helix pomatia*). Twenty traps were set up for 24 and 48 hours on the identical places on the same days of July and August in three consecutive years (1995–1997); flies were also

reared from the dead snails left out two days. The number and species composition of the flies on a dead snail likely depend much more on whether a snail died in the close vicinity of a fresh corpse some time earlier than on the physical or environmental factors of the micro-site.

The species numbers found on four types of sources is summarised in Table 3 and compared with species number estimation made by the Chao 2 and the first order jackknife method. When analysing data shown in Table 1, all the sources sampled are taken into consideration. The species richness calculations summarised in Table 4, however, only include the number of the adult flies captured on tinder fungi, on fox faeces, on deer faeces and on rotten or mouldy fungi.

Some faunistic results

A by-product of our studies is that dozens of species and genera were found as new for the fauna of Hungary (numerous species even new to science have been found hitherto). PAPP (1999) recorded eight genera and 15 species as new for the Hungarian fauna (*Elephantomyia edwardsi* (MEIGEN, 1818), the genera *Phalacro-*

Table 1. Number of species, individuals and samples collected from 1995 to 1998

Source	species	specimens	samples	remarks
Dead *Helix* snails	91	5013	240	see table 2
Fox dung	67	844	45	11 negative samples
Deer dung	73	569	39	
Tinder fungi	61	2708	50	
Rotten or mouldy fungi	113	1503	20	
Vespa crabro nests	19	8225	2	see PAPP (2000)
Other dung[1]	30	87	5	
Dead animals[2]	22	68	4	
Wounds of trees, bleeding stubs of trees	60	601	73	(47 + and * samples)
Apple marc	43	191+	20	(plus Drosophilidae 2571 ex.)
Other sources[3]	770	6		
Total	–	20579	504	(plus at least 91 empty samples)

*Combined samples

[1]One week old human faeces, rabbit litter thrown into a forest, wild boar dung (2), *Mustela* sp. dung

[2]Dead fox, dead frog, dead *Anguis fragilis*, owl pellet

[3]On mouldy sap of oak and hornbeam stubs (2+1), on *Meloe violaceus* (2)

Table 2. Dipterous individuals trapped during 24 hours on dead *Helix* snails combined with the numbers of flies reared from dead *Helix* snails exposed for 48 hours (20 samples each) (see also PAPP & TÓTHMÉRÉSZ, in prep.)

	1995	1996	1997	total
July, 1 day	254	110	424	788
August, 1st day	82	218	187	486
August, 2nd day	214	410	131	754
Flies reared	1870	338	775	2983
Altogether	2420	1076	1517	5013

Total number of species: 91; in one series max. 37 species

cera, Ditomyia, Phthinia, Ectrepesthoneura, Novakia, Sceptonia with one species each, the genus *Monoclona* with three species and the peculiar species *Dicranomyia ornata* (MEIGEN)). In the same paper numerous mycetophilids (in the genera *Neoempheria, Acnemia, Polylepta, Apolephthisa*) are mentioned, which are significant contributions to the collection of the Hungarian Natural History Museum.

Table 3. Non-parametric estimations of species richness. N: number of dipterous individuals captured on the source on that day, S_0: number of species actually found in that sample series; n: number of samples; L: number of single occurrences; M: number of double occurrences; Chao2: species number estimated by the Chao2 method; Jack1: species number estimated by the first order jackknife method

Locality, time (year/month/day)	N	S_0	n	L	M	Chao2	Jack1
Tinder fungus, total no of species: 61, N = 2708							
G-V,F-v., 96/05/07	374	18	6	7	8	21.1	23.8
G-V,F-v., 96/06/04	346	20	5	14	1	216	31.2
G-V,F-v., 98/05/09	318	16	7	6	5	19.6	21.1
Fox faeces, total no of species: 67, N = 844							
G-V,F-v., 95/10/31	297	11	15	5	3	15.2	15.7
G-V,F-v., 97/11/02	140	6	8	3	1	10.5	8.6
Szo,K-h., 98/09/27	102	16	7	7	1	65.0	22.0
Deer faeces, total no of species: 73, N = 569							
G-V,F-v., 97/09/28	179	31	8	16	4	63.0	45.0
Szo,K-h., 98/10/23	111	11	6	3	3	12.5	13.5
G-V,F-v., 96/09/11	52	21	4	16	5	46.6	33.0
Rotting or mouldy fungi, total no of species: 113, N = 1503							
VM,K-v., 95/10/15	502	65	4	27	14	91.0	85.3
Sze,K-v., 96/08/08	257	38	6	14	7	52.0	49.7

Some other species and genera new for the Hungarian fauna are as follow: *Keroplatus testaceus*, *Xylophagus compeditus*, *Rhaphium sp.*, *Oncopygius distans* (LOEW) (also first record of this genus), *Phaonia cincta* ZETTERSTEDT. *Xenolimosina setaria* (VILLENEUVE) represents also a separate sphaerocerid genus new to Hungary and even to the Carpathian Basin. Its only known locality in Hungary is Gánt, Fáni-valley, where it was first collected in 1992 and three years later (Oct 31, 1995). It is important to know that this species maintained its small population there.

The species of the family Phoridae play an important role in the dipterous population of almost all of the small-sized sources. We knew even in the planning phase of the project that we do not possess the taxonomic base for their study (a collection of named species, expertise, etc.). Consequently, we sorted the unnamed specimens in the HNHM into genera, identified several species and compiled a literature base. This work resulted in the publication of a list of species of the family Phoridae in Hungary (ÁDÁM & PAPP 1996) including three genera new to Hungary (*Aenigmatias, Plectanocnema* (by *P. nudipes* (BECKER)), *Woodiphora*).

The number of the rare species whose representatives were captured is very high. I would like to mention only *Sycorax silacea, Xylophagus ater, Opetia nigra, Chymomyza caudatula, Ch. fuscimana, Gigalimosina flaviceps, Anagnota bicolor, Steganina hypoleuca, Phyllomyza longipalpis, Fannia aequilineata.*

Sampling on wounds and bleeding stubs of trees did not result in a data set proper for quantitative analysis. A high number of wounds were found empty and this is why samples were combined (adult flies captured on several trees combined into one sample). The species composition on these wounds we found very interesting, for we discovered there are four *Aulacigaster* species in the Palearctic (*A. afghanorum* sp. n., *A. falcata* sp. n., *A. neoleucopeza* MATHIS et FREIDBERG, *A. leucopeza* MEIGEN; PAPP 1998*a*), instead of one (*A. leucopeza*). Also a species of the Drosophilidae new to science, which develop in the oozing sap, was described (*Scaptodrosophila abdita* PAPP *et al.*, 1999). Another paper was published on the life-habits of the species of Periscelididae and I also captured the formerly unknown larvae of *Periscelis nigra minor* ssp. n. and *Periscelis winnertzi* EGGER.

DISCUSSION

Difficulties in finding small-sized sources resulted in a loose data set; that is, only a few kinds of sources were found in high numbers. Those are dead snails (baiting and trapping), fox and deer faeces, tinder fungi, rotten or mouldy fungi, and wounds of deciduous trees (Tables 1 and 3).

Occurrences and frequencies

Occasionally an extremely high number of insects (flies) is found on or in a piece of the small-sized sources. For example, we reared 1295 dipterous individuals of 16 species from 4 litres volume of the debris in a wasp (*Vespa crabro*) nest, as well as 6930 specimens of 15 species from 9–10 litres of another nest (PAPP 2000). A sporophore (fruiting body) of a mushroom of c. 50 grams produces over 500 small flies (50000 mg *vs* 500×5 = 2500 mg living weight). We collected more than 7000 specimens of the staphylinid beetles from a medium-sized sporophore of a *Laetiporus sulphureus* tinder-fungus. These examples might help to understand the seemingly high abundance of numerous species in a common forest.

On the other hand, it became obvious at an early stage of our studies, that a significant part (about 20%) of those sources is empty and not exploited by any flies (Table 1). In some cases no insects were found on a seemingly proper micro-site (the empty source seemed just as good as another one that was richly occupied); even the dominant species characteristic of the given source were missing. In numerous cases the composition of the guild of one type of small-sized sources is different from site to site at a given time (as if there were no "cores" but "satellites" only; cf. HANSKI 1982). The explanation of these kind of unusual situations is that we experienced a very low representation of a minor part of the species pool instead of characteristic species in reproducible frequencies. This kind of a sample is not "typical": I would symbolise it as a small broken piece of earthenware from which the shape of the pot cannot be reconstructed. The virtual species pool is very large (cf. Table 4) if we regard all the species as members of the species pool which may appear on the given kind of small source. We can realise a part of this virtual pool by systematic collection of flies at a given site. By now we are sure that it would take years to obtain a significant part of that species pool. We can artificially improve collections by placing baits into the natural habitats. If properly done, baiting (e.g., BUCK 1994, BUCK *et al.* 1997, and also our dead snail sampling) provides useful data. However, the complete species pool of a given source with an ideal frequency vector is a fiction (as The Hyper Fox Faeces or The Hyper Dead Snail), an unattainable non-existing idealisation. I do not think that baiting or even manipulated baits would be proper tools for tests of general ecological relationships as was made by KNEIDEL (1984) and others.

The species composition, connectance (how many species would connect two kinds of small sized sources), etc., of the guilds are highly varied. The quality, size, persistency and place of renewal of the sources, the potential size of each dipterous population, their agility and ability to find new sources and composition of the local fauna (as a species pool) are the most important factors which determine actual frequencies found on extant sources. It seems that the abundant species

Table 4. Species and their total abundance in the samples of rotten fungi, fox faeces, deer faeces and tinder fungi

Rotten fungi		*Tephrochlamys flavipes*	1
Psychoda sp.	7	*Suillia affinis*	4
Tinearia alternata	16	*Suillia bicolor*	5
Trichocera relegationis	1	*Suillia fuscicornis*	1
Epidapus sp.	1	*Clusiodes albimana*	3
Sciaridae sp. 1	12	*Paraclusia tigrina*	1
Sciaridae sp. 2	19	*Sphaerocera curvipes*	3
Sciaridae sp. 3	4	*Ischiolepta pusilla*	9
Cecidomyiidae sp. 1	6	*Crumomyia nigra*	1
Cecidomyiidae sp. 2	5	*Crumomyia nitida*	1
Cecidomyiidae sp. 3	3	*Alloborborus pallifrons*	1
Macrocera fasciata	1	*Coproica ferruginata*	6
Macrocera sp.	1	*Coproica hirticula*	37
Neoclastobasis sibirica	1	*Coproica vagans*	2
Dynatosoma majus	1	*Trachyopella atomus*	2
Mycetophila fungorum	1	*Trachyopella kuntzei*	3
Mycetophila sp.	8	*Gonioneura spinipennis*	1
Allodia sp.	5	*Gigalimosina flaviceps*	1
Exechia sp.	4	*Terrilimosina schmitzi*	1
Phronia sp.	1	*Paralimosina fucata*	5
Rymosia sp.	1	*Minilimosina parvula*	5
Stigmatomeria crassicornis	2	*Pullimosina heteroneura*	9
Mycetophilidae sp. 1	9	*Pullimosina meijerei*	2
Mycetophilidae sp. 2	2	*Pullimosina moesta*	5
Mycetophilidae sp. 3	4	*Spelobia (S.) manicata*	3
Mycetophilidae sp. 4	1	*Spelobia (S.) palmata*	11
Mycetophilidae sp. 5	3	*Spelobia (S.) parapusio*	171
Chironomidae sp.	23	*Spelobia (S.) rufilabris*	3
Atrichopogon sp.	4	*S. (Bifronsina) bifrons*	4
Culicoides sp.	34	*Opalimosina czernyi*	12
Forcipomyia sp.	10	*Opalimosina liliputana*	4
Holoplagia bullata	1	*Opalimosina mirabilis*	1
Apiloscatopse cochleata	1	*Telomerina flavipes*	1
Apiloscatopse flavicollis	1	*Leptocera caenosa*	5
Scatopse notata	1	*Leptocera fontinalis*	5
Coboldia fuscipes	1	*Leptocera nigra*	9
Lonchoptera furcata	1	*Asteia amoena*	3
Platypezidae sp.	1	*Leiomyza dudai*	23
Megaselia sp. 1	18	*Leiomyza laevigata*	7
Megaselia sp. 2	10	*Leiomyza scatophagina*	1
Megaselia sp. 3	4	*Leucophenga maculata*	3
Megaselia sp. 4	1	*A. (Phortica) variegata*	7
Chaetopleurophora sp.	1	*Scaptomyza (P.) pallida*	2
Gymnophora sp.	3	*Mycodrosophila poecilogastra*	37
Triphleba sp.	1	*Lordiphosa fenestrarum*	14
Nemopoda nitidula	4	*Hirtodrosophila confusa*	98

Table 4 (continued)

Hirtodrosophila trivittata	22
Drosophila buscki	2
Drosophila immigrans	65
Drosophila kuntzei	25
Drosophila limbata	3
Drosophila phalerata	170
Drosophila testacea	205
Drosophila transversa	77
Liriomyza sp.	1
Phytomyza sp.	1
Meoneura neottiophila	3
Acartophthalmus nigrinus	23
Scathophaga stercoraria	2
Pegomyia sp.	2
Fannia monilis	4
Fannia parva	120
Thricops simplex	1
Hydrotaea sp.	1
Mydaea electa	1
Mydaea sp.	1
Helina sp.	1
Coenosiini sp.	1
Total	1503

Fox faeces

Pericoma sp.	2
Trichocera relegationis	7
Sciaridae sp. 1	6
Sciaridae sp. 2	1
Cecidomyiidae sp.	1
Camptocladius sp.	38
Chironomidae sp.	1
Culicoides sp.	1
Penthetria funebris	1
Apiloscatopse sp.	2
Scatopsidae sp.	2
Megaselia sp. 1	12
Megaselia sp. 2	4
Conicera sp.	1
Diplonevra sp.	1
Gymnophora sp.	1
Triphleba sp.	1
Dryomyza flaveola	19
Neuroctena anilis	1
Oldenbergiella seticerca	485
Neoleria ruficeps	8
Tephrochlamys tarsalis	1
Sphaerocera curvipes	12
Ischiolepta micropyga	1
Ischiolepta pusilla	2
Crumomyia nitida	1
Coproica ferruginata	10
Coproica hirticula	2
Coproica vagans	7
Gonioneura spinipennis	5
Limosina silvatica	2
Gigalimosina flaviceps	1
Paralimosina fucata	8
Pullimosina heteroneura	2
Pullimosina moesta	1
Spelobia clunipes	7
Spelobia manicata	2
Spelobia palmata	2
Leptocera oldenbergi	1
Amiota (A.) alboguttata	1
A. (Phortica) variegata	6
Acartophthalmus nigrinus	2
Meoneura neottiophila	1
Adia cinerella	7
Hylemya sp.	24
Anthomyiidae sp.	6
Fannia armata	30
Fannia ornata	2
Fannia parva	45
Muscina sp.	1
Thricops diaphanus	3
Thricops simplex	1
Hydrotaea cyrtoneurina	1
Hydrotaea dentipes	4
Hydrotaea irritans	15
Morellia hortorum	1
Morellia sp.	1
Eudasyphora cyanicolor	8
Phaonia pallida	1
Mydaea corni	2
Mydaea nubila	1
Mydaea urbana/electa	1
Calliphora vomitoria	8
Lucilia caesar	1
Rhinophorinae sp.	7
Tachinidae sp.	1
Lipoptena cervi	1
Total	844

Table 4 (continued)

Deer faeces	
Psychodidae sp.	1
Trichocera relegationis	2
Trichocera sp.	2
Sciara sp.	5
Sciaridae sp. 1	18
Sciaridae sp. 2	5
Cecidomyiidae sp.	3
Camptocladius sp.	28
Chironomidae sp.	10
Ceratopogonidae sp.	2
Crossopalpus nigritella	1
Megaselia sp. 1	15
Megaselia sp. 2	2
Conicera sp.	1
Diplonevra sp.	5
Gymnophora sp.	1
Hypocera mordellaria	8
Dryomyza flaveola	41
Neuroctena anilis	1
Lyciella rorida	1
Meroplius stercorarius	1
Oldenbergiella seticerca	1
Sphaerocera curvipes	17
Ischiolepta micropyga	2
Ischiolepta pusilla	3
Crumomyia nigra	3
Crumomyia nitida	4
Coproica ferruginata	3
Coproica hirticula	1
Coproica hirtula	1
Coproica vagans	2
Elachisoma bajzae	2
Chaetopodella scutellaris	10
Limosina silvatica	2
Gigalimosina flaviceps	10
Paralimosina fucata	11
Phthitia plumosula	1
Pullimosina meijerei	2
Spelobia clunipes	6
Spelobia manicata	32
Spelobia palmata	6
Spelobia sp. female	1
Opalimosina mirabilis	1
Opacifrons coxata	2
Leptocera nigra	2
Diastata fuscula	1
Campichoeta basalis	1
Drosophila transversa	1
Meoneura sp.	1
Thaumatomyia sp.	2
Hydrophoria sp.	3
Hylemya sp. 1	43
Hylemya sp. 2	3
Anthomyiidae sp.	2
Fannia armata	6
Fannia ornata	6
Fannia parva	141
Fannia sp.	14
Azelia triquetra	2
Azelia sp.	5
Hydrotaea irritans	7
Hydrotaea sp.	5
Thricops simplex	13
Musca autumnalis	1
Neomyia cornicina	1
Morellia hortorum	1
Eudasyphora cyanicolor	17
Polietes meridionalis	4
Mydaea sp.	3
Calliphora vomitoria	2
Lucilia ampullacea	1
Pollenia sp.	1
Sarcophaga lehmanni	1
Total	569

Tinder fungi	
Trichocera sp.	1
Ptychoptera	1
Sciaridae sp. 1	23
Sciaridae sp. 2	9
Cecidomyiidae sp.	5
Chironomidae sp.	3
Ceratopogonidae sp.	1
Ditomyia fasciata	1
Acnemia nitidicollis	1
Mycetophilidae gen. 1	4
Mycetophilidae gen. 2	2
Mycetophilidae sp. 3	1
Penthetria funebris	6
Colobostema nigripenne	1
Sylvicola cinctus	1
Actina	2
Platypalpus sp.	3

Hybotidae sp.	2	*Drosophila funebris*	1
Dolichopodidae sp.	8	*Drosophila kuntzei*	3
Megaselia sp. 1	12	*Drosophila littoralis*	1
Megaselia sp. 2	7	*Drosophila phalerata*	11
Megaselia sp. 3	5	*Drosophila testacea*	14
Megaselia sp. 4	2	*Drosophila transversa*	3
Phora sp.	1	*Odinia boletina*	54
Spiniphora sp.	1	*Acartophthalmus nigrinus*	2
Platypezidae sp.	1	*M. neottiophila/lamellata*	1
Lyciella rorida	2	*Tricimba cincta*	1
Tephrochlamys flavipes	1	*Anthomyia* sp.	1
Suillia affinis	1	*Hylemya* sp.	2
Clusiodes albimana	1	*Pegomyia* sp.	3
Clusiodes apicalis	2	Anthomyiidae sp. 1	1
Limosina silvatica	1	Anthomyiidae sp. 2	2
Paralimosina fucata	1	Anthomyiidae sp. 3	2
Spelobia parapusio	1	*Fannia parva*	58
Leucophenga maculata	29	*Fannia* sp. 1	5
A.(Phortica) variegata	2	*Fannia* sp. 2	2
Scaptomyza (P.) pallida	1	*Azelia* sp.	1
Mycodrosophila poecilogastra	263	*Mydaea* sp.	1
Hirtodrosophila confusa	2125		
Hirtodrosophila trivittata	5	Total	2708

populations form the texture of the community structure. In the low mountain forests of Hungary there are also dipterous species among the dominant phytophagous species (e.g., *Mikiola fagi* in beech forests, an assemblage of several species in mixed hornbeam-oak forests). Species like *Bibio marci*, several species of *Tipula* and *Fannia*, a good number of less abundant but common species of Lauxaniidae and Sciaridae are significant or at least not negligible in the decomposition of forest litter. If compared to the former ones, species populations living on/in the small sized feeding sources are rare and disorderly ("messy"). As a consequence of their rarity they are insignificant in matter turnover and energy flow. The species in guilds of small-sized sources superimpose a colourful pattern on the texture formed by the abundant forest species.

Since their presence/absence are incidental (that is so for several hundred species!), it is obvious that they cannot play a decisive role in the forest ecosystems. Their mere existence is a trouble for reductionists. However, if we are really concerned about the true nature of ecosystems, or about the knowledge of biodiversity on Earth (quality, quantity, evolution, etc.), they must not be neglected. In fact, their study seems indispensable for a better understanding of ecosystem structures and diversity maintenance.

Our results are not enough for a generalisation of the features of small sized source guilds, except that two basic types can be distinguished: (a) Guilds of sources that renew at places (micro-sites) year by year; for instance, tinder fungi on dead trees; (b) Guilds of sources that emerge by chance anywhere; for instance, droppings or dead snails.

It is important to note that the diversity of the two types is not different (in the mirror of the diversity index measures).

Based on our results, one of the main reasons of general rarity among insect species is that the infrequent and variable small-sized feeding sources produce a high number of rare species. Scaling must be one of the most important aspects in order to find their function. I mean, very small-sized emergence sources and extremely large sinks (the large forest area around the minute source) are to be expected.

From another aspect, the small-sized sources that are or seem to be scattered by chance at a given scale are probably found by adult Diptera only by chance as well. An overwhelming majority of those adults are lost during their searching flight. This is why the group (a) above is far more reproducible from year to year than species in guilds of group (b). This power of chance may also be a decisive experience for entomologists working on agricultural pests. In Hungary that was most characteristically expressed by Prof. T. JERMY, saying, "Do not you [theoretical ecologists] imagine too many regularities in Nature", cited by JUHÁSZ-NAGY (1986). Both sides may be right, though (cf. PAPP 1988). For example, in an earlier paper (PAPP & ÁDÁM 1996) we created a diagram of how sheep-runs are experienced by a lesser dung fly which now seems to be quite general and not just for coprophagous flies: Flies (and other insects) seek "new" sources and most of them are lost during this search. Those that have found such an object keep in contact with it via olfactory stimuli. That fact has two major consequences for the investigator: If anything bothers these flies, they fly away only a short distance so they can find this source again. Secondly, if the investigator attempts to collect all the insects that come to a source, it could take a long period of time to recruit from the environs. This could be critical in cool autumn weather when the mean recruitment period may be longer than the period of time during which a fresh piece of dung can be attractive for coprophagous flies.

Species diversity contribution of the small sized sources

We thought it important to make an estimate of the contribution of the species diversity of all the small-sized feeding sources (combined) to the diversity of forest Diptera in Hungary. Species number estimations, as for example those in

Table 3, are not good tools for this. In fact, Table 3 demonstrates how much these estimations deviate from the sample numbers necessary to judge a local subset of the species pool on that day. It is better to make a rough estimate by comparing and combining species lists (potential pool members) of all kinds of small-sized sources one by one.

Among all our collection sites, there were only two where we obtained enough data to be able to judge their contribution to the insect diversity of those low mountain forests. One of them is the Fáni-valley in Vértes Mts in Transdanubia, the other is the Keskenybükki-valley in the Börzsöny Mts in central North Hungary.

Since all the small-sized sources are dead organic matter, a key point of the estimations is the ratio of the phytophagous, predator and parasitoid species as well as those developing in dead organic materials. According to my former estimations, 16 per cent of the dipterous fauna of Hungary are phytophagous, approximately 25 per cent are predacious and parasitoid species. (All the dipterous fauna of Hungary is ca. 10000 species.) Consequently, 59 per cent belong to all those guilds which develop in dead organic materials.

DELY-DRASKOVITS reared 128 dipterous species from sporophores of fungi. I collected ca. 200 dipterous species on human faeces in some mountain creek valleys (PAPP 1993). I collected ca. 150 species on apple bait at the same sites (PAPP 1992: 40 spp. of drosophilids alone). There are almost no overlaps in the species composition of those guilds. The species found on tinder fungi, on sap runs of trees, on dead snails and on dead small mammals, in nests of birds and insects, and on various kinds of droppings, form an addition. And I have not mentioned the hundreds of species in dead decaying wood, which seems the richest in species (although most of them are not specific to the species of trees). We had to postpone studies on flies collectible on and developing in decaying wood, although those seem extremely important in the dipterous communities of forest ecosystems. According to an estimation of DELY-DRASKOVITS *et al.* (1991), excluding phytophagous species, this is the potential microhabitat of 80 per cent of forest Diptera. Whether this ratio is an overestimation or not, their study deserves a separate series of sampling and analysis.

Even if we hypothesise that representatives of at least 1000 at most 2000 species are present in large forests of low mountain brook valleys, the combined numbers of the species on small sized feeding sources form a majority of forest Diptera diversity in Hungary.

GENERAL SIGNIFICANCE

In response to the questions posed in the introduction *re:* repeatablilty of species composition of the guilds and structural characteristics of those assemblages, we can give a positive answer only in few cases: The drosophilid species *Hirtodrosophila confusa* is a dominant species of tinder fungi; and *Oldenbergiella seticerca* is characteristically dominant in the guild of fox faeces but only at the end of autumn. Otherwise, neither the name of the dominant species nor species composition is predictable.

When I made the project proposal for this study, I hypothesised that the data obtained from all guilds of small-sized food sources would be amenable to generalisation and that general terms would apply across guilds. In other words, are they units by the shared properties of their structure, or only by the human contemplation. Considering all the accumulated evidence, I question any claim for any kind of generalisation. Viewing the problem "from outside to inside", that is, as seen from the large-scale habitats like a beech forest, one may use names like "inclusions", "ecosystem chips", etc. However, I cannot give a proposal by which we would unite them by a general term. This agrees with a previous summary of views about this kind of generalisation (review by BALOGH 1953).

An overview of our data corroborate the opportunistic fitness guild definition by HAWKINS & MACMAHON (1989): "...guild still describes all organisms that use the same investigator-defined resource; the usefulness of the concept depends more on the investigator's acuity and care than it does on the organisms and their interactions in nature."

You may guess my answer to the question of the often-discussed relationship of diversity and ecosystem function: I do not believe that any kind of general relationships exist. And if I am right, none of the species on small-sized feeding sources are suitable for biomonitoring as a consequence of their highly variable abundance changes and largely unknown ecological background.

RARITY AND RARITOLOGY

It is no wonder that the insects that develop in small-sized sources are mostly rare species since the sources themselves are not abundant. And although rarity among insects is not always in direct relationship with the size of their breeding media, the insects we have studied seem to show all the features which characterise rare species and so their study is also relevant to rarity among living organisms in general.

In the past, most of the estimations of the ratio (or the real number) of the rare species in an ecosystem have missed their mark. These estimations work well only in the cases of sites where regular and long term studies have been performed. Otherwise, the ratio of the rare species is usually underestimated: at a given stage of studies we may know all the species of the dominant and subdominant species, but only the fore-part of the long row of rare ones. JERMY (1987) was among the first modern ecologists who re-called DARWIN's idea about the "vast number of species of all classes".

The most important lesson I derived from these studies is that we are wrong if our approach to the study of the insects found on and developing in small-sized sources is only based on our general ecological knowledge. Ecology is, by one of its definitions (DODSON *et al.* 1998), "the study of the relationships, distribution, and abundance of organisms, or groups of organisms, in an environment." This loose definition includes the study of the rare species, and they must not be neglected if we are really concerned with the knowledge of biodiversity on Earth. Needless to say, this kind of study is important for biological conservation, since all threatened species are rare.

I can corroborate the fears of former students that any study on rare species will not reveal general ecological relationships; we are still far from the realisation of general invariance rules valid for rare species.

Based on our data I was able to revise some considerations of the forms of rarity among insects (PAPP 1998*c*). I have concluded that those methods and attitudes that are usually successful and effective in ecological studies are not very successful or even usable in studies concerned with rare species. So I hypothesise the development of a new branch of ecology, namely raritology, the study of rare living organisms (PAPP 1998*b*). Those special ecologists, the raritologists, are the curious, resolute and humble researchers, who will be ready to strive after – and to spend much time for – small results without any hope of shedding light on "very important" general relationships of Nature winning the Nobel Prize. Thus, the development of raritology (study of rare species) as an individual branch of ecology is predicted (for I think, it is predictable).

In the future, studies on flies and other insects on and in small-sized feeding sources must have a perspective for the long term and be included as part of mainstream ecology instead of as a pioneer or isolated work. The delicate question will probably be who would finance this kind of long-term studies of uncertain outcome.

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AN INVENTORY OF TASTE IN CATERPILLARS: EACH SPECIES ITS OWN KEY*

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Food plant recognition in lepidopterous larvae is predominantly governed by the activity of eight taste neurones present in two sensilla styloconica located on each maxilla. This paper reviews the results of electrophysiological and behavioural studies made on various caterpillar species during the last 40 years. It appears that all species, even closely related ones, have different taste systems. Taste cells responding to general phagostimulants (e.g., carbohydrates) have been found in all species studied. In some species, highly specialized taste cells have been found that respond to plant taxon-specific secondary plant substances that act as 'token' stimuli for plant recognition. Taste cells responding to many different secondary plant substances occur in most species studied. Their activity deters feeding. Though the response profile of these taste cells is best described as generalized, they nevertheless show species-specific stimulus spectra. These generalist deterrent cells often play a crucial role in feeding behaviour, a conclusion which confirms JERMY's (1966) earlier inference on the preponderant role of inhibitory secondary plant substances in food-plant selection by herbivorous insects. The two most frequently studied neural coding mechanisms, 'labelled lines' and 'across-fibre patterning' have been inferred to operate in caterpillars. The first type is a likely coding mode in oligophagous species employing token stimulus receptors, whereas 'across-fibre patterning' most probably operates in all species confronted with choices between plant food of varying quality. The responses of each of the taste cell types to their specific stimuli may be modified by the presence of other plant constituents, indicating that a complex stimulus (plant sap) evokes a response that is unpredictable from knowledge of responses to single compounds. Variability in taste cell responsiveness is dependent on developmental stage, time of day, and feeding history. This indicates that caterpillar taste cells are not rigid systems, and even possess a 'peripheral memory'.

Key words: sensilla styloconica, chemoreception, Lepidoptera, electrophysiology

INTRODUCTION

A rich variety of green plants on this planet presents an abundant food source to herbivores. Myriads of insects have since their origin taken their share of it and, by doing so, probably contributed to the development of the unsurpassed chemical diversity hidden in the Plant Kingdom. Insects and plants, therefore, are more

* This paper has been prepared as a tribute to Dr. TIBOR JERMY, an esteemed scientist and dear friend, who, under many adverse circumstances, has maintained his scientific integrity and originality and has made a seminal and lasting contribution to the field of insect–plant biology.

firmly interwoven than has been thought for a long time. A conspicuous feature of herbivorous insects is a preponderance of food specialization in this group. Lepidoptera, comprising about 10 per cent of all animal species, form a striking illustration, since they are generally finicky eaters. The great majority of lepidopterous larvae are specialists with regard to the kind of food they accept: only one plant species, or a few species belonging either to the same genus (monophagy), or to the same family (oligophagy). Even generalist species are selective in their food choice and do show preferences for some plants over others.

Diet specialization is a fundamental aspect of an animal's biology and has at the same time far-reaching ecological implications. To properly value the ecological impact of food selection behaviour and its evolutionary significance, it is helpful, if not a dire necessity, to understand the underlying mechanism of this behaviour.

A plant's chemical composition is in many cases the most important source of information which herbivorous insects use to discriminate between host and non-host plants. Lepidopterous larvae have been known for a long time to use this kind of information (VERSCHAFFELT 1910). Caterpillars are in many respects also ideal insects to unravel some principles which govern food selection behaviour. Their size and amenability make them quite suitable for behavioural studies. Their sense of taste, an essential faculty in food recognition, is by a stroke of luck singularly simple and easily accessible to experimentation. Based on unique temporal patterns of firing it appeared possible to reliably discriminate between different taste cells in one and the same sensillum (PETERSON *et al.* 1993; GLENDINNING & HILLS 1997). Neurophysiological recordings from intact animals allow long-lasting experiments on individuals, which subsequently may be used for behavioural tests (GOTHILF & HANSON 1994). These characteristics have contributed to the fact that many efforts to elucidate the role of taste in herbivorous insects have employed caterpillars.

The aims of this paper are (1) to present an overview of our present knowledge of taste receptors in caterpillars, (2) to explain interspecific differences in their taste system in relation to food-plant preferences, (3) to discuss the concept of sensory codes which direct food selection behaviour, and (4) to indicate some avenues which may be pursued in order to obtain a full answer to the question why a caterpillar accepts certain plants while rejecting others.

After a brief discussion of the structure and function of all taste receptors in caterpillars this paper will focus on the responses of the two maxillary sensilla styloconica to a spectrum of chemicals known to occur in plants. The chemosensory properties of these sensilla will be discussed in relation to food-plant recognition.

THE SENSE OF TASTE: MORPHOLOGY AND FINE STRUCTURE

The sense of taste in lepidopterous larvae is located in sensilla on the maxillae and epipharynx (DETHIER 1937) and possibly in some receptors in the hypopharynx and deeper portions of the buccal cavity (KENT & HILDEBRAND 1987). Each maxilla has two lobes arising from the basal segment (palpiger). The medial lobe is the galea and the lateral three-segmented lobe is the maxillary palpus (Fig. 1).

Galea. Each galea bears two elongated blunt protuberances which each support a uniporous peg, commonly referred to as the medial and lateral sensilla styloconica (Fig. 2). Light microscopic and electronmicroscopic examination showed that each sensillum styloconicum is innervated by five bipolar neurones, one of which functions as a mechanoreceptor. The dendrites of the four remaining chemoreceptor cells extend into the lumen of the peg, and terminate at a short distance from a minute pore in the tip of the peg (SCHOONHOVEN & DETHIER 1966, DEVITT & SMITH 1982). A detailed description of the internal structure of the sensilla styloconica of *Mamestra configurata* is given by SHIELDS (1994). There is no evidence of close contacts or tight junctions between styloconic chemoreceptor cells, as has been observed in tarsal sensilla of adult cabbage root flies (ISIDORO *et al.* 1994).

In a beautifully illustrated report GRIMES and NEUNZIG (1986a) concluded from a comparative study on 41 species that on the outside both sensilla styloconica vary little among species and appear to be the most conservative structures among all (eight) sensilla on each galea.

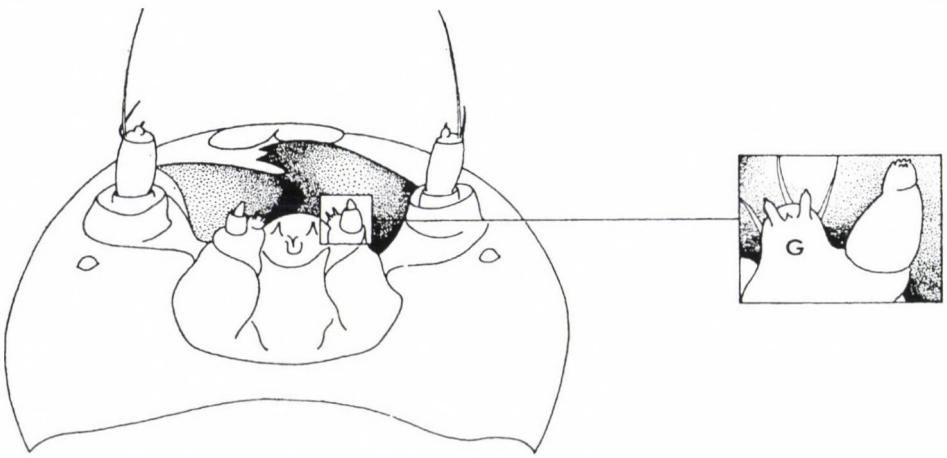

Fig. 1. Ventral view of a caterpillar head. G = galea, bearing two sensilla styloconica

Maxillary palpus. The third (distal) segment of the palpus bears a group of eight terminal sensilla basiconica, each innervated by 3–4 chemoreceptor neurones (SCHOONHOVEN & DETHIER 1966, DEVITT & SMITH 1982). Three of them have a grainy or pitted appearance, presumably due to the presence of pits which are entrances to underlying pores. It is speculated that these sensilla have an olfactory function, whereas the shape and smoothness of the remaining five uniporous sensilla indicate a role in contact chemoreception. In a more detailed study based on scanning electronmicroscopic images GRIMES and NEUNZIG (1986*b*) discern three different types of sensilla basiconica. They suggest that morphological differences observed between exophagous and endophagous species reflect functional differences with respect to taste and olfaction.

Epipharynx. One pair of dome-shaped epipharyngeal sensilla may be located on the epipharynx, the inner surface of the labrum. They have been described in larvae of *Bombyx mori* (GRANDI 1922, 1923), *Pieris brassicae* and *Manduca sexta* (MA 1972), *Malacosoma americana* (DETHIER 1975), and *Choristoneura fumiferana* (ALBERT 1980). Each sensillum is served by three neurones. These sensilla are not universally present in caterpillars, because they have been reported to be absent in *Mamestra brassicae* (BLOM 1978) and *Euxoa messoria* (DEVITT & SMITH 1982). The neurons innervating the epipharyngeal sensilla project on the frontal ganglion (MA 1972), tritocerebrum (MA 1976*a*, DE BOER *et al.* 1977) and suboesophageal ganglion (KENT & HILDEBRAND 1987).

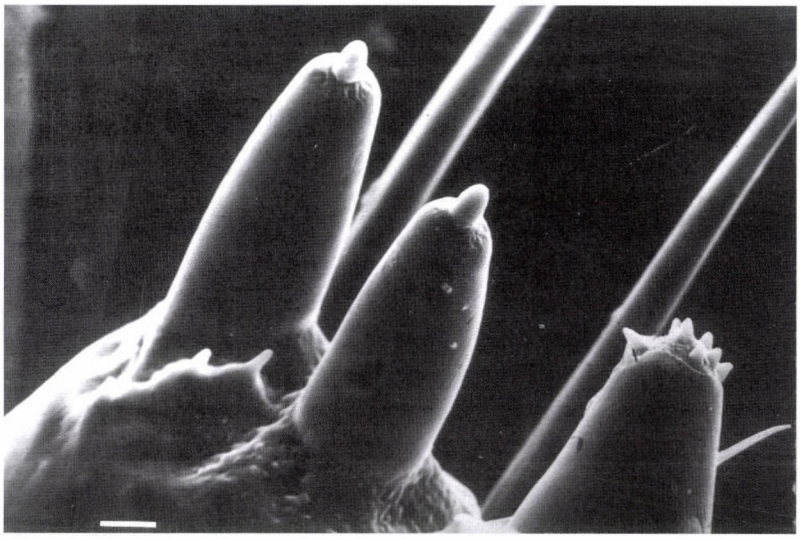

Fig. 2. Scanning electron micrograph of sensilla styloconica of *Spodoptera littoralis*. Scale = 10 μM (courtesy of W.M. BLANEY)

THE SENSE OF TASTE: BEHAVIOUR AND ELECTROPHYSIOLOGY

Physiological information on taste receptors located on the maxillary palps and epipharynx is pathetically limited.

Maxillary palpus. Behavioural experiments on *Lymantria dispar* (DETHIER 1937) and *B. mori* (ISHIKAWA *et al.* 1969) after removal of their maxillary palpi, provided evidence for the assumption that these appendages harbour olfactory receptors. This conclusion was confirmed unequivocally by recordings of increased neural activity in the palpi of *Manduca sexta* and *Hyalophora gloveri* in response to various plant odours (SCHOONHOVEN & DETHIER 1966, DETHIER & SCHOONHOVEN 1969). Similar results were obtained in *B. mori* (ISHIKAWA *et al.* 1969). Additionally, a gustatory role of some palpal sensilla could be inferred from the fact that topical application of some solutions caused changes in feeding behaviour (DETHIER 1937). Moreover, stimulation of the palpus with plant saps or dissolved chemicals elicited electrophysiological responses in *B. mori* (ISHIKAWA *et al.* 1969). More recently, GLENDINNING *et al.* (1998) published a detailed investigation of the responses from palpal chemoreceptors to compounds which deter feeding in *Manduca sexta* larvae.

Epipharynx. Early experiments in which the maxillae were surgically removed led to the unexpected observation that amputation of these appendages stimulated silkworms to eat plants that are normally rejected (TORII & MORII 1948). However, the fact that *Manduca sexta* caterpillars deprived of their maxillae still could discriminate between some host and non-host plants suggested the involvement of some hitherto unknown chemoreceptors in food selection behaviour (WALDBAUER & FRAENKEL 1961). When both maxillae as well as the antennae, bearing olfactory receptors, were extirpated, the ability to discriminate was still not completely lost (SCHOONHOVEN & DETHIER 1966). Therefore, it was hypothesized that the oral cavity also contains taste receptors. Only when, together with the maxillae and antennae, the labrum was removed, the loss of host discrimination appeared to be complete (DE BOER & HANSON 1987).

A taste function of the epipharyngeal sensilla has been proved by applying electrophysiological techniques in some taxonomically unrelated insect species. Thus, neural responses from these organs were obtained in *Pieris brassicae* (MA 1972), *Spodoptera exempta* (MA 1976a), *Manduca sexta* (DE BOER *et al.* 1977, GLENDINNING *et al.* 1999*b*, GLENDINNING *et al.* 2000), *Choristoneura fumiferana* (ALBERT 1980), *Bombyx mori*, and *Antheraea yamamai* (ASAOKA & AKAI 1991, ASAOKA & SHIBUYA 1995, ASAOKA 2000). All studies yielded evidence for the presence of three different taste cells, which were found to respond to deterrents and salts, and occasionally to other compounds as well.

SENSILLA STYLOCONICA: THE FUNCTIONS OF 8 TASTE CELLS

The two sensilla styloconica on each maxilla undoubtedly play a decisive role in hostplant selection behaviour. Therefore, though they contain only eight (paired) cells out of a total of approximately 59 (paired) chemoreceptory cells present in caterpillars (SCHOONHOVEN & DETHIER 1966), the function of these two sensilla has received more interest than all other chemoreceptors together. The main goal of most investigators has been to understand the sensory message which arises in these sensilla upon contact with a plant and which wholly or largely determines the insect's subsequent feeding response. To this end early students in this field recorded neural responses to saps from acceptable or unacceptable plants. To their disappointment they found these recordings, often showing impulses from all four cells, to be complex and too difficult to analyse to allow an in-depth analysis. Though different plant saps clearly evoked different impulse patterns, the character of the overall pattern of responses bore no orderly relationship to the acceptability or non-acceptability of the plants (ISHIKAWA 1966, SCHOONHOVEN & DETHIER 1966). Clearly, some detailed knowledge of the specificity spectra of all eight cells is needed before responses to complex stimuli, involving several receptors, may be understood. Thus, in the past decades most studies have concentrated on the identification of specific cells and their sensitivity to pure compounds or binary mixtures. Studies on responses to plant saps have been relatively rare (but see, e.g., SIMMONDS & BLANEY 1991).

Even the determination of the specificity ranges of individual cells has been found to be more difficult than anticipated. The analysis of a receptor's specificity range is impeded by the fact that many factors may affect a receptor's quantitative responsiveness. Factors that may exert profound effects on receptor sensitivity include larval stadium (e.g., differences between 4th and 6th instar: PANZUTO & ALBERT 1997, 1998), developmental stage (e.g., receptors of mid-instar larvae showing maximal responses: SIMMONDS *et al.* 1991), time of day (SCHOONHOVEN *et al.* 1991), nutritional status, and experience. Populations of different origin may also show qualitative and quantitative differences in responsiveness (e.g., WIECZOREK 1976). On top of that one usually encounters, also under fully standardized conditions, considerable interindividual variation, as well as marked intra-individual (i.e. measurements on the same individual) variation (e.g., SCHOONHOVEN 1976, SIMMONDS & BLANEY 1991, FRAZIER 1992, MENKEN & ROESSINGH 1998). Last but not least inhibitory or synergistic interactions commonly transmute receptor responsiveness when it is exposed to two (or more) compounds simultaneously. Despite this multitude of receptor modulating factors our knowledge of stimulus specificity and sensitivity of many taste cells has made ample

progress and provided fascinating new insights into their role of the process of food recognition, as will be shown in the following.

SPECIFICITY RANGES OF STYLOCONIC TASTE CELLS

In the course of years a typology of styloconic taste cells has been made for over 20 caterpillar species, inviting a comparison of the results (Table 1). It should be kept in mind, however, that different authors have often tested different sets of chemicals, thereby reducing the comparability of their results. There is also little uniformity in cell labelling. To establish whether or not two compounds stimulate one and the same cell, it is necessary to test them as a mixture. This has not been done for all possible combinations of stimulants on which Table 1 is based, and therefore some uncertainties remain.

Evidently the characterization of most taste cells is only partially complete. Even the taste spectra of some of the most thoroughly investigated species, e.g. *Pieris brassicae* and *Manduca sexta*, cannot be considered to be fully known. In spite of such gaps Table 1 shows some clear patterns among this not only taxonomically, but also behaviourally (specialists *versus* generalists) diverse group of insects. Responses to salt (NaCl and KCl) occur in all species tested. Some authors consider salt responses to originate in so-called deterrent (D) cells, another cell type of universal occurrence.

Receptor cells responding to one (sucrose, glucose or fructose; 'S', 'G' or 'F') or more ('sugars') carbohydrates likewise occur in all species tested. Many, but not all species have inositol cells. Specialized amino acid cells have been described only for some species, but not all listed species have been tested for their responsiveness to this group of chemicals. In some instances taste cells were found which specifically respond to host-plant specific secondary plant substances. For example, *Pieris brassicae* and *P. rapae* larvae possess two glucosinolate cells and most *Yponomeuta* species have dulcitol and/or sorbitol receptors, responding to the predominant carbohydrate in their host plants.

Sugars and, though to a lesser extent, inositol are general feeding stimulants. Clearly insects are equipped with taste cells which are tuned to detect feeding stimulants (sugars, inositol, amino acids, secondary plant substances occurring in their host plants) as well as cells (D cells and, to some extent, salt cells) signalling the presence and quantities of compounds which reduce or inhibit feeding.

A general pattern emerges when all cells are labelled according to their either stimulating or inhibiting effect on feeding, as suggested by BERNAYS and CHAPMAN (2001*a*). According to this classification each sensillum styloconicum in most cat-

Table 1. Typology of taste cells in the maxillary sensilla styloconica of selected lepidopterous larvae. AA = amino acids; CAT = catalpol; Chlor. A = chlorogenic acid; D = deterrents; gD = generalist deterrent cell; sD = specialized deterrent cell; glucosinol = glucosinolates; ar. glucosinol. = aromatic glucosinolates; PO = populin; SA = salicin; sugars = cell responds to >3 carbohydrates; S = sucrose; G = glucose; F = fructose

	Medial sensillum				Lateral sensillum			
	1	2	3	4	1	2	3	4
Adoxophyes orana (1)[a]			salt	salt	S	AA	inositol	phloridzin
Choristoneura fumiferana (2,3,4)	water	proline	salt	salt	sugars	AA	water	salt
Yponomeuta cagnagellus[b] (5)		dulcitol	D	salt	S	dulcitol	D	salt
Y. malinellus (5)			D	salt	S	sorbitol	D	salt
Chilo partellus (6)	water		Chlor.A	salt	S			salt
Eldana saccharina (6, 7)	water	S		salt	S		D	salt
Maruca testulalis (6)	water			salt	S			salt
Bombyx mori (8)	water	salt	D	salt	sugars	inositol	G	salt
Philosamia cynthia (9)	G	inositol	salt	salt	S	inositol	G	salt
Pieris brassicae (9,10,11,12,13)	sugars	ar. glucosinol	gD	salt	S	AA	glucosinol	sD
P. rapae (12,13,14,15)	sugars	ar. glucosinol	gD	salt	sugars	AA	glucosinol	sD
Operophtera brumata (9)	glycosides		salt	salt		inositol		
Manduca sexta (9,16, 17,18, 19)	G	inositol	D	salt	S/G	inositol	D	salt
Laothoe populi (1)	PO/SA		D		S	AA	PO/SA	
Grammia geneura (20,21,22)	sugars/AA/CAT		D	D	F	AA	D	D
Euproctis phaeorrhoea (9)	glycosides	inositol		salt	S	inositol		salt
Heliothis virescens (23,24)	S/alanine	inositol	D	D	S	alanine	D	D
H. armigera (23)	S	alanine	D	D	S	alanine	D	D
Mamestra brassicae (25,26)	sinigrin	inositol	D	salt	sugars	salt	D	salt

Table 1 (continued)

	Medial sensillum				Lateral sensillum			
	1	2	3	4	1	2	3	4
M. configurata (27)		inositol		salt	S	salt	sinigrin	salt
Spodoptera exempta (6,7,23, 28)	S	inositol	D		S	adenosine	D	
S. littoralis (23)	S	alanine	D	D	S	alanine	D	D
S. frugiperda (23)	S	alanine	D	D	S	alanine	D	D
S. litura (29)	F	inositol	salt	salt	sugars	water	D	salt
Trichoplusia ni (27)			sinigrin	salt	S		sinigrin	salt

[a]Data from: (1) SCHOONHOVEN 1973; (2) ALBERT 1980; (3) ALBERT & PARISELLA 1988*a*; (4) PANZUTO & ALBERT 1997, 1998; (5) VAN DRONGELEN 1979; (6) WALADDE *et al.* 1989; (7) DEN OTTER 1992; (8) ISHIKAWA 1963, 1967; (9) SCHOONHOVEN 1969*c*; (10) SCHOONHOVEN 1967, 1969*a*; (11) MA 1972; (12) VAN LOON 1990; (13) VAN LOON & SCHOONHOVEN 1999; (14) VAN LOON & VAN EEUWIJK 1989; (15) VAN LOON unpubl.; (16) SCHOONHOVEN & DETHIER 1966; (17) PETERSON *et al.* 1993; (18) GLENDINNING *et al.* 1999*b*; (19) FRAZIER 1986; (20) BERNAYS *et al.* 2000*a*; (21) BERNAYS & CHAPMAN 2001*b*; (22) BERNAYS & CHAPMAN 2001*a*; (23) SIMMONDS & BLANEY 1991; (24) BERNAYS & CHAPMAN 2000; (25) WIECZOREK 1976; (26) BLOM 1978; (27) SHIELDS & MITCHELL 1995; (28) MA 1976*a*, 1977*a*; (29) HIRAO *et al.* 1992

[b]Results on 7 other *Yponomeuta* species are presented in VAN DRONGELEN 1979

erpillar species contains two feeding stimulating and two deterrent cells (SIMMONDS & BLANEY 1991, BERNAYS & CHAPMAN 2001*a*). Such grouping, though satisfying our sense of unity in nature, hides the endless variation which exists among species. Detailed comparisons of their taste spectra show that each species is suited with a unique chemoreceptor system, as will be amplified in the next sections.

SUGAR CELLS

Plants generally contain sucrose and its constituent monosaccharides glucose and fructose as primary metabolites resulting from their photosynthetic activity. These compounds function as strong phagostimulants to most herbivorous insects, equipped with specialized receptors to detect sugars. Table 1 shows that all species tested have a sugar cell (cell #1 in the lateral taste hair) which responds to one or more kinds of sugar. In several instances a second sugar cell is found in the medial sensillum (cell #1). The stimulus ranges of the sugar cells have been investigated only in a limited number of species. Various mono-, di-, and trisaccharides may stimulate the sugar cell in some insects (Table 2), whereas in other species this receptor responds exclusively to sucrose (Table 3) or glucose ('G' in Table 1) or fructose ('F'). It should be noted, however, that a number of cells designated as sucrose ('S') cells in Table 1 have been identified by stimulation with sucrose only, and thus may possess a wider stimulus range. Though sucrose is a strong stimulant to most lepidopterous larvae, some species are insensitive to it. *Helicoverpa zea* does not electrophysiologically respond to sucrose, but it does to glucose (DETHIER & KUCH 1971). Other species are stimulated by sucrose only and appear insensitive to other sugars (DEN OTTER 1992).

Most caterpillar sugar cells have a threshold sensitivity of 0.1–1 mM and reach saturation at about 100 times higher concentrations. These cells thus are most sensitive over a range of about two orders of magnitude, a span that nicely covers the range of sugar levels generally present in green leaves, i.e., 10–50 mM/l (Table 4).

An important conclusion emerging from Tables 2 and 3 is, despite the limited information available, that the response properties of sugar cells vary widely between species. Also, when a species has two sugar-sensitive cells these cells appear to differ in their response characteristics with respect to quality and/or quantity of their stimuli (Tables 1–3).

A more detailed analysis of responsiveness to various sugars in relation to age showed that changes may occur with development. A striking example concerns the spruce budworm, *Choristoneura fumiferana*. The order of stimulating ef-

fectiveness of a number of sugars for fourth-instar larvae differs from that of sixth-instar larvae. This change is correlated with temporal changes in carbohydrate composition of their food plants (PANZUTO & ALBERT 1997).

Some non-sugar organic compounds which stimulate human sugar receptors appear to be ineffective when applied to caterpillar sugar cells. Saccharin in con-

Table 2. Stimulus spectra of sugar cells in the maxillary sensilla styloconica to various carbohydrates. M = medial and L = lateral sensillum

	P. brassicae (1)[a]		*P. rapae* (2)		*D. pini* (1)		*C. fumiferana* (3)		*B. mori* (4)	*M. brassicae* (5)
	M	L	M	L	M	L	M	L	L	L
Pentoses										
D-arabinose	o	o			+	o			++	+
L-arabinose	o	o	+	+	+	o	o	+	+	+
L-fucose	++	o	+++	+	+++	+++				+
D-ribose	o	o	+	o	o	+			±	
D-xylose	o	o	o	+	+++	o	o	+	±	
Hexoses										
D-fructose	+	o	++	o	+	o	o	+++	+	+
D-galactose	o	o	o	o	++	o	o	+	+	+
D-glucose	+	++	+	++	+++	+	o	++	++	+
D-mannose	o	o	o	o	+	o			±	o
L-sorbose	+	o	+	++	+	+			+/++	
Disaccharides										
Lactose	o	o	o	o	o	+			±	o
D-maltose	o	o	o	+++	o	o			+++	+
Sucrose	++	+++	++	+++	+	+++	o	+++	++++	+
D-trehalose	o	o	o	+			+		+	o
Melibiose							o	++	±	
Trisaccharides										
Melezitose	o	o			o	+			+	
Raffinose	o	o			o	o	o	++	+	
Polyhydric alcohols										
Inositol	o	o	o	o	+++	o	+++	+++	o	
D-sorbitol	o	o	o	o			+	+	±	

+++ = strong reaction, ++ = medium reaction, + mild reaction, ± little or no reaction, o = no reaction

[a](1) MA 1972; (2) VAN LOON unpubl.; (3) PANZUTO & ALBERT 1997; (4) ISHIKAWA 1967; (5) WIECZOREK 1976

centrations up to 10 mM does not stimulate taste cells in *Manduca sexta* or *Pieris brassicae*. Sodium cyclamate is also inactive in *Philosamia cynthia* and *P. brassicae* larvae, although in the latter another receptor cell (presumably the amino acid cell) is stimulated (SCHOONHOVEN 1974). This corresponds with the observation that saccharin does not stimulate feeding in behavioural tests (EGER 1937). The finding that in vertebrates non-sugar sweeteners act via a different transduction pathway from that used for sugars (BERNHARDT *et al.* 1996) suggests that this pathway is absent from insect sugar receptors. Likewise, thaumatin, a botanical protein very sweet to man, does not elicit responses from styloconic sugar cells in *P. brassicae* and gymnemic acid, a compound that suppresses sugar sensitivity in vertebrates, does not affect electrophysiological responses to sugar in *P. brassicae*

Table 3. Carbohydrates ranked in order of effectiveness for different sugar receptors. M = medial and L = lateral sensillum styloconicum

P. brassicae (1)	M:	fucose > sucrose > glucose > fructose (15 other sugars do not stimulate)
	L:	sucrose > glucose (17 other sugars do not stimulate)
P. rapae (2)	M:	fucose > sucrose = fructose > glucose = ribose = arabinose (8 other sugars do not stimulate)
	L:	sucrose = maltose > glucose = sorbose > arabinose = fucose = xylose (7 other sugars do not stimulate)
D. pini (1)	M:	xylose > glucose > fucose = inositol = galactose > sucrose > arabinose = fructose > mannose (8 other sugars do not stimulate)
	L:	sucrose > fucose > glucose > ribose = sorbose (12 other sugars do not stimulate)
C. fumiferana (3)	L (4th instar):	melibiose > sucrose > raffinose > fructose > inositol > glucose > L-arabinose = xylose = galactose > sorbitol
	L (6th instar):	sucrose > fructose > inositiol > raffinose > glucose = melibiose > sorbitol > L-arabinose > xylose = galactose
B. mori (4)	L:	sucrose > maltose > glucose = D-arabinose = rhamnose > sorbose > L-arabinose = fructose = galactose = trehalose = melezitose
E. saccharina (5)	M:	sucrose (12 other sugars do not stimulate)
	L:	sucrose (12 other sugars do not stimulate)
C. partellus (5)	L:	sucrose (12 other sugars do not stimulate)
M. testulalis (5)	L:	sucrose (12 other sugars do not stimulate)
S. exempta (5)	L:	sucrose (12 other sugars do not stimulate)

(1) MA 1972; (2) VAN LOON unpubl.; (3)PANZUTO & ALBERT 1997; (4) ISHIKAWA 1963; (5) DEN OTTER 1992

or *M. sexta*, again indicating basic differences in transduction processes (SCHOONHOVEN 1974, SCHIFFMAN 1997).

Few studies on herbivorous insects have addressed the causes of differences in stimulating capacity between different sugars for one receptor cell, or differences between receptor cells in their responsiveness to the same sugar. LAM and FRAZIER (1991) conclude from a structure-activity study that the difference in responsiveness to glucose between the glucose-sensitive cell located in the medial sensillum styloconicum of *M. sexta* and the cell in its lateral hair responding to su-

Table 4. Sensitivity thresholds and saturation levels of some sugar cells. L = lateral and M = medial sensillum

			Threshold	Plateau	Kb	
		Sugar	(mM)	(mM)	(mM)	Reference[a]
B. mori	L	sucrose	0.1	10		(1)
		glucose	2			
		fructose	5–10			
P. brassicae	L	sucrose	1	100	50	(2)
		glucose	10	300		
	M	sucrose	10			(2)
P. rapae	L	sucrose	0.1	20	0.5	(3)
		glucose	0.1	100	1.0	
	M	sucrose	0.5	32	1.0	(3)
D. pini	M	glucose	<0.5	50	30	(4)
M. sexta	M	glucose	0.5	100	8	(5)
C. fumiferana	L	sucrose	<0.5	50	1.5	(6)
S. exempta	L	sucrose	<0.1			(7)
M. testulalis	L	sucrose	<0.1	10		(7)
E. saccharina	L	sucrose	0.1	100		(7)
	M	sucrose	0.1	10		
C. partellus	L	sucrose	0.1	100		(7)
H. virescens	L	sucrose	0.5	10		(8)
H. subflexa	L	sucrose	0.5	10		(8)
G. geneura	M	sucrose	<0.1	50		(9)
		(serine)[b]	<0.1	10		
		(catalpol)[b]	0.01	5		

[a](1) ISHIKAWA 1963; ASAOKA 2000; (2) MA 1972; (3) VAN LOON unpubl.; (4) MENCO *et al.* 1974; (5) FRAZIER 1986; (6) ALBERT & PARISELLA 1988*a*; (7) DEN OTTER 1992; (8) BERNAYS & CHAPMAN 2000; (9) BERNAYS *et al.* 2000*a*

[b]Compounds stimulate sucrose-sensitive cell

crose and glucose can be attributed to differences in topographical binding-site characteristics.

Several studies have shown that feeding behaviour is quantitatively related to sensory input, as may be expected for a major and in most cases even dominant phagostimulant (e.g., BLOM 1978). The rank order of the major sugars for behavioural preferences in spruce budworm larvae correlates with that for firing frequency of the sugar-sensitive neuron in its lateral sensillum styloconicum (PANZUTO & ALBERT 1997), another indication of the importance of input from this cell to the gustation processing centre.

Table 5. Responses to inositol in medial (M) and lateral (L) sensilla styloconica

Species	M	L	Reference[a]
Cossus cossus (Cossidae)	+	–	(1)
Adoxophyes orana (Tortricidae)	–	+	(2)
Choristoneura fumiferana (Tortricidae)	+	+	(3)
Euchaetias egle (Oecophoridae)	–	–	(4)
Calpodes ethilus (Hesperiidae)	–	+	(5)
Dendrolimus pini (Lasiocampidae)	+	–	(6)
Malacosoma americana (Lasiocampidae)	+	+	(5)
Bombyx mori (Bombycidae)	–	+	(7)
Philosamia cynthia (Saturniidae)	+	+	(2)
Papilio troilus (Papilionidae)	+	–	(4)
P. glaucus (Papilionidae)		–	(4)
P. polyxenes (Papilionidae)	+	+	(4)
Pieris brassicae (Pieridae)	–	–	(6)
P. rapae (Pieridae)	–	–	(8)
Danaus plexippus (Danaidae)	–	+	(4)
Bupalus piniarius (Geometridae)	–	+	(6)
Operophtera brumata (Geometridae)	–	+	(2)
Celerio euphorbiae (Sphingidae)	+	+	(1)
Ceratomia catalpae (Sphingidae)	+	+	(4)
Manduca sexta (Sphingidae)	+	+	(2)
Sphinx ligustri (Sphingidae)	+	+	(1)
Estimene acrea (Arctiidae)	+	–	(4)
Grammia geneura (Arctiidae)	–	–	(9)
Isia isabella (Arctiidae)	+	+	(4)
Euproctis chrysorrhoea (Lymantriidae)	+	+	(1)
Lymantria dispar (Lymantriidae)	+	+	(4)

Table 5 (continued)

Species	M	L	Reference[a]
Leucoma salicis (Lymantriidae)	+	–	(1)
Episema caeruleocephala (Noctuidae)	+	–	(1)
Helicoverpa zea (Noctuidae)	+	–	(4)
H. virescens (Noctuidae)	+	–	(10)
H. subflexa (Noctuidae)	+	–	(10)
Mamestra brassicae (Noctuidae)	+	+	(6)
M. configurata (Noctuidae)	+	–	(11)
Spodoptera exempta (Noctuidae)	+	–	(12)
S. littoralis (Noctuidae)	+	+	(13)
Trichoplusia ni (Noctuidae)	–	–	(11)

[a](1) SCHOONHOVEN 1973; (2) SCHOONHOVEN 1969*c*; (3) PANZUTO & ALBERT 1997; (4) DETHIER 1973; (5) DETHIER & KUCH 1971; (6) MA 1972; (7) ISHIKAWA 1963; (8) VAN LOON unpubl.; (9) BERNAYS & CHAPMAN 2001*a*; (10) BERNAYS & CHAPMAN 2000; (11) SHIELDS & MITCHELL 1995; (12) MA 1977*a*; (13) SCHOONHOVEN *et al.* 1991

SUGAR ALCOHOL CELLS

Since ISHIKAWA's initiating paper (1963) on taste receptors in the silkworm, in which he reported the presence of, among others, a specific inositol-sensitive cell, many species of caterpillar have been found to possess a cell that vigorously responds to inositol (Table 5). In some cases, for instance in *Dendrolimus pini* (MA 1972, MENCO *et al.* 1974) and *Choristoneura fumiferana* (PANZUTO & ALBERT 1997), inositol stimulates the sugar cell. Usually, however, inositol stimulates one or even two specialized, so-called inositol cells. Their specificity spectra have been studied in a few species only, but it is generally assumed that they are highly specific. Thus, out of the nine stereo-isomeric configurations of inositol, only myo- and epi-inositol stimulated the inositol cell in *B. mori* (JAKINOVICH & AGRANOFF 1971, 1972). Both inositol cells in *M. sexta* are insensitive to the cyclitols mannitol, sorbitol, pinitol and quebrachitol (GLENDINNING *et al.* 2000).

The sensitivity of inositol cells is generally fairly high and comparable to threshold levels found in sugar cells, i.e., 0.1 mM (ISHIKAWA 1967, DEN OTTER 1992, BERNAYS *et al.* 1998). Their dynamic range (i.e., the steepest part of the concentration/response curve) overlaps with the known range of inositol concentrations in plant tissues, i.e., 0.5–10 mM (MORRÉ *et al.* 1990, NELSON & BERNAYS 1998). Thus, these cells are well equipped to quantitatively determine the presence of inositol in food plants.

The finding that many caterpillars devote out of their styloconic complement of only eight cells one or even two taste cells to inositol perception, suggests that inositol, an ubiquitous plant constituent (LOEWUS & MURTHY 2000), is an important signal in host-plant recognition and/or assessing plant nutritional value. It does indeed stimulate feeding behaviour when added to an artificial diet or smeared on an otherwise unacceptable plant leaf (e.g., SCHOONHOVEN 1969*c*, HAMAMURA 1970, GLENDINNING *et al.* 2000). However, the effects on feeding behaviour can only partially explain why caterpillars spend so much sensory input capacity on this simple compound. Inositol is known to occupy a multifunctional role in plant metabolism and to affect in manifold ways growth and development (LOEWUS & MURTHY 2000). Possibly inositol levels signal to the insect some important feature of a plant other than its nutritional value *per se* (NELSON & BERNAYS 1998, GLENDINNING *et al.* 2000).

Table 6. Presence of sorbitol-sensitive taste cells in medial (M) or lateral (L) sensillum styloconicum

Species	Feeding range[a]	Food plants	Sorbitol cell		Reference[b]
			M	L	
Malacosoma americana	O	mainly Rosaceae	o	+	(1)
Episema caeruleocephala	O	Rosaceae	o	+	(2)
Lymantria dispar	P	Rosaceous and other trees	+	o	(3)
Yponomeuta evonymellus	M	*Prunus padus* (Ros.)	o	+	(4)
Y. malinellus	M	*Malus* spp. (Ros.)	o	+	(4)
Y. padellus	O	Rosaceae	o	+	(4)
Y. mahalebellus	M	*Prunus mahaleb* (Ros.)	o	+	(4)
Y. cagnagellus	M	*Euonymus europaeus* (Celas.)	o	o	(4)
Y. irrorellus	M	*E. europaeus*	o	o	(4)
Y. plumbellus	M	*E. europaeus*	o	o	(4)
Y. rorellus	M	*Salix* spp. (Salic.)	o	o	(4)
Y. vigintipunctatus	M	*Sedum telephium* (Crass.)	o	o	(4)
Estigmene acrea	P	herbaceous plants	o	o	(3)
Choristoneura fumiferana	O	*Picea* spp. (Pinac.)	o	+	(5)
Dendrolimus pini	O	*Pinus* spp. (Pinac.)	o	o	(6)
Pieris brassicae	O	Cruciferae	o	o	(7)
Manduca sexta	O	Solanaceae	o	o	(8)
Papilio troilus	P	various trees	o	o	(1)

[a]O = oligophagous, P = polyphagous, and M = monophagous

[b](1) DETHIER 1973; (2) SCHOONHOVEN 1973; (3) DETHIER & KUCH 1971; (4) VAN DRONGELEN 1979; (5) PANZUTO & ALBERT 1997; (6) MENCO *et al.* 1974; (7) MA 1972; (8) GLENDINNING 2000

Some other sugar alcohols play a dominant role in certain caterpillar–host-plant relationships. Taste cells which typically respond to sorbitol or dulcitol, compounds which occur at high concentrations in Rosaceae and Celastraceae respectively, are present in species which feed exclusively or to a greater extent on plants belonging to these taxa, whereas species feeding on other plant taxa lack such receptors (Table 6). A well documented example of specialized sorbitol and dulcitol cells is provided in an electrophysiological inventory covering nine *Yponomeuta* species, all feeding specialists (VAN DRONGELEN 1979). Four species bound to rosaceous plant species possess sorbitol-specific taste cells, whereas the remaining five species lack such receptors. Three of the latter species feed monophagously on *Euonymus europaeus*, a shrub which is characterized by large amounts of dulcitol (a stereoisomer of sorbitol). These species are equipped with specific dulcitol-sensitive receptor cells in their lateral and, in two species, also in their medial sensilla styloconica (VAN DRONGELEN *l. c.*).

AMINO ACID CELLS

Since several amino acids stimulate feeding behaviour in various herbivorous insects (BERNAYS & SIMPSON 1982, ALBERT & PARISELLA 1988*b*, HIRAO & ARAI 1990) one may expect to find among an insect's chemoreceptor system neurons which respond either directly to amino acids, or whose responses to other compounds are modified by the presence of amino acids. Both modes of perception have been found to coexist in several caterpillar species.

Table 7 lists the results of studies in which the stimulus ranges of styloconic cells for a series of amino acids were determined in some detail. A glance at the table immediately reveals striking differences between species. Even two species considered to be closely related, *Pieris brassicae* and *P. rapae*, show several significant differences in their responses to the same set of amino acids. A second noteworthy feature is that all species respond to some nutritionally essential as well as non-essential amino acids. In both *Pieris* species the responses to the essential amino acids are stronger than to the non-essential ones, but this balance is reversed in, for instance, *Ecrisia acrea*. The signalling function of these compounds is presumably more important to the insect than exact knowledge of the presence of nutritionally relevant chemicals.

The picture arising from Table 7 is, however, very incomplete. It only presents data from one of the two sensilla styloconica, whereas it is known that in several cases the complementary sensillum also responds to one or more amino acids. Thus, in *P. brassicae* and *P. rapae* two of the dominant free amino acids in their

food plants, i.e., aspartic acid and glutamic acid, stimulate a cell in the medial sensillum rather than the amino acid cell in the lateral hair (VAN LOON & VAN EEUWIJK 1989). Another example is provided by larvae of *Choristoneura fumiferana*. All amino acids tested, except proline, stimulate a cell located in the other hair. Proline, on the other hand, evokes vigorous responses in the medial sensil-

Table 7. Amino acid receptors in maxillary chemosensilla of selected lepidopterous larvae[a]. L = lateral and M = medial sensillum styloconicum. Arterisks* indicate essential amino acids. (P.b.: *Pieris brassicae*; P.r.: *Pieris rapae*; H.z.: *Helicoverpa zea*; E.a.: *Ecrisia acrea*; M.a.: *Malacosoma americana*; D.p.: *Danaus plexippus*; P.p.: *Papilio polyxenes*; L.d.: *Lymantria dispar*; C.e.: *Calpodes ethlius*, A.o.: *Adoxophyes orana*; C.f.: *Choristoneura fumiferana*, G.g.: *Grammia geneura*)

	P.b. L (1,2)[c]	P.r. L (2,3)	H.z. L (3)	E.a. M (3)	M.a. M (3)	D.p. L (3)	P.p. L (3)	L.d. L (3)	C.e. L (3)	A.o. L (4)	C.f.[b] L (5)	G.g. L (6)
Arginine*	o	o	o	o	+	–	–	–	++		o	++
Histidine*	+++	+	o	o	o		o	o		+	+	+++
Isoleucine*	++	++	o	o	o	o	o	+		++		o
Leucine*	++	+++	++	+	o	o	o	o		+++	+	++
Lysine*	o	o										++
Methionine*	++	+++	++	+	o	++	o	–	++	+	+	++
Phenylalanine*	+++	+	o	++	o	o	o	o		o	+	o
Threonine*	+	o	o	+	o	++	++	+		o		+
Tryptophan*	++	+	o	+	o	o	+	o		+		o
Valine*	++	++	–	+	++	++	o	o		++	+	o
Alanine	++	++	o	+++	+++	++	o	o	–		+	+
Asparagine	++	++										o
Aspartic acid	o	o	o	o	+	o	o	o	++		+	+
Cysteine	+	o		++	o		–	o	++			
Cystine			++	o	+	+	o	o	+		+	o
Glutamic acid	o	o	o	++	++	o	–	o	o		+	++
Glycine	+	o	o	++	–	o	–	o			+	+
Proline	++	++	o	++	++	+++	o	o	++		o	o
Serine	++	++	o	+++	o	+++	++	o			+	o
Tyrosine	o	o	+	+	o	o	o	o			+	o

[a]+++ = strong reaction, ++ = medium reaction, + mild reaction, o = no reaction, – = inhibition as compared to control

[b]Different compounds were tested at different concentrations

[c]Data from (1) SCHOONHOVEN 1969*a*; (2) VAN LOON & VAN EEUWIJK 1989; (3) DETHIER & KUCH 1971; (4) SCHOONHOVEN 1973; (5) PANZUTO & ALBERT 1998; (6) BERNAYS & CHAPMAN 2001*a*

lum. In behavioural tests proline strongly stimulates feeding activity in this insect (PANZUTO & ALBERT 1998).

Some amino acids appear to stimulate 'sugar' cells. An interesting case of such a versatile receptor cell is present in *Grammia geneura* larvae. These insects have, in addition to an amino acid cell in their lateral sensillum styloconicum, in the other sensillum a neuron which responds to seven (out of 20) amino acids. The same cell can be stimulated by sucrose, glucose, and trehalose, and, remarkably, also by catalpol. The latter compound, an iridoid glycoside, occurs in a favoured food plant of this species. Because of its multiple specificity BERNAYS and CHAPMAN (2001*a*) named this cell a 'phagostimulatory cell', rather than a 'sugar' or 'amino acid' cell.

As has been described above for sugar cells the dose-response curves of some representative amino acids show a section of increasing responsiveness which spans a concentration range of about two orders of magnitude. In the case of *Pieris* the observed sensitivity ranges cover the concentrations of the compounds concerned as found in cabbage leaves (VAN LOON & VAN EEUWIJK 1989).

The relevance of amino acid receptors may be questioned in view of the fact that relatively small amounts of free amino acids occur in living plant tissues, and herbivores depend for their nitrogen requirements mainly on digestion of proteins. On the other hand, free amino acids are more readily available than proteins which need to be digested first, a process which involves energy. An indication of the fact that the amount of soluble nitrogen is important to an insect is deduced from better growth of *Pieris rapae* larvae on plants in which the tissues contained a greater proportion of the total nitrogen in soluble form than in control plants with similar levels of total nitrogen (SLANSKY & FEENY 1977). Furthermore, quantity and composition of the free amino acid pool may signal the nutritional status of a plant and as such form an important source of information to herbivores. In this context it is interesting to note that proline, though a non-essential amino acid for insects, is compared to other amino acids often a strong stimulus, which in *C. fumiferana* is even perceived via a separate channel. This very compound appears to play an important role in plants under water stress conditions and is known to accumulate in stressed plants (CYR *et al.* 1990). Conceivably, an insect obtains information on a plant's physiological status by measuring its proline level (PANZUTO & ALBERT 1998).

Several authors (e.g., DETHIER & KUCH 1971, HIRAO & ARAI 1990, BERNAYS & CHAPMAN 2001*a*) have reported that some amino acids may affect the impulse activity (positively or negatively) of various receptor types. Furthermore, cases are known in which a particular amino acid stimulates a deterrent cell (e.g., HIRAO & ARAI 1990). The observation that valine, though a strong stimulant of the amino

acid cell in *C. fumiferana*, appears to be a feeding deterrent in behavioural tests, may be attributed to its multiple effects on more than one cell type (PANZUTO & ALBERT 1998).

In conclusion, perception of amino acids is rarely if ever effected via a simple and highly specific chemosensory pathway. The finding that plant-like mixtures of amino acids stimulate two, and sometimes even three cells within the lateral sensillum of *Grammia geneura* (BERNAYS & CHAPMAN 2001*b*) fits into this inference. That multicomponent mixtures often evoke complex responses is hardly surprising in view of the fact that amino acids are structurally much more dissimilar than their common name suggests. Apart from that, their physiological roles in plants are multifaceted, and last but not least, their absolute and relative quantities vary greatly among plant species, as well as within plants, depending on developmental and physiological condition. Altogether, it is to be expected, also taking into account their different feeding habits, that amino acid perception among insect species shows little uniformity.

RECEPTORS FOR SIGN OR TOKEN STIMULI

In a pioneer study VERSCHAFFELT (1910) showed that certain specific secondary plant substances serve as cues used by some insects to recognise their food plants. It took half a century before the first chemosensory responses were recorded to one of the compounds which VERSCHAFFELT identified as a *sine qua non* for attack by insects specialized on these plants. He used sinigrin, a glucosinolate occurring in cruciferous plants, to entice *P. brassicae* larvae to feed on normally rejected plant species. Glucosinolates stimulate one neuron in each sensillum styloconicum of this insect, which thus function as phagostimulatory receptors for host-specific compounds (SCHOONHOVEN 1967). The cell located in the lateral sensillum responds to all tested glucosinolates with thresholds of ca. 0.1 mM. The cell in the medial sensillum reacts only to aromatic glucosinolates. This difference in specificity ranges allows the insect in principle to determine the ratio between total glucosinolates and aromatic glucosinolates. (Aromatic glucosinolates are induced in response to damage.)

After the elucidation of glucosinolates as pivotal in a crucifer-herbivore association the search for specific phagostimulants in other plant families was intensified. Although some striking cases have been reported, they are relatively rare in view of the interest in insect-plant relationships during the past decades (STÄDLER 1992, see also MÜLLER & RENWICK 2001). Within the Lepidoptera the most distinct case is found in the association of a number of insect species with Rosaceae.

The larvae of eight taxonomically diverse lepidopterans that feed only or at least mainly on rosaceous plants have receptors for sorbitol, the predominant soluble carbohydrate typical of this family, whereas such receptors do not occur in other insects (Table 6).

As discussed earlier the presence of sorbitol receptors in some *Yponomeuta* species specialized on rosaceous hosts is mirrored in dulcitol receptors in related *Yponomeuta* species, which feed only on *Euonymus europaeus*, a plant with dulcitol as its primary carbohydrate. These insects thus have, in addition to a sucrose receptor, sorbitol and/or dulcitol specific cells which signal the presence of a host-specific phagostimulant and which is at the same time an important nutrient (VAN DRONGELEN 1979). The dulcitol receptor cell responds to stimulus concentrations as present in its food plant with a maximum firing rate (Fig. 3). This indicates that it functions as a gauge which records the presence or absence of a sign stimulus, rather than measuring stimulus intensity.

An interesting taste cell type has been found in larvae of *Spodoptera exempta*. A cell which is specifically stimulated by adenosine and adenine provides a chemosensory basis for the fact that these compounds stimulate food uptake in this insect. This receptor is insensitive to purine or pyrimidine compounds or derivatives, including nucleotides and nucleosides (MA 1977*a*, MA & KUBO 1977). Whether or not we are dealing with an exceptional type of feeding stimulant

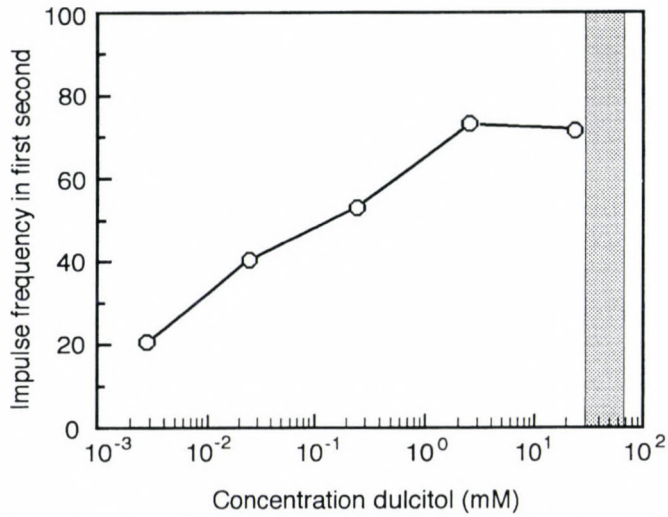

Fig. 3. Dose-response curve for dulcitol of the dulcitol-sensitive cell in the lateral sensillum styloconicum of *Yponomeuta cagnagellus*. The range of dulcitol concentrations in its host plant, *Euonymus europaeus*, lies within the shaded part of the figure (after MENKEN & ROESSINGH, 1998)

is unknown, because these compounds have rarely been included in feeding assays. Based on evidence from some related *Spodoptera* spp. MA (1977*a*) hypothesized that adenosine which occurs at a concentration of ca. 0.2 mMoles/1000g fresh maize leaves, is a more common phagostimulant for insects with grasses in their diet.

As referred to above, catalpol, a compound typically occurring in *Plantago* spp., stimulates at natural concentrations a phagostimulatory cell in *Grammia geneura*. This species, although polyphagous, shows a preference for *Plantago* over several other food plants. Catalpol, when added to a neutral substrate, stimulates feeding activity (BERNAYS *et al.* 2000*a*).

Table 8. Response spectra of deterrent neurones in four caterpillar species belonging to different food specialization categories, to four classes of secondary plant substances[a]

	B. mori (1)[b]	*P. brassicae* (2, 3, 4)	*M. sexta* (5)	*M. brassicae* (6, 7, 8)
	M[c]	O	O	P
Alkaloids				
Quinine	+	+	–	
Strychnine	+	+	–	+
Conessine	+	+	–	–
Caffein	+	-	+	
Nicotine	+	+	–	
Terpenoids/steroids				
Azadirachtin		+	–	–
ß-Ecdysone	+	+		+
Digitoxin		+		–
Phenolics, flavonoids				
Salicin	+	–	+	+
Rutin	+	–	–	
Quercitrin	+			–
Phloridzin	–	+	+	
Malvin		–	+	
Glucosinolates				
Glucocapparin		–	–	+
Glucotropaeolin		–	+	+

[a]Most chemicals were tested at concentrations of 1-10 mM or as saturated solutions

[b]Data taken from: (1) ISHIKAWA 1966; (2) MA 1969, 1972; (3) VAN LOON 1990; (4) VAN LOON & SCHOONHOVEN 1999; (5) SCHOONHOVEN 1973, 1981; (6) WIECZOREK 1976; (7) DESCOINS & MARION-POLL 1999; (8) VAN LOON unpubl.

[c]M = monophagous; O = oligophagous; P = polyphagous

The relative paucity of examples discovered up till now of host-plant specific compounds that serve as feeding stimulants may be due to the limited research capacity devoted to this subject, but it could also very well be that clear and simple relationships between insects and their host plants based on one or a few chemicals are less widespread than is often presumed. After all, many groups of minor plant compounds have fairly wide distributions, and relatively few have a sufficiently restricted distribution range to use them as a specific enough characteristic of a certain plant taxon (SWAIN 1972). This implies that when an insect cannot rely on a simple and unequivocal chemical flag, it would have to rely on a chemosensory system that obtains more subtle and at the same time more complex information of a plant's chemical composition to distinguish hosts from non-hosts.

DETERRENT CELLS

All herbivorous insects have deterrent (D) receptors which upon stimulation reduce or fully stop feeding activity. These cells fulfil a central role in host-plant recognition, or rather in identifying non-hosts, and have since their discovery (ISHIKAWA 1966) attracted much interest. The fairly extensive literature on the sensory coding of feeding deterrents in various insects is reviewed by FRAZIER (1986, 1992) and SCHOONHOVEN *et al.* (1992).

The apparent simplicity of host-nonhost discrimination by D cells hides a multifarious complexity. First, the response patterns of D cells vary greatly among species, even if they are closely related, both qualitatively (VAN DRONGELEN 1979) and quantitatively (Fig. 4) (DETHIER & KUCH 1971, VAN LOON 1990). Second, in those cases where a range of compounds has been tested, the D cell is sensitive to compounds belonging to more than one chemical class. At the same time, in none of these cases does this cell respond to all chemical classes tested or even to all the compounds within a class (Table 8). Thus, although the stimulus spectra of D cells are often remarkably broad with a seemingly capricious response pattern, they nonetheless display specificity.

Deterrent cells naturally vary in their specificity depending on species and stimulus type. When these cells indeed function as an identification device to perceive secondary plant compounds which may occur in non-hosts their specificity ranges are expected to overlap with the concentration ranges of these compounds as commonly encountered in plants. Table 9 shows threshold values and saturation levels for chemicals which are the strongest stimuli known for the insects mentioned. It may be concluded from this very limited set of data that threshold concentrations are commonly below 1 mM. In some cases this value is even about

1000 times lower and ranks among the lowest reported for insect taste cells (by comparison: human taste threshold for quinine is about 0.00075 mM).

There are many indications that food specialists feature a greater sensitivity to deterrents than polyphagous species (e.g., BERNAYS & CHAPMAN 1994, BERNAYS *et al.* 2000*b*) and, as JERMY more specifically stated, that "the sensitivity of chemoreceptors to deterrents is a general factor determining the host range of chewing phytophagous insects" (JERMY 1966, p. 9). However, to conclude that the data of Table 9 support this hypothesis would be premature, because the high sensitivities observed in the oligophagous species may also be due to the fact that the stimulus spectra of these species have been investigated much more thoroughly than those of the generalist species. It may very well be that much stronger deterrents for the latter species will be found when more compounds are tested.

The concentration range between threshold and maximum firing intensity spans two to three orders of magnitude, and is thus comparable to ranges as determined for sugar cells (Table 4).

An essential difference between D cells and phagostimulatory cells is found in the time characteristics of their responses. Deterrent cells generally show greater latency in their response than phagostimulatory cells (e.g., MA 1972, GLENDINNG & HILLS 1997, DESCOINS & MARION-POLL 1999). Two other features which de-

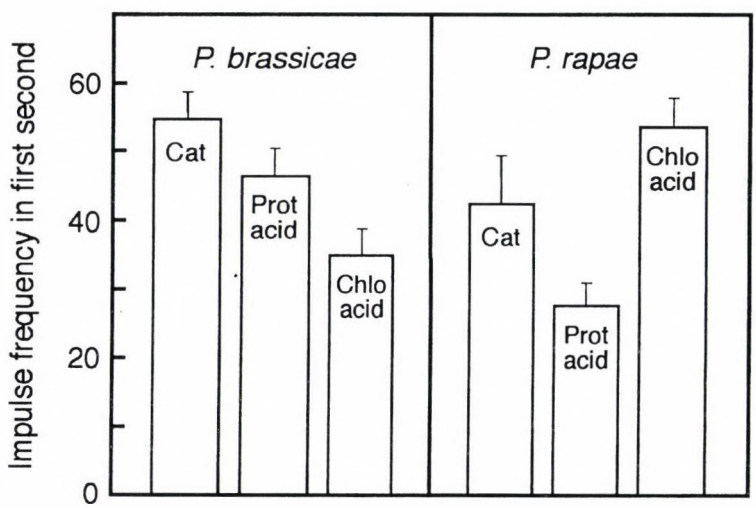

Fig. 4. Comparison of relative effectiveness of catechin (cat), protocatechuic acid (prot acid), and chlorogenic acid (chlo acid) on specialized deterrent cell in the lateral sensilla styloconica of two *Pieris* species. The three compounds were tested at 1 mM on *P. brassicae* and at 2.5 mM on *P. rapae* (data from VAN LOON 1990)

Table 9. Sensitivity thresholds and saturation levels of some deterrent cells. L = lateral and M = medial sensillum styloconicum; O = oligophagous and P = polyphagous

		Feeding range	Stimulus	Threshold (mM)	Plateau (mM)	References[a]
B. mori	M	O	strychnine	0.0001		(1)
P. brassicae	L	O	helveticoside	0.0002	0.03	(2)
	M	O	strychnine	0.001	0.02	(3)
M. sexta	L	O	aristolochic acid	0.0003		(4)
	M	O	caffeine	0.03	5	(4)
T. ni	L	P	sinigrin	0.02	5	(5)
	M	P	sinigrin	0.06	10	(5)
H. virescens	L	P	sinigrin	0.1	5	(6)
M. configurata	L	P	sinigrin	0.16	30	(5)
M. brassicae	L	P	sinigrin	0.5	500	(7)

[a]Data from (1) ISHIKAWA 1966; (2) VAN LOON & SCHOONHOVEN 1999; (3) MA 1972; (4) GLENDINNING *et al.* 1999*b*; (5) SHIELDS & MITCHELL 1995; (6) BERNAYS & CHAPMAN 2000; (7) WIECZOREK 1967

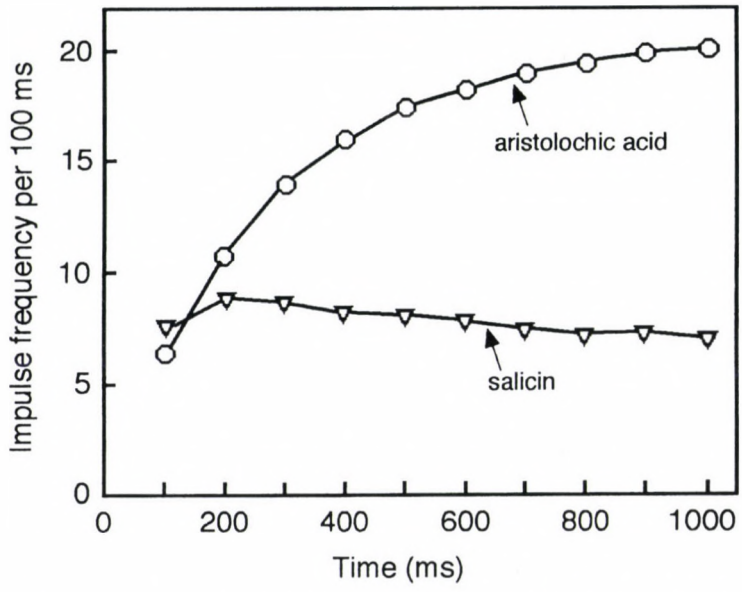

Fig. 5. Impulse frequencies elicited during the first second of stimulation by 10 µM aristolochic acid and 10 mM salicin in the D cell of the medial sensillum styloconicum of *Manduca sexta* (after GLENDINNING & HILLS 1997)

terrent cells may show upon stimulation by certain compounds are a slow increase in impulse frequency (Fig. 5), and an increase in impulse amplitude with stimulus concentration (PETERSON *et al.* 1993, VAN LOON & SCHOONHOVEN 1999). Impulse amplitude changes are most likely irrelevant in the central integration process, but the slow start of impulse formation in D cells as compared to phagostimulatory cells is probably of importance. Another characteristic of D cells is their low adaptation rate (e.g., ISHIKAWA 1966, SCHOONHOVEN 1977, SHIELDS & MITCHELL 1995, DESCOINS & MARION-POLL 1999). The phasic-tonic relationship of a D cell, after it has reached its maximum activity in response to a given deterrent at a given concentration, differs from that of phagostimulatory cells (Fig. 6A), a characteristic which has a very marked effect on the ratio of impulse frequencies between the D cells and those responding to phagostimulants (Fig. 6B). As a consequence, the "taste" of a mixture of, for instance, sucrose and strychnine changes gradually, becoming more repulsive as time passes. Low levels of deter-

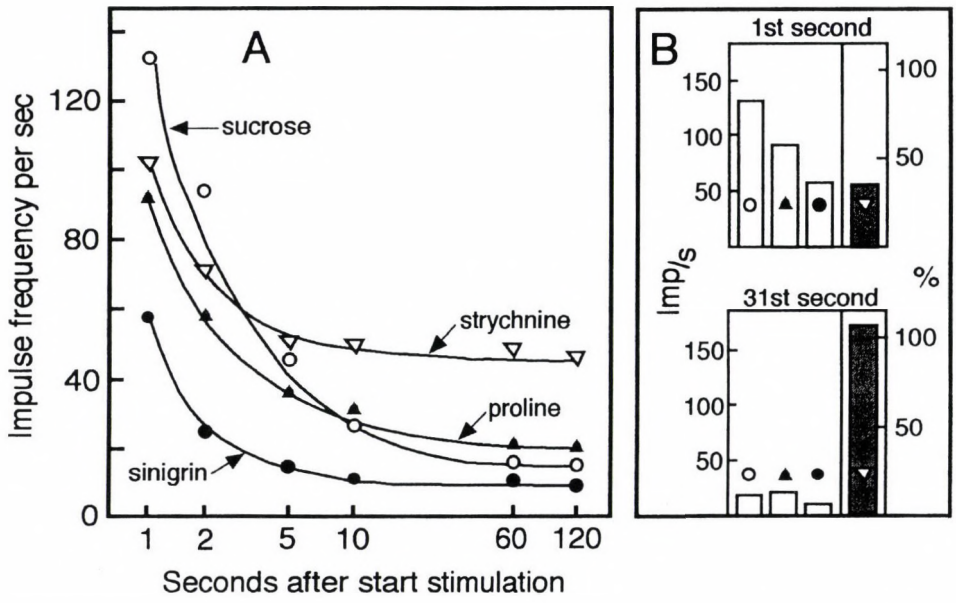

Fig. 6. (A) Adapatation curves of some chemoreceptory cells in the sensilla styloconica of *Pieris brassicae*. Stimuli: 0.003 mM strychnine, 100 mM proline, 10 mM sucrose, and 10 mM sinigrin. (B) Responses of four cell types during the 1st and 31st second of stimulation with a mixture of the same four chemicals, provided no interactions between the stimuli occur. The response intensity of the D cell (shaded) upon stimulation by strychnine is expressed as percentage of the summated impulse frequencies of the three phagostimulatory cells upon stimulation by sucrose, proline and siningrin, respectively (after SCHOONHOVEN 1977)

rents, though not preventive of feeding, may by way of this physiological mechanism reduce the lengths of feeding bouts. Shorter than normal feeding periods have often been recorded on deterrent foods that were eaten to some extent (BERNAYS *et al.* 2000*b*).

The decisive role of D cells in feeding behaviour is unambiguously supported by observations of a close correspondence between impulse frequencies recorded in D cells upon stimulation by a deterrent at various concentrations, and the feeding intensity on diets containing various amounts of the same compound (BLOM 1978, PETERSON *et al.* 1993, LUO *et al.* 1995, MESSCHENDORP *et al.* 1996, BERNAYS & CHAPMAN 2000).

SALT CELLS

Most if not all sensilla styloconica show neural activity when stimulated with salt solutions. KCl or NaCl are commonly used as an electrolyte enhancing electrical conduction of the recording electrode. These compounds, at the fairly high concentrations of 50 or 100 mM, stimulate one or two cells which have been labelled as 'salt' cells. Impulses from these cells are in most recordings characterized by relatively small amplitudes. ISHIKAWA (1963) suggested that they function as an anion and a cation cell. He found that the stimulating effect of the salts tested was dominated by the cations involved, and that monovalent cations were more effective stimuli than divalent cations.

Few studies report dose/response curves for one or more salts. A study on *Grammia geneura* shows increasing activity in two salt cells in response to KCl at concentrations ranging from 10 to 1000 mM. NaCl produced also responses in the two cells with slightly higher firing rates than KCl (BERNAYS & CHAPMAN 2001*a*). Interestingly, these authors conclude that salts and deterrents stimulate the same cells. PETERSON *et al.* (1993) also consider one of the two 'salt' cells in the medial sensillum of *Manduca sexta* to be in fact a D cell, and DETHIER (1973) reported that salicin, populin, and sinigrin tend to stimulate the 'primary salt cell' in the lateral sensillum of *Danaus plexippus*. Incongruent with these inferences is the fact that responses to salts display a temporal pattern quite different from that characterizing the majority of D cells (see previous section).

Obviously, sensory responses to salts have attracted only limited attention, which may be due to their supposedly minor role in host-plant selection. Moreover, salt responses appear often to be more or less suppressed when tested in mixtures with, for example, sucrose. It could be argued, therefore, that the role of salts

under natural conditions, that is as a component of leaf tissue sap, is of limited importance.

The view, recently expressed by BERNAYS and CHAPMAN (2001*a*), that salt cells have to be regarded as synonymous with D cells, opens a new perspective, which merits further investigation.

WATER CELLS

Water cells form perhaps the most mysterious cell type recognised so far among styloconic taste cells. Its existence has been reported in early papers on styloconic taste cells (ISHIKAWA & HIRAO 1963, SCHOONHOVEN & DETHIER 1966), although in some cases they have later been relabelled as salt cells. New instances of water cells have recently been described for several lepidopterous larvae (DEN OTTER 1992, PANZUTO & ALBERT 1998).

The presence of a water cell was concluded from stimulations with low salt concentrations or even distilled water (hence its sometimes used alternative name: 'low-salt cell'). Characteristically, water cells exposed to increasing salt concentrations are increasingly inhibited and may become fully suppressed, as was seen in *Bombyx mori* upon stimulation by 10 mM NaCl. Sugars and amino acids may inhibit this cell too (ISHIKAWA 1967, PANZUTO & ALBERT 1998).

It remains to be worked out whether 'water' cells under more natural conditions respond to compounds other than pure water, and then have to be renamed.

PLANT ACIDS

All plants contain organic acids, although the quantities and types of acid vary among species and with physiological state. Ascorbic acid is a common plant constituent, and, in contrast to other organic acids, an essential nutrient for most caterpillars. It stimulates feeding activity in, for instance, *Pieris brassicae* larvae (MA 1972). Therefore, any analysis of a caterpillar's gustatory sense should include responses to ascorbic acid and preferably some other common plant acids as well. However, few studies on this type of stimuli are available. DETHIER and KUCH (1971) and DETHIER (1973) have tested ascorbic acid, malic acid, oxalic acid, succinic acid and nicotinic acid on several caterpillar species. They noticed in several instances some increase of neural activity, and occasionally an inhibition of the salt cells as compared to control stimuli. No attempt was made to assign the observed action potentials to specific cell types. Caterpillars of *Choristoneura*

fumiferana respond to shikimic acid, a known feeding stimulant for this species. It is again unclear what cell type is involved (ALBERT 1980). Recently, BERNAYS *et al.* (1998) found that citric acid, oxalic acid and ascorbic acid may reduce salt responses and/or stimulate the D cells in *Manduca sexta* larvae. These responses, however, were largely ascribed to pH and not to specific effects of any of these compounds. Ascorbic acid at concentrations as it occurs in plant tissues consistently reduced responses to glucose and inositol.

The meagre information we have on sensory effects of plant acids does not provide evidence for the presence of a specific acid cell in caterpillars. At the present state of our knowledge it seems most likely that acids at natural concentrations primarily exert an effect on feeding behaviour by modulating the responses of various cell types. Besides, they may stimulate D cells at higher concentrations.

INHIBITORY AND SYNERGISTIC INTERACTIONS

When a styloconic sensillum is stimulated by a mixture of two compounds its neural response is often different from what would be expected on the basis of responses to the same compounds when tested singly. The presence of sucrose appeared to reduce the impulse frequency of the salt cell in *Bombyx mori*, and when the concentration of salt is increased, the intensity of responses of the sugar cell is reduced (ISHIKAWA 1963). Since ISHIKAWA's observation numerous examples of such negative interactions have been published. Thus, deterrents may inhibit sugar cells (Fig. 7) (e.g., FRAZIER 1986, VAN LOON 1990, HIRAO & ARAI 1991, MESSCHENDORP *et al.* 1996), and sugars and salts may inhibit D cells (e.g., SIMMONDS & BLANEY 1983, SHIELDS & MITCHELL 1995, GLENDINNING *et al.* 2000). Not only concentration of the inhibitory compound determines the degree of an inhibition, as shown in Fig. 7, but also exposure time. Three taste cells in *Pieris brassicae* responding to phagostimulants showed a gradual decrease of sensitivity when exposed to 1 mM polygodial, a drimane isolated from *Polygonum hydropiper*, for periods of up to 30 minutes. Its lateral glucosinolate receptor then showed a 20% lower sensitivity to sinigrin, while for the sugar cell and the amino acids cell reductions of about 50% were attained (SCHOONHOVEN & YAN 1989).

Another type of modification of normal chemosensory function caused by some feeding deterrents was first described by MA (1977*b*) after studying the effect of warburganal on phagostimulatory cells of *Spodoptera exempta*. This drimane compound appeared to distort the normal function of several cells, resulting in irregular patterns and eventually, depending on concentration and duration of exposure, to 'bursting' activity. The question, however, whether or not this type

of response, observed with relatively high concentrations and/or long stimulation periods, also occurs under natural conditions, remains to be solved (SCHOONHOVEN *et al.* 1992). The fact that tomatine, a constituent of one of the food plants of *Manduca sexta*, at low concentrations (i.e., 0.1 mM) causes within 30 seconds bursting activity in both sensilla, but is in behavioural experiments a (weak) phagostimulant (PETERSON *et al.* 1993) also seems inconsistent with the assumption that bursting patterns are normal physiological reactions.

Two compounds which both stimulate the same cell may when mixed also evoke a weaker response than expected from tests with the single compounds. A mixture of sucrose and glucose elicits a significantly lower impulse frequency than sucrose at the same concentration alone (ISHIKAWA 1967). Similar inhibitory interactions have been described for binary mixtures of compounds which stimulate, for instance, an amino acid cell [lysine and histidine (BERNAYS & CHAPMAN 2001*b*)] or deterrent cells [caffeine and salicin (SCHOONHOVEN 1978)].

Conversely, some combinations, for instance, inositol and glucose, or serine and alanine resulted in stronger than expected responses of respectively sugar and amino acids cells (MENCO *et al.* 1974, BERNAYS & CHAPMAN 2001*b*).

Deterrent compounds that on their own do not stimulate any neuron within a sensillum may also decrease the responsiveness of a cell responding to a nutrient, as exemplified by sinigrin inhibiting the inositol cell in *Heliothis virescens* (BERNAYS & CHAPMAN 2000).

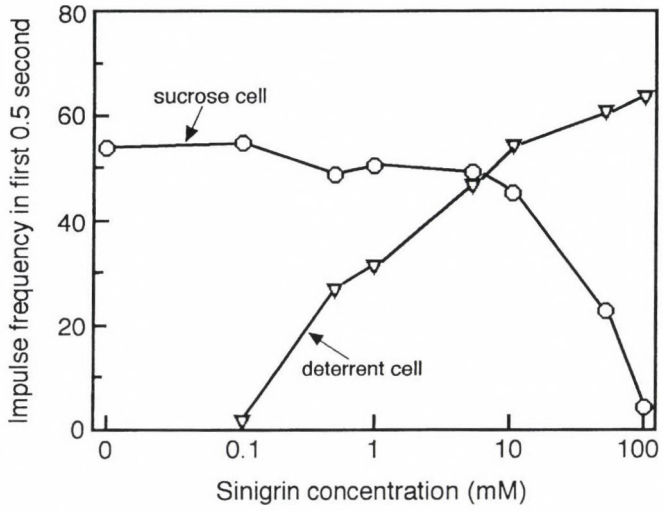

Fig. 7. Impulse frequencies of the sucrose-sensitive and deterrent cells in the lateral sensillum styloconicum of *Heliothis subflexa* upon stimulation with 5 mM sucrose mixed with different concentrations of sinigrin (after BERNAYS & CHAPMAN 2000)

Two compounds may also interact via a synergistic mechanism and induce a stronger neural response than each compound on its own would have done. Thus, the presence of sucrose greatly increased the response of the cell that in *Isia isabella* preferentially responds to sinigrin (DETHIER & KUCH 1971). Interestingly, a synergistic interaction between two chemicals at low concentrations may with increasing concentrations become reversed to an antagonistic interaction. This happens in the silkworm when strychnine at a fixed concentration is mixed with NaCl at varying concentrations. Increasing NaCl levels up till 40 mM NaCl induce an increase in firing frequency of the D cell in response to strychnine, whereas NaCl at a concentration of 100 mM and above inhibit the D cell (ISHIKAWA 1966).

The physiological mechanism underlying inhibitory (or excitatory) interactions when two cells are stimulated simultaneously is unknown. Mutual electrotonic influences may be involved, since in a dipterous insect direct contacts have been observed between chemosensory cell somata (ISIDORO *et al.* 1994). Direct physiological interactions between receptor cells occur in tibial chemosensilla of a grasshopper (WHITE *et al.* 1990).

The phenomenon of stimulus interactions resulting in inhibitions of one or more cells is reminiscent of lateral inhibition known from visual systems (HARTLINE *et al.* 1961). Likewise, inhibitory (and synergistic) relationships between chemicals may serve to sharpen the chemical image, the *Gestalt*, of a complex stimulus, thus providing the central nervous system (CNS) a partly pre-treated message.

The examples presented in this paragraph serve to stress the widespread occurrence of interactions between two or more chemicals, which probably take place at the receptor level. These mixture effects obviously hamper the analysis of responses to natural stimuli by the caterpillar's taste system because of the unpredictability of direction and degree of interplay between all contributing chemicals.

TASTE CELL CATEGORIES

Our approach of an analysis of taste cells in animals is coloured by the traditional concept of the four primary taste qualities: sweet, sour, salty, and bitter. The kinds of stimuli first chosen to investigate insect chemoreceptors and the denomination of cells responding to them reflect this background. Deterrent cells in caterpillars are still called by some researchers 'bitter' cells, since they often respond to compounds which taste bitter to humans.

In the foregoing paragraphs an attempt was made to categorize taste cells in lepidopterous larvae based on their responses to various ranges of chemicals (c.f. Table 1). Two distinct features of the caterpillar's gustatory apparatus have emerged. (1) Many more cell types can be distinguished than the four taste categories commonly recognised in man. Cells responding to a number (but not all) sugars have been found, but also cells narrowly tuned to glucose, or fructose, or sucrose, or inositol. Cells responding to many feeding deterrents occur side by side with cells responding to only some deterrents. Cation, anion, and water cells have been identified, as well as amino acid cells and glucosinolate cells. Though some of these types may on further analysis turn out to be equivalents, the perception of a multitude of taste cells remains. It thus appears impossible to classify caterpillar taste cells into a few discrete types, though the other extreme with each taste cell being unique in its properties defies our notion of phyletic relationships between caterpillars. (2) There is a pronounced variability of cell types across caterpillar species, the relevance of which may be appreciated especially in the context of sensory coding principles and evolutionary origins, both topics to be discussed later.

It should be noticed that the response specificity of even well-studied cells in most cases have not been tested exhaustively with a wide diversity of compounds. Examples of cells responding to apparently unusual stimuli underline the importance of testing ideally a broad range of chemicals on each cell. There is, as mentioned before, the cell responding to some sugars, several amino acids, and catalpol (BERNAYS & CHAPMAN 2001*a*). The observation of ribose stimulating the inositol cell in *Spodoptera exempta* (DEN OTTER 1992) contrasts with the generally found high specificity of inositol cells. Deterrent cells in particular may be stimulated by very differently structured compounds. Therefore, each gustatory receptor responds to a variety of compounds in a manner that is not constrained by chemical relationships. Nevertheless, the often used and convenient categorization is probably generally valid, although it clearly should not be regarded as implying an absolute and rigid classification.

Taste cells respond primarily to their specific stimuli, but are also affected by compounds which modulate receptor activity, as discussed in the previous section. These modulating compounds are to be regarded as 'latent' stimuli, which form a hidden fraction of the specificity range of a taste cell. Influences of these compounds come to the surface only during tasting complex stimuli as when contacting plant contents (SCHOONHOVEN 1987).

There is evidence that plant volatiles may also stimulate caterpillar taste cells (STÄDLER & HANSON 1975). Because the maxillae move rhythmically in coordination with mandible movements, the sensilla styloconica may be exposed several times per second to the surrounding air in alternation with contacts with plant ma-

terial. Plant volatiles conceivably modulate the sensory pattern elicited by the extruding leaf sap. This aspect needs further investigation to assess its significance for sensory coding.

Table 10. Effects of dietary history on sensitivity of maxillary taste cells. M = medial and L = lateral sensillum styloconicum

Species		Control food	Experimental food	Stimulus	Sensitivity change (%)[a]	Reference[b]
M. sexta	M	Tomato foliage	Art. diet	Tomato leaf sap	+35	(1)
	M	Art. diet	Art. diet + 10 mM inositol	50 mM inositol	–42	(1)
	L	Art. diet	Art. diet + 10 mM salicin	10 mM salicin	–34	(1)
	L	Art. diet	Art. diet + 5 mM caffeine (2 days)	5 mM caffeine	–70	(2)
	L	*Solanum* foliage	Tomato foliage	Solanum leaf sap	+72	(3)
S. littoralis	M	Art. diet	Art. diet + 20 mM nicotine	20 mM nicotine	–50	(4)
	L	Art. diet	Art. diet + 20 mM nicotine	20 mM nicotine	–42	(4)
	M	Art. diet	Art. diet + 0.01 mM azad. (2 days)	0.01 mM azadirachtin	–41	(5)
	L	Art. diet	Sugar-free art. diet (4-12 h)	100 mM sucrose	+170	(6)
	M	Cabbage	Art. diet	1 mM sinigrin	–56	(7)
S. exempta	M	Art. diet	Art. diet + 0.01 mM azad. (2 days)	0.01 mM azadirachtin	–52	(5)
P. brassicae	M	Cabbage	Art. diet	5 mM chlorogenic acid	–36	(8)
	L	Cabbage	Art. diet	5 mM chlorogenic acid	–32	(8)
	L	Cabbage	Art. diet	5 mM proline	–16	(8)

[a]Based on total impulse frequencies per sensillum

[b]Data from (1) SCHOONHOVEN 1969*b*; (2) GLENDINNING *et al.* 1999a; (3) STÄDLER & HANSON 1976; (4) BLANEY & SIMMONDS 1987a; (5) SIMMONDS & BLANEY 1983; (6) SIMMONDS *et al.* 1992; (7) SCHOONHOVEN *et al.* 1987; (8) VAN LOON 1990

CHANGES IN RECEPTOR SENSITIVITY

Chemoreceptors encode stimulus intensity in frequency of impulses which are propagated to the CNS. Curiously, in lepidopteran taste cells this frequency control process does not reflect a fixed and constant sensitivity, but appears to vary with the insect's feeding history. Table 10 summarizes some salient results of experiments in which the sensitivity of one identifiable cell or an assembly of cells has been compared between groups of caterpillars which were fed different food types. Insects reared on different host plants showed highly significant differences in their total impulse frequencies to plant saps. Also insects fed a standard artificial diet containing low levels of a feeding deterrent or phagostimulant (inositol) show desensitisation of the specific receptors for these compounds, whereas conditioning on a phagostimulant-deficient diet sensitised the, in this case, sugar receptor. Apparently this phenomenon is a general property of taste cells in caterpillars since it occurs across species and cell types. Sensitivity changes develop within periods of hours to days. A more detailed analysis of this process in the D cell of *Manduca sexta* revealed that exposure to caffeine reduced its sensitivity to caffeine as well as salicin, but not to aristolochic acid (SCHOONHOVEN 1969*b*, GLENDINNING *et al.* 1999*a*), indicating that different transduction pathways are involved.

In addition to an influence of feeding history many other variables may also alter taste cell sensitivity (BLANEY *et al.* 1986), including age (BLANEY & SIMMONDS 1987*a*), time of day (SIMMONDS *et al.* 1991), satiety level (SCHOONHOVEN *et al.* 1987), and nutritional requirements. Caterpillars which were fed protein-free food showed an increased sensitivity to stimulation with an amino acid mixture, while in insects fed carbohydrate-free food sensitivity to sucrose stimulation was increased (SIMMONDS *et al.* 1992). Obviously, nutrient-specific feedback mechanisms exist which render deprived insects more sensitive to specific food components, a form of 'specific hunger'. Probably nutrients in the receptor lymph, supposedly reflecting haemolymph composition, modulate taste cell responsiveness, as is the case for amino acids in locusts (SIMPSON & SIMPSON 1992) and sugars in blow flies (AMAKAWA 2001).

The phenomenon of sensitivity modulation in response to previous experience or physiological condition, though complicating the search for the sensory code, reveals a new perspective of sensory function. Rather than transmitting a constant and predictable message, the receptors modify the sensory input to the CNS in such a way that several factors, which need to be considered by the CNS when preparing its instruction for behavioural response, have already been taken into account. Evidently, decision processes are not restricted to the CNS, but in-

volve also other components of the neural system, i.e., receptors. This results in a more efficient use of the total neural assembly an insect possesses.

NEURAL INTEGRATION OF SENSORY INPUT

As may be concluded from the previous sections we have good information on sensory input to the CNS and a fair knowledge of behavioural output. This logically raises the question where and how chemosensory input is processed and integrated with other central neuronal activity, such as that associated with satiety level, prior to the initiation of motor output which drives feeding behaviour.

The axons of all maxillary taste receptors project directly without synapsing, into the suboesophageal ganglion (SOG) (KENT & HILDEBRAND 1987, MITCHELL *et al.* 1999). The SOG also provides motor output to those mouthparts immediately involved in the feeding process (BLANEY & SIMMONDS 1987*b*, GRISS *et al.* 1991, ROHRBACHER 1994). It is inferred that much of the central processing of various types of input (including that of the taste cells) takes place in the SOG. However, since inputs from other parts of the CNS, e.g., the frontal ganglion and olfactory lobes, also contribute to feeding behaviour including host-plant recognition, the assumption that a 'feeding centre' is situated in the SOG is still premature. Experimental evidence is badly needed.

The maxillary taste cells show, with the notable exception of the generalist D cells, rather narrow specificity ranges. Most cells generate a neural output that can be correlated in a dose-dependent manner with either acceptance or rejection of their adequate stimuli. Thus chemosensory input guiding feeding preferences consists of positive and negative signals from various chemical stimuli, and changes in the balance of these chemicals may change preference. (It is not *a priori* to be excluded that some cell types have a bimodal effect on food intake: low impulse frequencies lead to phagostimulation and high impulse frequencies cause feeding inhibition). This conflict between positive and negative input is in principle resolved in the CNS, though peripheral interactions have already contributed to the outcome. Thus 10 mM inositol totally counteracts the inhibitory effect of 10 mM caffeine in *Manduca sexta* through a central evaluation of gustatory input (in this case the compounds do not interact at the periphery) (GLENDINNING *et al.* 2000).

From experiments on different caterpillar species it may be concluded that information (as number of spikes per unit of time) from various cells reaching the CNS is here summated algebraically (SCHOONHOVEN & BLOM 1988, SIMMONDS *et al.* 1991). Presumably the cells signalling rejection are connected to a circuit with inhibitory synapses whereas acceptance signals enter circuits with excitatory

synapses. Such a simple model of sensory integration, based on electrophysiological and behavioural data obtained on *Pieris brassicae* larvae (BLOM 1978), appears to explain quite nicely the results of experiments with single chemicals (Fig. 8). When peripheral interactions occur, as commonly observed for mixtures of chemicals or plant saps, the input from different cells will be modified quantitatively, but this will not alter the principle of simple central summation, which still can lead to an appropriate response. In contrast, DE BOER (1993) concludes from behavioural studies employing selective ablations of various sensilla, that feeding on plant material involves a central processing mechanism based on differentially weighting of sensory inputs via different channels, instead of a simple additive procedure. The different opinions are probably due to differences in the methodol-

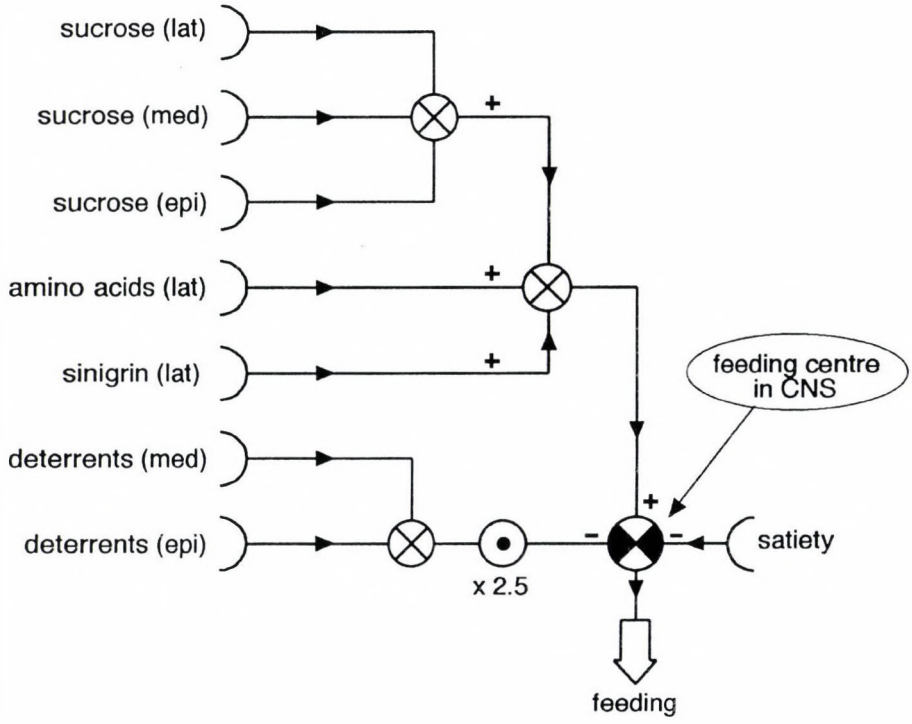

Fig. 8. Model of integration of sensory inputs from taste cells located in the lateral (lat) and medial (med) sensilla styloconica and the epipharyngeal organs (epi) as it might occur in the CNS of *Pieris brassicae* caterpillars. Inputs from the D cells would have negative effects and tend to inhibit feeding. One impulse reaching the CNS from the D cells neutralizes 2.5 impulses originating in one of the phagostimulatory receptors. Satiety has also an inhibitory effect. The balance between negative (inhibitory) and positive (stimulatory) inputs determines whether or not the insect will feed (after SCHOONHOVEN & BLOM 1988)

ogy used. The results from *Pieris brassicae* were based on experiments with single compounds, which are known to stimulate specific cells. The results from *Manduca sexta* were obtained with complex stimuli, i.e., plant material. Conceivably, neural integration depends on a simple arithmetic process, but when additional information via other lines is superimposed on the basic response, the origin of this information becomes important. This would explain the discrepant conclusions reached by BLOM (1978) and DE BOER (1993)

Another approach to unravelling the sensory code starts from impulse patterns evoked by plant saps. A simple comparison of total impulse frequencies in both sensilla styloconica showed that in *Manduca sexta* saps from acceptable plants stimulate the medial sensillum more strongly than the lateral sensillum, in contrast to unacceptable plants, which show a reversed ratio of neural activity (SCHOONHOVEN & DETHIER 1966). A more refined method employing computer techniques was chosen by DETHIER and CRNJAR (1982). These authors detected different temporal patterns in the responses of six receptors when stimulated by three different host-plant species. They suggest that these temporal response characteristics hold additional information for processing by the CNS, and eventual host discrimination.

Food-plant discrimination is submaximal or even absent for some plant combinations after unilateral removal of all chemoreceptors in *Manduca sexta*. DE BOER (1991) deduced from this observation that feeding decisions are based on both quantitative and qualitative aspects of chemosensory input. Unilateral maxillectomy in *Spodoptera exempta* larvae, likewise, produces an intermediate response in length of time before a non-food plant will be accepted, as compared to bilaterally or sham operated insects (MA 1976*b*). Apparently bilateral chemosensory input, rather than representing functional redundancy, provides useful information which is taken into account in the central decision process. The fact that some chemosensory pathways cross over to the contralateral side of the CNS (KENT & HILDEBRAND 1987) may result in the 'feeding centre' in unilaterally ablated insects receiving distorted or incomplete information.

Clearly our insight into the central integration process is still very primitive. It can only be expressed in rather general terms, for instance by saying that insects possess an innate profile of host-plant taste, or by using the metaphor of a 'key-lock' system, in which the key stands for a complex sensory pattern and the lock for an innate profile shaped to only accept neural patterns as elicited by host plants (SCHOONHOVEN 1987). This symbolization is incongruent with the model of simple algebraic summation of impulse frequencies, as this neglects their origins in specific cells. It seems unlikely that information on impulse origin will not be used in central decision processes. Further analysis of total response patterns to

simple mixtures and plant saps, as begun by DETHIER and CRNJAR (1982), in conjunction with behavioural studies, may prove to be a fruitful approach to understanding the mode of operation of the caterpillar's 'feeding centre'.

Discussions on coding in chemosensory systems often focus on three hypothetical codes for the representation of chemical messages sent to the CNS. They are (1) primary tastes exist, (2) taste and smells are represented in an analytical or labelled-line pattern, and (3) taste and smells are represented as a synthetic or across-fibre pattern of neural activity (FRAZIER 1992). It should be realized that these three models are not mutually exclusive and thus may operate within the same gustatory system. From the data presented on taste cells in caterpillars the labelled-line concept is applicable to several identified cell types, e.g., the D cells and sign stimulus cells. However, the coding mode based on across-fibre patterns seems also to operate to some extent in caterpillars and might help to better understand the roles of, for instance, the water and salt cells. Because olfactory cells in *Manduca sexta* larvae have very broad and overlapping response specificities (DETHIER & SCHOONHOVEN 1969, ITAGAKI & HILDEBRAND 1990), here across-fibre patterning must be the operative mechanism.

EVOLUTION

Of all organisms, the insects show the greatest diversity of diets. Among herbivorous species even generalists have marked preferences in diet (BRUES 1946, SCHOONHOVEN *et al.* 1998) and specialists are notorious for the most rigid restrictions. Their feeding habits have evolved amidst an unsurpassed diversity of green plants which harbour, unseen to the human eye, a still vaster diversity of chemicals. This could only happen when the gustatory sense is sufficiently versatile to adapt to the needs of each insect species. Conceivably, differences in food-plant selection between species are based on different central processing principles of invariable sensory inputs, or, alternatively, different feeding habits between species depend on differences in their gustatory systems, each adapted to a particular diet. Both models may also be combined to a third model, which appears to reflect the situation in caterpillars. The sense of taste (and smell), in close interplay with the central processing mechanism, is finely tuned to recognising a specific insect's host plant(s). The decisive role of the CNS is strikingly illustrated in a comparative study of two sister species, *Heliothis virescens*, a generalist feeding on plants from many families, and *H. subflexa*, which is restricted to one plant genus. The differences in diet breadth between the two species could in this case not be attributed to

different properties of their styloconic taste cells and thus must be due to differences in the central processing of sensory input (BERNAYS & CHAPMAN 2000).

The variation in gustatory profiles across species, as exemplified in Table 1, indicates great evolutionary flexibility of the sensory apparatus, which would make it relatively easy for a herbivore to switch to a new food source (provided this is not impeded by other constraints, e.g., nutritional inadequacy). The great inter-individual variation in both sensory responses and behavioural reactions observed under strict standardized experimental conditions, even if this variability is only partly genetic, provides ample opportunity for the evolution of new feeding preferences. The exploitation of new food sources could then result in the development of a new species. There is irrefutable evidence for speciation according to this scenario (MENKEN & ROESSINGH 1998, ROESSINGH *et al.* 1999).

The role of the D cells merits special attention, because host recognition is often primarily determined by the absence of deterrents, as the pioneering studies by JERMY (1958, 1966, 1984) have shown. In silkworms, a classic case of a strictly monophagous insect, mutant strains have been selected with a broader diet than parent lines. The D cell in these strains have lost their sensitivity to some, but not all deterrent compounds tested (ASAOKA 2000). The broad specificity ranges of D cells supposedly depend on the presence at the dendritic membrane of different receptor sites for the perception of different compounds (reviewed in FRAZIER 1992, SCHOONHOVEN *et al.* 1992).

Host-plant switching must be accompanied by a loss of sensitivity of the D cells to compounds which typically occur in the new host plant. This is nicely illustrated in *Yponomeuta rorellus* larvae, which are restricted feeders on *Salix* spp. Their D cells are significantly less sensitive to salicin than those of their sister species. Likewise, *Yponomeuta malinellus*, occurring on *Malus*, is insensitive to the *Malus*-specific compound phloridzin, that stimulates the D cell in eight related *Yponomeuta* species, which reject *Malus* (VAN DRONGELEN 1979). When *Y. cagnagellus* (host: *Euonymus*) was experimentally crossed with *Y. malinellus* (host: *Malus*) the D cells of their offspring showed an intermediate sensitivity to phloridzin (VAN DRONGELEN & VAN LOON 1980).

ASAOKA's (2000) observation of partial insensitivity of the D cell in the silkworm ties in with the demonstration of two excitatory transduction pathways in the D cells of *Manduca sexta* (GLENDINNING & HILLS 1997). In vertebrates, cells responding to bitter substances contain a large repertoire of different taste receptors, linked to gustducin, a G protein implicated in bitter signalling. Some gustducin-linked receptors have also been identified in insect cells (CHANDRASHEKAR *et al.* 2000) and may be operative in the systems just mentioned.

Loss of sensitivity to certain feeding deterrents is one aspect of a change in food-plant preference. Another step is developing a preference for a host-plant compound that usually acts as a deterrent (Fig. 9). Glucosinolates present a well-defined example. These compounds are general feeding deterrents to many insects which do not feed on cruciferous plants. Some polyphagous species which do feed on e.g., cabbage have deterrent cells which respond to sinigrin, but in the presence of sucrose and inositol these cells may be sufficiently inhibited to allow the insect to unreservedly feed on this plant (SHIELDS & MITCHELL 1995). In insects specialized on crucifers the D cell has become fully unresponsive to glucosinolates. Instead separate cells are now sensitive to these host-plant specific chemicals (SCHOONHOVEN 1967). Were the latter cells at one time D cells whose input in the CNS underwent a sign transformation at the synaptic level? Or did "loose receptor sites" (TALLAMY *et al.* 1999) on glucose-sensitive cells begin to accept glucosinolates as novel stimuli? With respect to the possibility of central nervous sign transformation, changes at the integrative level are known to occur. There is a silkworm strain that has normally functioning D cells, but nevertheless exhibits an expanded food-plant range (ISHIKAWA *et al.* 1963). There is no *a priori*

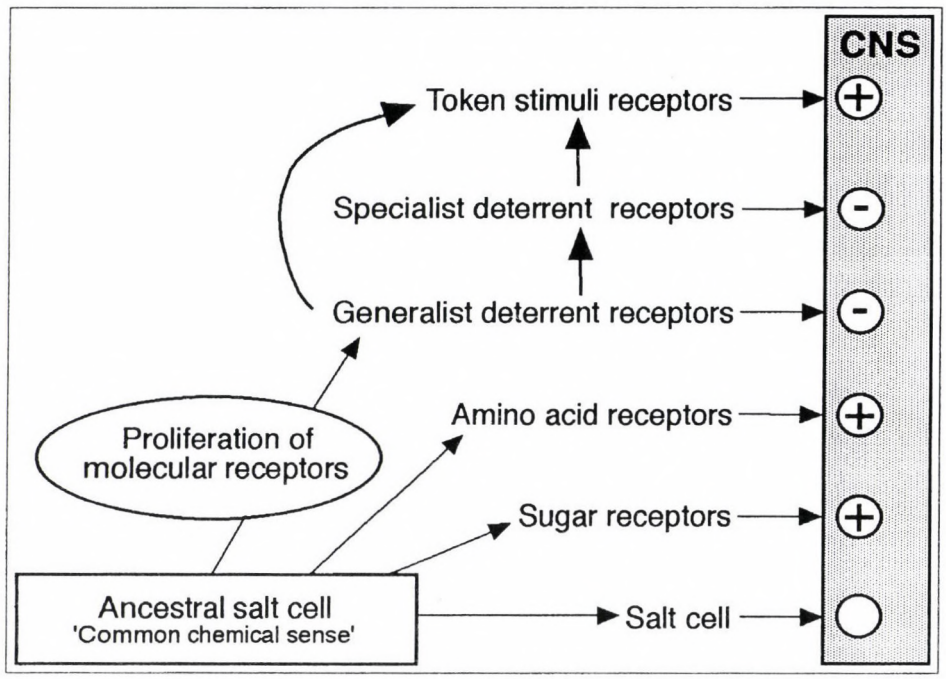

Fig. 9. Evolution of gustatory receptors in specialist herbivores

reason to expect that changes in the central processing mechanism are more difficult to realize than peripheral changes.

JERMY, in a thought-provoking review, stresses the prime role of heritable changes of chemoreceptors in insect evolution. He points out that evolution of host-plant specialization is not primarily due to ecological selective forces, but rather to a behavioural change governed by the insect's ability to recognise new potential food plants as a result of mutations (*sensu lato*) that change the function of an insect's sensory system. Only then selection starts and the new genotype may become successful if it can tolerate the many ecological and physiological constraints to which it will be subjected (JERMY 1993). The importance of this type of evolutionary mechanisms may once more be stressed by citing the concluding sentences of BERNAYS and CHAPMAN's book on host-plant selection by phytophagous insects (1994, p. 284): "The evolution of behavioral patterns is an evolution of properties of the nervous system. The precise details of how insects perceive the plant world, how they channel and integrate information, and finally how they behave in response to the information, will provide the details necessary to develop ideas further on how the behavior of host-plant choice in insects may have evolved."

CONCLUSIONS AND FUTURE DIRECTIONS

Lepidopterous larvae with their relatively simple gustatory sense offer an ideal system to analyse peripheral and central mechanisms governing feeding behaviour. Considering the bilateral eight-neuron taste system it is striking that subtle taste discrimination, evidently present in many caterpillar species, is allowed by so few cells. The lateral and medial sensilla have similar functionalities but yet show differentiation in their specificity ranges for both stimulant and deterrent receptors. In only few cases have the consequences for discrimination capacity been studied in detail (VAN LOON & SCHOONHOVEN 1999). Here we focussed on the maxillary sensilla styloconica, but it must be stressed that maxillary palp receptors as well as epipharyngeal sensilla undoubtedly contribute to even more subtle discrimination power (DE BOER & HANSON 1987, DE BOER 1993, GLENDINNING *et al.* 1998, VAN LOON unpubl.). The striking diversity of taste cell types, reflecting a great adaptability to the many plant substances nature offers, forms a crucial aspect of the role of herbivorous insects in terrestrial ecosystems.

The multitude of plant compounds acting as deterrents and recognised by JERMY (*in litt.*) as pivotal in many insect-plant interactions, stimulate some taste cells with broad, though well-defined specificity ranges. A molecular analysis of

their receptor sites is within sight, which aims at clarifying how these cells practise their impressive chemosensory repertoire, as is now being made in *Caenorhabditis elegans*, a nematode which with 20–30 chemosensory neurons can detect hundreds of chemicals (TROEMEL 1999).

Although the sense of taste in caterpillars has been studied during the past 40 years by just a few research groups, a clear picture has emerged, as the information presented in this paper shows. Of course intriguing and important questions remain to be solved. For instance, it is difficult to understand why inositol receptors receive the conspicuous position exhibited in most caterpillar species. These cells, from which recording is usually remarkably easy, merit further attention. Deterrent cells, in view of their clear-cut role in preference and rejection behaviour, are also most interesting elements of caterpillar taste systems. A comparative study on sensitivity thresholds in phylogenetically related monophagous and polyphagous species could answer the question whether diet breadth is related to receptor sensitivity (cf. Table 9) or depends on central decision-making processes in food-plant acceptance behaviour. Deciphering sensory codes from recordings of stimulations with plant saps is another line of research which will shed light on the mechanism of food selection behaviour; if the caterpillar brain can decode the sensory message, our computers should be able to do it as well.

The beguiling simplicity of chemoreception in caterpillars shrouds a captivating complexity of receptor diversity, neural interactions, temporal characteristics, and peripheral memory. The rich harvest of some decades of research opens exciting vistas on behavioural analysis in an ecological and evolutionary context, as well as on the molecular basis of the most universal sense in animals: chemoreception.

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SENSORY BASIS OF HOST-PLANT SELECTION: IN SEARCH OF THE "FINGERPRINTS" RELATED TO OVIPOSITION OF THE CABBAGE ROOT FLY

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The oviposition preference of the cabbage root fly, *Delia radicum* (Diptera, Anthomyiidae), was studied using leaf surface extracts of 24 different plant species that covered the whole span of preference rankings. The oviposition data were related to the content of the extract fractions containing either the glucosinolates or CIF ("cabbage identification factor", 1,2-dihydro-3-thia-4,10,10b-triaza-cyclopenta[.a.]fluorene-1-carboxylic acid). We observed a significant correlation between oviposition preference and the leaf surface content of benzyl and indolyl glucosinolates, substances that belong to the most active stimulants in oviposition assays, and in electrophysiological recordings from the tarsal $D_{4,3}$-sensilla. However, there was not a significant correlation between the extract fraction containing CIF and the recorded neural activity in the tarsal C_5-sensillum containing the CIF sensitive neuron. When this lack of correlation was investigated it was revealed that the leaf surfaces of two unacceptable host plants, *Capsella bursa-pastoris* and *Tropaeolum majus*, contain inhibitory compounds. Our data strongly support the hypothesis put forward by T. JERMY that "fingerprints" (specific mixtures of stimulatory and inhibitory plant compounds) mediate host-plant selection.

Key words: Cruciferae, leaf surface, glucosinolates, 1,2-dihydro-3-thia-4,10,10b-triaza-cyclopenta[.a.]fluorene-1-carboxylic acid (CIF1), tarsal contact chemoreceptor sensilla, inhibitors

INTRODUCTION

In his discussion of the evolution of insect/host-plant relationships JERMY (1984) hypothesised that the main role of secondary plant substances in insect/host relationships is to form the 'fingerprint', the specific pattern or biochemical profile by which the insect recognises the plants. This statement is based on the postulate that "Host plant specificity in phytophagous insects is determined mainly by the botanical distribution of plant substances ..." (JERMY 1983). In the same paper, JERMY also stresses the importance of plant compounds that inhibit feeding or oviposition.

In recent years we were able to isolate and identify compounds from the leaf surface of *Brassica oleracea*, one of the major cultivated host plants that elicit oviposition by the cabbage root fly, *Delia radicum* (ROESSINGH *et al.* 1992, HURTER *et al.* 1999, DE JONG *et al.* 2000). Further, BAUR *et al.* (1996) found that

the content of the so-called CIF compounds ("cabbage identification factor"; 1,2-dihydro-3-thia-4,10,10b-triaza-cyclopenta[.a.]fluorene-1-carboxylic acid; Fig. 1) in four *Brassica* species is related to the oviposition preference of the cabbage root fly. However, *Brassica* species are not the only host plants for this fly. As shown by FINCH and ACKLEY (1977) many different wild crucifers and related plants are attacked. In endeavouring to correlate the observed preference of the fly with the presence or absence of quantifiable oviposition stimulants we had an opportunity to test JERMY's hypotheses concerning the role of secondary plant metabolites in host-plant selection of herbivorous insects.

MATERIALS AND METHODS

Oviposition behaviour

Insects: These tests were performed using *Delia radicum* from our continuous laboratory culture (restarted with field-collected maggots in 1996) and surrogate leaves treated with leaf surface extracts of the selected plants, as previously described by ROESSINGH *et al.* (1992). In each cage (70×70×70 cm) about 100 mature female flies and an equal number of males were kept at 21°C, 80% r.h., and LD 16:8h. The flies had access to a source of water, 10% sugar water on filter paper and a mixture of raw cane sugar, yeast hydrolysate, and water (4:1:1) applied on absorbent tissue strips.

Oviposition choice assay: The choice assays were performed in three separate, partially overlapping sets of 12 extract surrogate leaves and each set was replicated at least 7 times. After counting the eggs, the position of each treatment was re-randomised within the cages. *Brassica oleracea* convar. *botrytis* "CC-Cross" at two concentrations, 1.25 gle (gram leaf equivalent) and 0.125 gle and a control (methanol) were included as standards in all 3 sets. All the other extracts were applied at only one concentration of 1 gle. In all three sets of extracts bioassayed, one preferred host plant, one poor host plant and a non-host plant (*Allium porrum*) were included. This procedure resulted in 7–25 individual egg counts per plant species. For each treatment, the percentage of the total number of eggs laid on the date of counting was calculated; these percentages were averaged and correlated with other measurements using the non-parametric Spearman rank correlation test (corrected for ties if necessary).

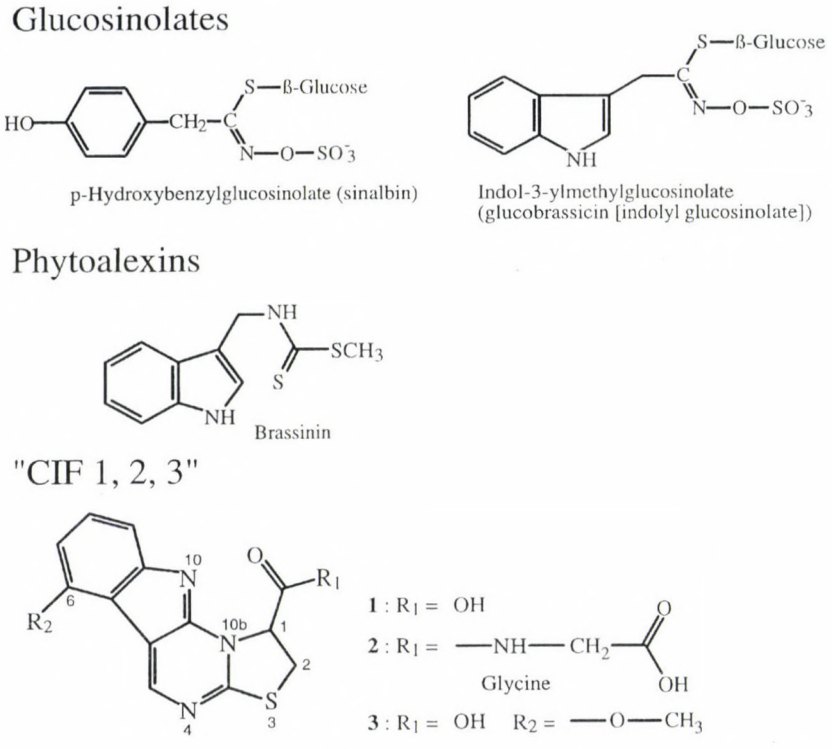
No-choice oviposition assay: We utilised the same acrylic cages (50×50×50 cm) that were used by KOSTÁL *et al.* (2000). The surrogates, extracts, water, and food source were the same as used in the choice experiments and in the rearing cages. One surrogate plant was installed per cage and the eggs were counted daily from day 5 to 12 following emergence. Leaf surface extracts of *Brassica oleracea* (CC cross), *Capsella bursa-pastoris*, *Iberis amara*, *Raphanus raphanistrum*, *Sisymbrium officinale*, and *Tropaeolum majus* were tested in 3 independent repetitions with 35, 24 and 30 females and about 20 males per cage. The daily counts were divided by the number of live females and averaged. The average number of eggs were correlated to the other measures using the Spearman rank correlation test.

Inhibitory (deterrency) assays: The inhibitory effect of leaf surface extracts was tested in an oviposition choice test with three types of treatment applied on surrogate leaves: leaf extract (1.25 gle/leaf), pure sinigrin (Roth, Karlsruhe) at 1 µmol/leaf (397 µg/leaf), and a mixture of the extract and

sinigrin with each at the same concentration as in the single treatments (1.25 gle extract and 1 µmol sinigrin). Each treatment was repeated three times per cage (total of 9 surrogate leaves). After counting the eggs on four consecutive days the position of the leaves was re-randomised within the cage. The egg counts of each day were, as with the preference tests, converted into percentages and averaged. The extract treatment was compared with pure sinigrin or the mixture using the Mann-Whitney test.

Electrophysiology

Tip recordings from the tarsal C_5- sensillum of female flies were obtained using the same technique and set up as described recently by DE JONG *et al.* (2000). All the nerve impulses (spikes) recorded were counted in the first second after contact of the recording electrode with the tip of the sensillum using our spike train analysis software (STA). No attempt was made to discriminate between different spikes because we recorded mostly spikes of one shape. We investigated a total of 26 sensilla, from which we excluded those six preparations that gave < 40 spikes in the first second of stimulation with 10 ng/ml CIF1. The number of spikes recorded from each C_5-sensilla is expressed as percent of the response to 10 ng/ml CIF 1 (= 100 %) for each of the 20 sensilla.



1: 1,2-Dihydro-3-thia-4,10,10b-triaza-cyclopenta[.a.]fluorene-1-carboxylic acid

Fig. 1. Chemical formulas of a benzyl and an indolyl glucosinolate, a crucifer phytoalexin, and CIF 1, 2, 3

Plants

All the seeds of the wild plants (Capparidaceae, Cruciferae, Resedaceae, Tropaeolaceae) were obtained from the botanical garden of the University of Zürich. The seeds of cultivated plants were from the Federal Research Station Wädenswil: *Allium porrum* (convar. "ZEFA") and Zürich – Reckenholz: *Brassica napus* (var. "Eurol", winter cultivar with seeds low in erucic acid and glucosinolates) and *Brassica rapa* (convar. "Hanko"). *Brassica oleracea* var. botrytis (convar. "CC-Cross") was purchased from a local seed distributor.

Larval performance

We attempted to relate our oviposition data with the performance of the cabbage root fly larvae on the roots of the plants tested. To this end we used the published data of FINCH and ACKLEY (1977). These investigators inoculated 83 species of Cruciferae with cabbage root fly eggs in a glasshouse to determine which species could support the larvae. For each plant the number of pupae was recorded and we used these values as a measure of larval performance.

Chemical extraction and analysis

We used the same extraction procedure as described by STÄDLER and ROESSINGH (1991) and BAUR *et al.* (1996) to obtain wax-free methanolic leaf-surface extracts. These extracts were used in all the oviposition assays. The glucosinolate fraction of the extracts was separated from the fraction containing the CIF (DE JONG *et al.* 2000) compounds using an ion exchange chromatographic separation technique at atmospheric pressure. This method was developed and tested by BAUR *et al.* (1996) using *Brassica* genotypes. The glucosinolates were analysed qualitatively and quantitatively recently by GRIFFITHS *et al.* (2001). These analytical data are used in the present paper for the correlation with oviposition and sensory data.

RESULTS

Oviposition choice assays

The ranking in oviposition preference is presented in Figure 2 and summarised in Table1. The data show dramatic differences between the different plant extracts. *Sisymbrium officinale*, a wild crucifer, was the most preferred. *Brassica rapa* (kale-rape), a cultivated host plant, was only third but still in the most attractive group. These oviposition preferences correlated well (Spearman rank correlation Rho=0.644, p=0.020; Table 1) with the data on larval performance (number of pupae produced by the inoculated eggs) in the same plant species (FINCH & ACKLEY 1977). Thus, the females showed an overall preference for extracts from plants, which supported good development of the larvae on the roots. It appeared moreover that for the flies the plant extracts used were truly representative of the leaves of the plants tested.

Table 1. Summary of choice assays in response to plant extracts

	Family	Mean % eggs[1]	% CIF[2]	% pupae[3]
Readily accepted hosts				
Sisymbrium officinale	Cruciferae	74.0(8)	68.3	20
Barbarea vulgaris	Cruciferae	44.0(7)	38.5	32
Brassica rapa silvestris 'Hanko'	Cruciferae	33.0(7)	80.6	26
Lepidium campestre	Cruciferae	20.1(10)	20.9	–
Raphanus raphanistrum	Cruciferae	11.0(18)	51.1	32
Lepidium sativum	Cruciferae	8.1(10)	17.6	–
Sinapis arvensis	Cruciferae	7.8(18)	45.5	9
Brassica oleracea botrytis 'CC-Cross'	Cruciferae	7.1(25)	–	38
Brassica napus 'Eurol'	Cruciferae	6.5(7)	95.8	33
Cochlearia officinalis	Cruciferae	6.1(18)	34.8	32
Poor crucifer hosts				
Isatis tinctoria	Cruciferae	4.4(10)	37.2	0
Alyssum saxatile 'Gold Dust'	Cruciferae	4.0(7)	22.3	0
Iberis amara	Cruciferae	2.9(18)	–	0
Erysimum cheiranthoides	Cruciferae	2.2(10)	–	0
Brassica oleracea acephala 'Fribor'	Cruciferae	1.7(7)	–	–
Rorippa silvestris	Cruciferae	1.3(8)	47.1	–
Thlaspi arvense	Cruciferae	1.3(7)	68.8	–
Rorippa islandica	Cruciferae	0.9(8)	63.3	–
Crucifer non-host				
Capsella bursa-pastoris	Cruciferae	0.4(17)	34.5	0
Readily accepted non-crucifer hosts				
Cleome spinosa	Capparidaceae	5.9(7)	105.0	–
Poor non-crucifer hosts				
Reseda luteola	Resedaceae	2.0(8)	40.6	6
Non-crucifer non-hosts				
Tropaeolum majus	Tropaeolaceae	0.1(7)	32.9	–
Allium porrum	Liliaceae	0.1(8)	20.3	–
MeOH	–	0.3(25)	5.7	–

[1]The number of repetitions are in parentheses

[2]Mean CIF spikes (N= 20) stimulated by CIF fraction of plant extracts in percentage of 10 ng CIF1 / ml

[3]Mean pupal production angular transformation of % of eggs producing pupae (FINCH & ACKLEY 1977)

GRIFFITHS *et al.* (2001) has compared oviposition preference with analytical data on the glucosinolate fraction of the leaf surface extracts of the 19 plants shown in Figure 2. The amounts of 28 individual glucosinolates were determined, clustered according to the functional groups of the side chains (Fig. 1), and correlated with the mean percent oviposition preference. For the combined content of benzyl and indolyl glucosinolates, this correlation was clearly significant (Fig. 2: Rho=0.520; p=0.023), but not for the aliphatic glucosinolates (p=0.9) nor the glucosinolates with an additional sulphur molecule (methylthio; sulphonyl (p=0.13).

Contrary to our expectations, these oviposition data appeared to be unrelated to responses of the chemosensory neuron sensitive to CIF. This is illustrated in Figure 2 which shows that spike activity did not significantly correlate with oviposition preference (Rho=0.23, p=0.3). The high CIF activity of *Brassica napus*,

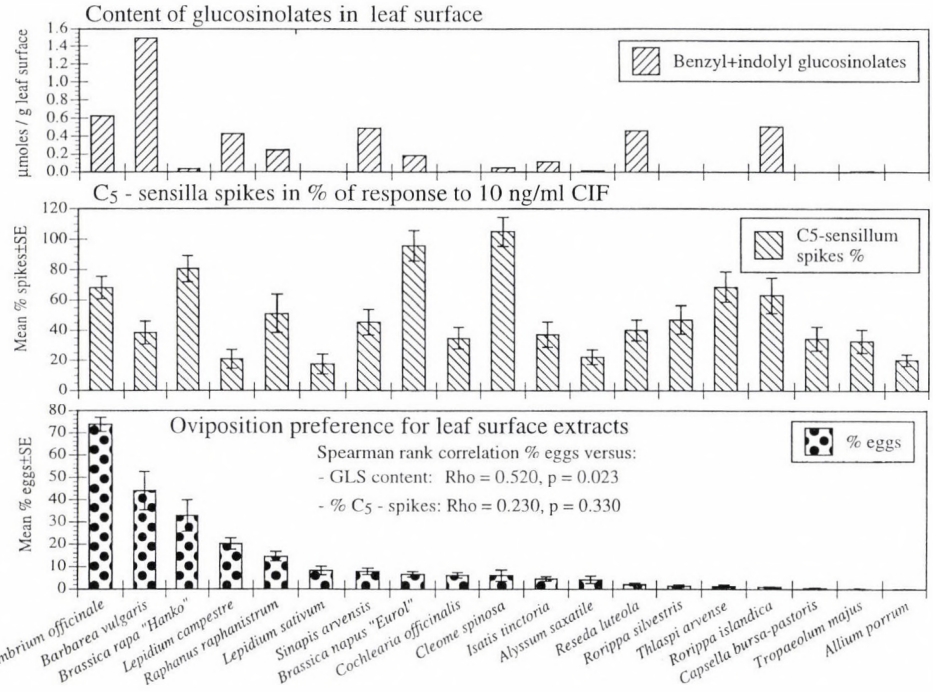


Fig. 2. Oviposition choice experiments related to analytical data of leaf surface extracts of 19 plants of the Capparidaceae, Cruciferae, Resedaceae, Tropaeolaceae and Liliaceae. The contents of the glucosinolates are derived from the data of GRIFFITHS *et al.* (2001). The spikes recorded from the C_5 sensilla are relative to (% of) the response to 10 ng/ml CIF 1 of the same sensilla. Oviposition preference is presented as % of total egg counts on 12 surrogate plants

Cleome spinosa, *Thlaspi arvense*, and *Rorippa islandica,* combined with their low oviposition preference value, were largely responsible for the low correlation. These plants were, by chance, excluded by the FINCH and ACKLEY's study (1977) (Table 1) on larval success, and therefore it is not surprising that their data correlated significantly with the CIF chemosensory response for the 12 plants that overlapped the two studies (Rho=0.615, p=0.043; Table 1).

Oviposition no-choice assays

Choice experiments can be problematic because the ranking is based on the selection of plants offered. We therefore performed no-choice experiments for several plants spanning the total range of stimulatory effectiveness in the choice

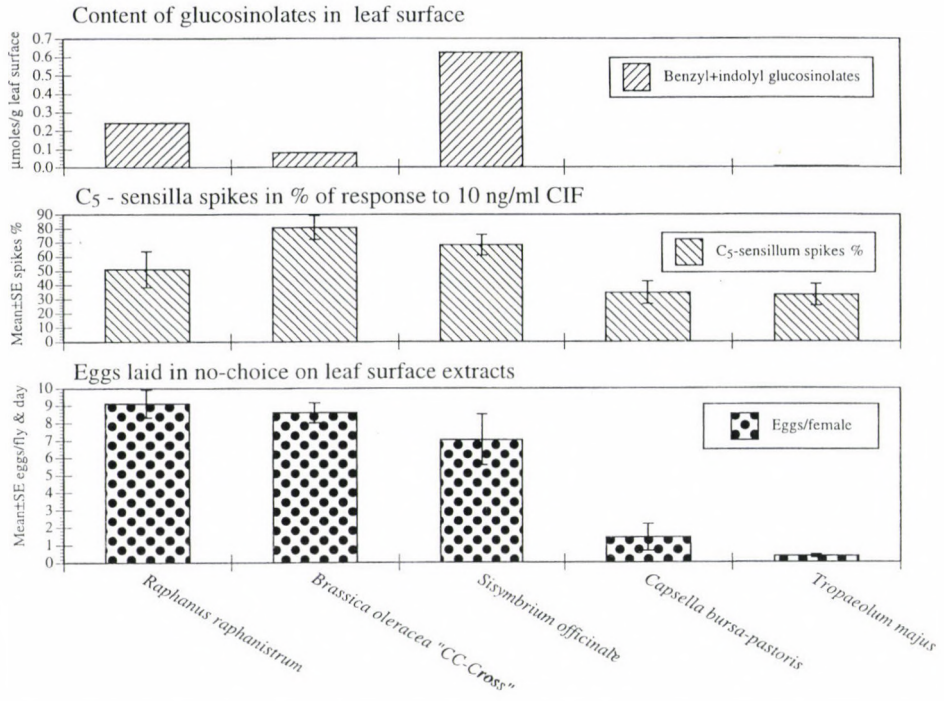


Fig. 3. Oviposition no-choice experiments related to analytical data of leaf surface extracts of and sensory responses to 5 selected plants. The analytical glucosinolate data for *B. oleracea* were derived from the data of ROESSINGH *et al.* (1992). The spikes were recorded from C_5 sensilla in response to the indicated plants, except that the data shown for *Brassica oleracea* CC-Cross were derived from those of *Brassica napus* as we had no data from the former. (These two plants are according to the results of DE JONG *et al.* 2000 equally attractive for the flies and both contain substantial amounts of CIF)

experiments. The data confirm in principle the choice experiment in the sense that the highly preferred plant extracts yielded many more eggs per female than the rarely chosen plant extracts (Fig. 3). Remarkable about the daily egg counts was the uniformity of the data. We observed no obvious difference in the ranking of egg production between the different days up to day 12 when the experiment ended. The wild crucifer *Sisymbrium officinale* was again a very stimulatory plant extract, but it was not significantly different from the other preferred plants, wild radish (*Raphanus raphanistrum*) and cauliflower (*Brassica oleracea*). Neither shepherd's purse (*Capsella bursa-pastoris*) nor *Tropaeolum majus*, two relatively unacceptable plants, were very stimulatory in the no-choice situation.

The comparison between the number of eggs, the plant content of glucosinolates, and "CIF spikes" shows clearly that the three most stimulatory plants contained more glucosinolates and stimulated more spikes in the C_5-sensillum than average. The Spearman rank correlations between the eggs per female and the CIF spike activity was relatively high (Rho=0.700, p=0.1615). The same was true for the benzyl- plus indolyl-glucosinolates (Rho=0.600, p=0.2301), but due to the smaller number of plants (N=5) tested, and a not perfect fit in the ranking, these correlation tests were not significant.

Inhibitory compounds

The data in Figure 2 and 3 show that the extracts of some plants that were not preferred (e.g., *Rorippa islandica*) did contain measurable amounts of glucosinolates or stimulated the receptor neurons in the C_5-sensillum. Thus it is surprising that they did not stimulate oviposition. A possible explanation for the weak effect of the total extract might be the occurrence of inhibitory (repellent or deterrent in the sense of DETHIER *et al.* 1960) compounds. To determine if this was the case, extracts were mixed with sinigrin, a commercially available glucosinolate that acts as a moderate stimulant for the cabbage root fly (ROESSINGH *et al.* 1992). The mixture was given in a choice experiment with pure sinigrin and the extract alone.

In the tests of two plants (*Capsella* and *Tropaeolum*) sinigrin alone was more stimulating than the extract mixed with sinigrin. The results in Figure 4 clearly demonstrate that these extracts contained one or several compounds that inhibited the stimulatory effect of the glucosinolate sinigrin. The females preferred, as expected, the mixtures to the extract alone in both plants, although in the case of *Tropaeolum* not significantly. In the case of *Erysimum cheiranthoides* (not shown in Figure 2, due to lack of analytical data) and *Rorippa islandica* no significant signs of an inhibitory effect of the extract were noted. The extract of *Iberis amara* (also not shown in Fig. 2) was in the oviposition choice experiments about as ac-

tive as *Brassica oleracea* at a tenth of its normal concentration (0.1 gle). In the experiment giving rise to Figure 4, the *Iberis* extract was significantly more stimulatory than a) the mixture with sinigrin and b) sinigrin alone. The finding b) might be the result of stimulatory activity of an additional compound(s) in the extract. The reason why the mixture with sinigrin a) was less stimulatory than the extract remains unexplained.

DISCUSSION

Comparison with field data

The ranking of plant extracts in oviposition choice was similar to the developmental data (pupae produced around the roots) of FINCH and ACKLEY (1977). Of course, there were some exceptions and this is not surprising because plant susceptibility or the attractiveness for the cabbage root fly depends on many factors, such as the plant varieties used, the plant growth conditions and age, and probably even on the genetics of the flies used. In our study all these conditions were different from those of FINCH and ACKLEY (1977). One surprising finding was that the species *Sisymbrium officinale* that yielded the most attractive extract in our study

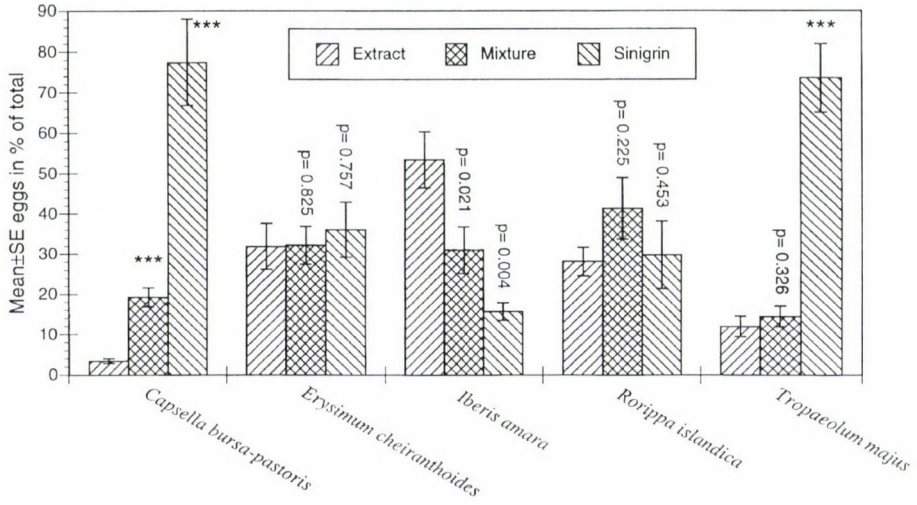


Fig. 4. Oviposition preference for surrogate leaves treated with either leaf surface extract (1.25gle), pure 1 µmol of sinigrin or a mixture of the extract and the sinigrin solution with each at the same concentration as in the single treatments. The p values shown were derived from the Mann-Whitney test for the difference to the extract treatment. *** p = 0.001

was clearly not the best host plant in the comparison of FINCH and ACKLEY (1977). Oil seed rape (*Brassica napus*) was in our choice tests an acceptable, although not one of the best host plants. There is the possibility that this was due to the type of cultivar chosen ("Eurol") a "double low" cultivar containing very little glucosinolate in the pods. The field studies of SKINNER and FINCH (1988) and of DOSDALL *et al.* (2000) confirm that oilseed rape (both *B. napus* and *B. rapa*) is susceptible to infestations by the cabbage root fly and can be damaged severely. Also in agreement with our results are the oviposition preference data obtained by DOANE and CHAPMAN (1962) in the field. These authors compared *Brassica napus* (*napobrassica*) (rutabaga), *B. rapa* (turnip), *B. nigra* (black mustard), *B. oleracea* (cauliflower), and *Raphanus sativus* (radish) and reported that *Brassica napus* and *B. rapa* consistently received the most eggs when counted on five dates during the growth period.

Another interesting comparison can be drawn from the work by NAIR *et al.* (1973), who studied oviposition and development of the cabbage root fly on 13 cruciferous weeds. These data were only partially derived from the same species that we used in our experiments. It is remarkable however, that the wild crucifer *Barbarea vulgaris*, in agreement with our study, was also very attractive and yielded many pupae. It was also more attractive than the rutabaga tested. Thus it seems safe to conclude that the surrogate treated with extracts, as used in our experiments, produced preferences very similar to those elicited by real plants. This would in turn validate the results of the comparable investigation of *Brassica* genotypes carried out by BAUR *et al.* (1996).

Comparison choice versus no-choice

Plants or extracts offered in a choice assay influence the relative preference (for detailed discussion of design problems see SINGER 1986). We tried therefore to take this into account by using multiple sets with plants varying in attractiveness based on the published data on the fly's performance (production of pupae by FINCH & ACKLEY 1977; plant resistance and oviposition by DOANE & CHAPMAN 1962). Our results show that no-choice experiments can supplement multiple choice tests very effectively but can not replace them because in an "emergency" the fly might oviposit on non-attractive plants ZOHREN (1968).

Glucosinolates

Although glucosinolates are less stimulatory than the CIFs of comparable doses (ROESSINGH *et al.* 1992, 1997), the present results show that this class of

compounds seems to have a significant influence on the host-plant choice of *Delia radicum*. In our study only the content of benzyl and indolyl GLS (Fig. 1) correlated significantly with oviposition choice. These same compounds are also the most active in eliciting oviposition behaviour as well as in electrophysiological assays (tarsal D4,3-sensilla) (ROESSINGH *et al.* 1992).

Some glucosinolate studies did not find a correlation with oviposition. For example, NAIR *et al.* (1976) tested six cruciferous plant species and found that the total glucosinolate concentrations in the leaves did not correlate with the oviposition response of cabbage root flies. The authors suggested that the presence or absence of plant inhibitors might explain the lack of correlation between glucosinolates and oviposition. It is not clear whether there was no correlation due to the role of inhibitors or because the authors determined only the total content of glucosinolates and did not consider the different functional groups. In our view the latter reason may well be relevant since we also found a much less significant correlation between the total glucosinolates than between specific groups of glucosinolates and oviposition preference. Thus at least for *Delia radicum*, it is necessary to differentiate individual glucosinolates, as we have recently reported (GRIFFITHS *et al.* 2001).

ELLIS *et al.* (1980) analysed the relationship between egg-laying and the amount of specific glucosinolates in radish (*Raphanus sativus*) populations with variable resistance to the maggots. Oviposition was significantly correlated with total amounts of 4-methylthio-3-butenyl isothiocyanate and 1-cyano-4-methylthio-3-butene (the hydrolysis products of glucoerucin respectively glucodehydroerucin) when tested on 6 dates after sowing. These compounds are methylthio glucosinolates that were in our data set only loosely correlated (Rho=0.340; p=0.1285) with oviposition preference. This does not, however contradict our results first of all because the authors compared genotypes within a plant species, *Raphanus sativus*, at different ages whereas we investigated differences between species and genera. Secondly, our choice of plants included only wild radish, *Raphanus raphinistrum*, and no cultivated varieties, as studied by ELLIS *et al.* (1980).

Glucosinolate concentrations can be manipulated by the selection of varieties. For example, special breeding programs produce pods and seeds of oilseed rape cultivars that vary strongly in glucosinolate content. It is quite possible that the relatively low preference for the variety "Eurol" of *Brassica napus* was caused by its low glucosinolate content of its leaf surface. But this need not be so: FIELDSEND and MILFORD (1994) found that other "double low" oilseed rape cultivars have low glucosinolate contents mainly in the floral tissue and pods,

whereas the leaves can have glucosinolate contents as high as the "single low" cultivars.

As reviewed recently by MOYES *et al.* (2000) and NIELSEN *et al.* (2001) correlations between glucosinolate contents and herbivore preference have been found also in some other insect and mollusc species. MOYES *et al.* (2000) examined the patterns of herbivory and the glucosinolate profiles of individual wild *Brassica oleracea* plants of different populations and habitats of the Dorset coast. A range of glucosinolate profiles were determined and the data were related to the proportion of damage by different herbivores. In the case of one specialist herbivore, *Selania leplastriana* (Tortricidae, Olethreutinae), the attacked plants contained significantly higher levels of 2-hydroxy-3-butenylglucosinolate and 3-indolylmethylglucosinolate than the uninfested plants. In relation to our study, it is remarkable that the preference of this moth species was also related to the indolyl glucosinolates. But, MOYES *et al.* (2000) found no significant influence of the different glucosinolates on the choice of the other herbivores observed (*Pieris* spp., slugs, snails, flea beetles, aphids).

NIELSEN *et al.* (2001) compared wild with transgenic *Arabidopsis thaliana* plants that, due to the introduced gene, contained sinalbin, which is not found in this plant in nature but is highly stimulatory when presented alone. Despite the four-fold increase in content of this glucosinolate, the tested flea beetles (*Phyllotreta* spp.) did not discriminate between transgenic and wild-type plants. In contrast to our study the effect of the glucosinolates was studied in plants of the same species. It might be that changes in stimulus concentration are less important for the intra-species than the inter-species and inter-genera discrimination.

CIF

In view of our earlier results (BAUR *et al.* 1996) with *Brassica* genotypes we expected a significant correlation between the oviposition choice data and the CIF content, estimated with the electrophysiological recordings from the C_5-sensillum. Several reasons can be put forward to account for the lack of a clear correlation: 1) The fractionation of plant extracts, other than those of *Brassica* might have been incomplete. Thus some CIF may have partitioned differently and not been tested. Also, some of the glucosinolates may have separated with the CIF fraction. Since the C_5-sensillum contains a chemoreceptor neuron that was shown to be sensitive to glucosinolates (ROESSINGH *et al.* 1997), CIF estimations may consequently have been too high. 2) Other compounds possibly stimulate the CIF sensitive neuron or another neuron with similarly shaped nerve impulses. Signs of this are the relatively high spike counts in responses to non-crucifers, such as *Allium porrum*

that most likely do not contain CIF, but elicited a spike activity (per 1st second, mean±SE: 21±4.4) that was significantly higher than in the control (KCl 10 mM: 5±1.8). This indicates that in the leek extract, and probably also in extracts from other plants, unidentified compounds are present that stimulate receptor cells in the C_5-sensillum. 3) Other substances not yet identified, volatile (DE JONG & STÄDLER 1999) or non-volatile compounds, could have affected the oviposition behaviour as well. Finally 4) the CIF fraction should have contained no glucosinolates, but certainly it did include many other plant compounds that could interact with the four receptor neurons that are present in the C_5-sensillum (ISIDORO *et al.* 1994). These interactions could lead to an increase or reduction of the spike activity of the stimulated cell(s). Several authors have observed such interactions between compounds acting in the same sensillum. SCHOONHOVEN and JERMY (1977) discovered a negative interaction of a secondary plant metabolite (strychnine) on a sucrose sensitive receptor neuron. Positive interactions have been observed less frequently, but they also exist: DETHIER and KUCH (1971) found that the contact chemoreceptor neurons of phytophagous caterpillars show signs of synergism nearly as often as inhibition. Thus, it seems likely that the response of the mostly active CIF receptor neuron to the CIF fraction of the plant extracts could have been influenced in different ways by other compounds present in the extract. In conclusion, our recordings from the C_5-sensillum of the cabbage root fly have to be interpreted with caution. The obvious resolution to these uncertainties would be a chemical analysis of the CIF fraction of each plant extract. Although this would in principle be possible using HPLC-MS, according to the unpublished results of GRIFFITHS *et al.*, the method is not reliably repeatable across plant species due to technical difficulties caused by interactions with unknown components of the plant extracts tested.

Inhibitors

As concluded from the experiments summarised in Figure 4 *Capsella bursa-pastoris* and *Tropaeolum majus* do indeed contain compounds inhibiting oviposition. This would explain why these plants are not very stimulatory in the oviposition assays despite their relatively high CIF activity. The finding is yet another example of inhibitory compounds from both host and non-host plants that can reduce oviposition or feeding responses. We have not yet identified the compounds but as the studies by RENWICK and colleagues show, different crucifers may contain inhibitory compounds that can affect crucifer specialist insects like *Pieris rapae* (RENWICK 1996). Identical or similar compounds might also be involved in the cabbage root fly – plant relationship. The general importance of in-

hibitors in host-plant selection has long ago been postulated by JERMY (1966, 1983, 1984) and our study adds further weight to his conclusion.

Patterns of compounds

The unexpected stimulatory effect of *Iberis amara* extracts (Fig. 4) is in need of an explanation. The presence of additional stimulants in this extract might account for the fact that the mixture of extract and sinigrin was more stimulating than sinigrin alone. But it is difficult to understand why the extract alone is significantly more stimulatory than the mixture with sinigrin. One explanation might be that the stimulatory component in the extract was active as part of a pattern and that adding sinigrin might change this pattern so that it became less attractive. An example suggestive of an insect able to discriminate between different glucosinolates is the adult small white butterfly, *Pieris rapae* which has two separate receptor neurons distinct in their sensitivity to specific glucosinolates (STÄDLER *et al.* 1995). The combined activity of the two neurons produces a pattern that correlates with the observed behavioural response of the butterflies to individual glucosinolates. Perhaps adding a glucosinolate that is not highly stimulatory, such as sinigrin, could change this response pattern sufficiently to reduce the behavioural response to a plant extract. This would also be in line with the conclusion of NIELSEN *et al.* (2001) that special emphasis should be given on the effect of variations in glucosinolate profiles as well as on other plant factors that modulate insect responses.

The pattern recognition hypothesis may also apply to the cabbage root fly. A variety of phytochemicals are cues for the fly to find and oviposit on a host plant. We know that compounds of different volatility (DE JONG & STÄDLER 1999) and chemical identity, such as the glucosinolates, the CIFs and the phytoalexins (Fig. 1) (BAUR *et al.* 1998), are active stimulants. In the present study, the three preferred hosts tested in the no-choice assay contain greater amounts of both CIF and indolyl glucosinolates, suggesting that multiple chemical stimuli are important in eliciting accurate oviposition. We conclude, therefore, that the results of our study on host-plant selection by the cabbage root fly underscores the conclusion reached by TIBOR JERMY that secondary plant substances form specific patterns, or 'fingerprints', which mediate the insect/host relationships of herbivorous insects (JERMY 1983, 1984).

*

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INDUCTION OF FEEDING PREFERENCE IN LARVAE OF THE PATCH BUTTERFLY, CHLOSYNE LACINIA

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Induction of preference, a phenomenon first described by TIBOR JERMY, was demonstrated in larvae of the patch butterfly, *Chlosyne lacinia*. Using choice tests pioneered by JERMY (the "disc test") to assay preferences, a strong induction was shown with three plant pairs. Several factors affecting induction were investigated: critical time windows, switching food plants, the amount of feeding necessary to produce a change in preference, and the effect of feeding just prior to the choice test. No early critical window ("imprinting") was found; both the amount and recency of feeding were found to be significant factors for induction and may interact. The importance of the induction of preference is discussed.

Key words: feeding behaviour, induction of preference, phytophagous insects, Nymphalidae, *Chlosyne lacinia*

INTRODUCTION

Phytophagous feeders comprise approximately 50% of all living insect species (DETHIER 1954) and close to 100% of Lepidoptera (SCHOONHOVEN *et al.* 1998). Most of these are specialists and have strong feeding preferences that result in various degrees of host specificity. Some of these feed on agriculturally important crops with significant economic consequences in both crop loss and the costs of insect control; the latter is often compounded by concomitant environmental degradation. Thus, given the economic and environmental importance of the feeding behaviour of phytophagous insects, the need to acquire a basic understanding of its mechanisms seems compelling.

One of the interesting aspects of insect feeding behaviour is that feeding preference shows plasticity. Behavioural plasticity is not something that is usually associated with insects, and so there has been some reluctance to accept it as part of the insect behavioural repertoire. Early evidence of preference alteration due to switches in larval food plants at first appeared in brief notes in the literature (reviewed by JERMY *et al.* 1968, JERMY 1987). As the bulk of evidence became substantial, TIBOR JERMY questioned whether these results were due to plasticity (individuals actually changing their preference), or to stringent selection (survival of

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a group of animals having a wider range of food tolerance). Therefore he proposed that future experiments monitor post-switch mortality to ensure that selection was not occurring. On research leave in VINCE DETHIER's laboratory in 1966 at the University of Pennsylvania in Philadelphia, he clearly demonstrated plasticity: Feeding experience by a caterpillar on a plant species resulted in increased preference for that plant (JERMY *et al.* 1968). The authors found this in two species of Lepidoptera, *Manduca sexta* and *Heliothis zea* (now *Helicoverpa zea*). These workers termed this phenomenon induction of preference to distinguish it from synonymous terms (e.g., conditioning) which may have special meaning in the behavioural literature.

Induction of preference has since been described in other species (see review by JERMY 1987) and possible mechanisms have been proposed (STÄDLER & HANSON 1976, 1978, DEBOER & HANSON 1984, 1988, DEBOER 1992, DEL CAMPO & RENWICK 2000, DEL CAMPO *et al.* 2001). However, many aspects of the phenomenon have not been fully explored. For example, is there a critical time window for exposure, as there is in vertebrate imprinting? Is there a threshold amount of feeding on an inducing plant that is required for the manifestation of induction? Does induction increase with exposure (cumulative effect)? Is recency of feeding a factor in induction, or only quantity of feeding? Experiments designed to test hypotheses generated by these and other questions were performed on larvae of the patch butterfly, *Chlosyne lacinia* GEYER using a modification of the behavioural choice test pioneered by TIBOR JERMY (JERMY 1961).

METHODS AND MATERIALS

Animals and culturing

The experiments were performed with caterpillars of the nymphalid patch butterfly *Chlosyne lacinia* GEYER, native to Texas, Central and South America. Larvae were collected from sunflower (*Helianthus annuus*) in and around Austin, Texas, and reared in continuous culture in the laboratory under controlled conditions of light (L:D 16:8) and temperature (ca. 20–23°C) during spring, summer and early fall (NECK 1977). Both the cultures and the larvae undergoing induction were reared on leaves. Growth and mortality rates were found to be comparable among the four host plants.

In rearing larvae for experiments, care was taken to circumvent brood effects. Egg masses were collected from oviposition cages, allowed to hatch in the absence of plants and distributed in equal numbers to the rearing plants. Thus if adverse effects of inbreeding, previous generation diet or other effects did occur, each culture would be equally affected.

Plants

The plants for the culture and experiments were locally collected host plants (Compositae): *Helianthus annuus* (henceforth abbreviated "*H*"), the common sunflower; *Ambrosia trifida* (abbreviated "*A*"), the common ragweed; *Zexmenia hispida* (abbreviated "*Z*"); and occasionally *Ximenesia enceloides* (abbreviated "*X*").

Testing procedures and calculations

The procedure for testing food preference was a modification of the JERMY disc test (JERMY 1961, JERMY *et al.* 1968). Two-choice tests were set up in plastic petri dishes of nine cm diameter for testing fifth instar larvae. Smaller dishes were used for testing for the lower instars. Four leaf discs of 8.5 mm diameter were punched from leaves of each of the two plant species to be examined. Smaller punch-outs were used with lower instars. The leaves destined for leaf discs were carefully selected from the top 1/3 of the plant to eliminate senescent leaves.

The leaf discs were arranged with the two plant species alternating around the inside circumference of the petri dish. This arrangement ensures that an active larva has an equal chance of encountering each leaf species. The small size of the leaf discs required multiple encounters with each leaf species to reach criterion, thus measuring choice and not feeding duration. In the center of each dish was placed a small circle of moist filter paper to prevent desiccation of the leaf discs.

Insects to be tested were removed from the culture at the end of the last rearing instar in the non-feeding premoult stage. They were placed in isolation without food and tested soon after moulting into the next instar. To start the test, a single larva was placed in the center of the dish, and leaf consumption was observed at approximately hourly intervals thereafter. At the time when one of the plant species was about 50% consumed (the equivalent of two discs) by a given larva, its test was terminated and the amount eaten of each plant species was visually estimated and recorded. These were summed on each plant, and the percentage of total consumption of each plant was calculated for each animal as an indirect measure of its choice, as follows:

Percent total consumption of plant #1 = (consumption of plant #1) / (consumption of plants #1 plus #2).

A similar calculation was done for consumption of plant #2. Means and standard errors were calculated for N animals. The "Choice Index" is the difference between the two means and has a range of –100 to +100. The "Induction Index" is the absolute value of the difference between Choice Indices of the two larval cohorts and has a range of 0 to 200. Statistical evaluations used the Wilcoxon non-parametric tests (signed rank test for P-choice, rank-sum test for P-induction) since the data distributions were similar but generally not normal.

Experiments

The basic induction of preference experiment tested the preferences of two cohorts of insects each reared on separate host plant species. The rearing plants were also the test plants. Five variations of the basic experiment were performed, as explained in the Results. All trials to be compared within each variation were performed within a few weeks of each other to avoid seasonal variation in plant quality.

RESULTS

Can a preference be induced in the patch butterfly, *Chlosyne lacinia*? Larvae reared for four instars on sunflower (*Helianthus annuus*, *H*) or ragweed (*Ambrosia trifida*, *A*) demonstrated a classic induction of preference response when given a choice test on this plant pair in early fifth instar: Larvae reared on *H* strongly preferred *H* whereas those reared on *A* strongly preferred *A* (Fig. 1). There was a large difference in feeding scores (Induction Index) for the two cohorts indicating a significant induction of preference ($P<0.001$; Table 1). Naïve control animals reared on another host plant, *Ximenesia enceloides*, *X*, but tested on the same plant pair showed a preference intermediate to that of *H* and *A* (Fig. 1, right pair of columns). Similar results also were seen with plant pairs *Z:H* and *A:Z* (*Z* is *Zexmenia hispida*) with large Induction Indices ($P<0.001$;Table 1); naïve controls also showed intermediate preferences in these experiments.

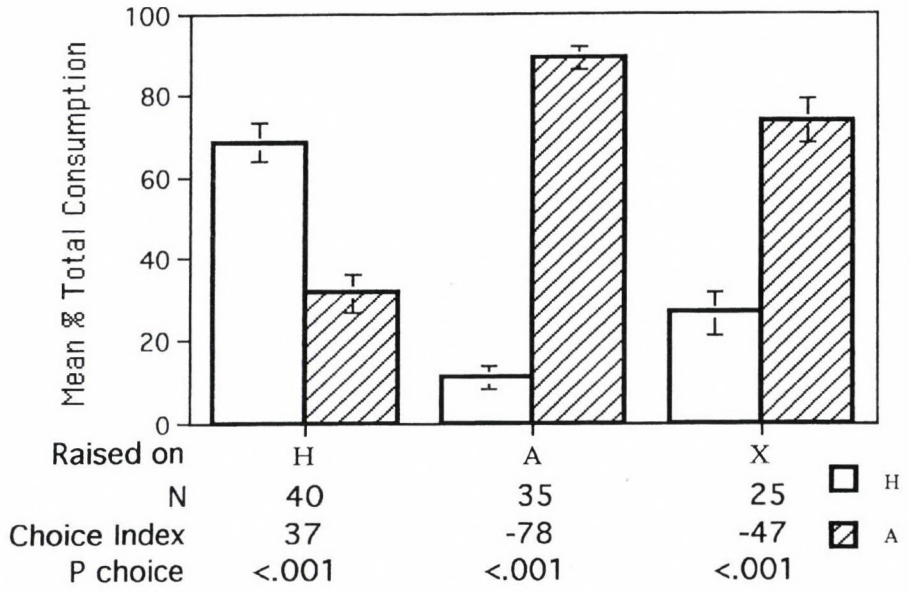

Fig. 1. Induction of preference in larvae of *Chlosyne lacinia*. Graphs depict the consumption of the two test plants (each expressed as percent of total consumption) during the choice test administered to a cohort of larvae raised on the designated host plant. Columns represent means for N larvae ±SE. Legend: Raised on = the plant on which that cohort of animals was reared for four instars. N = number of larvae tested. Choice Index = difference in feeding scores on the plant pair tested (range: –100 to +100). P choice = significance of difference in choice between test plants. See Materials and Methods for plant species abbreviations. All larvae were tested in early fifth instar. Note that rearing larvae on a plant increases its feeding preference for that plant

Table 1. Indices and statistics for the experiments showing induction of preference of six cohorts of *Chlosyne lacinia* larvae reared and tested on three pairs of host plants. See Materials and Methods for plant species abbreviations

Tested on	H:A		H:Z		A:Z	
Raised on	H	A	H	Z	A	Z
Number	40	35	41	46	11	21
Choice index	37	–78	34	85	21	–89
P choice	<.001	<.001	<.001	<.001	NS	<.001
Induction index	115		51		110	
P induction	<.001		<.001		<.001	

A separate set of experiments sought to determine whether earlier instars could also manifest an induction of preference. Larvae were reared on an inducing plant for two instars and tested in early third instar. These experiments also showed strong inductions of preference for *H:A* ($P<0.001$, $N=66$) and *H:Z* ($P<0.001$, $N=79$).

Does the strength of induction increase with duration of feeding on the inducing plant? Larvae reared on *H* show an increased preference for *H* with each additional instar of feeding on it (Fig. 2*a*). Thus, either induction increases with each instar of rearing on the inducing food, or else a specific increase in preference for *H* is a normal developmental phenomenon. Sibs reared on *A*, however, did not show an increased preference for *H* during development (Fig. 2*b*); thus, we conclude that the increase in preference for *H* in Fig. 2*a* is due to an increased induction with each additional instar of rearing on the inducing plant. Presumably this also would hold true for *A* but is not manifested in Fig. 2*b* because *A* is already so highly preferred to *H* in the early instars that no further increase in preference for *A* could take place.

Can a preference be changed by switching host plants? The original observations in the literature indicated that switching host plants results in a preference change towards the new host. To further investigate these reports and to determine if there is a requisite time period or quantity of feeding, we switched host plants after each instar and tested in the fifth instar. Our results confirm these early reports: Switching from *A* to *H* and vice versa does indeed change the preference (Fig. 3*a,b*: compare left pair of columns with right pair). These data also show that the feeding experience in the fourth instar accounts for all of the observed induction. Similar results from other plant pairs are reported in Table 2.

Occasionally we observed failure of induction or manifestation thereof. This occurred only when one member of the plant pair is very highly preferred over the other. For example, in the plant pair *H:Z* depicted in Fig. 3*c*, no induction was seen,

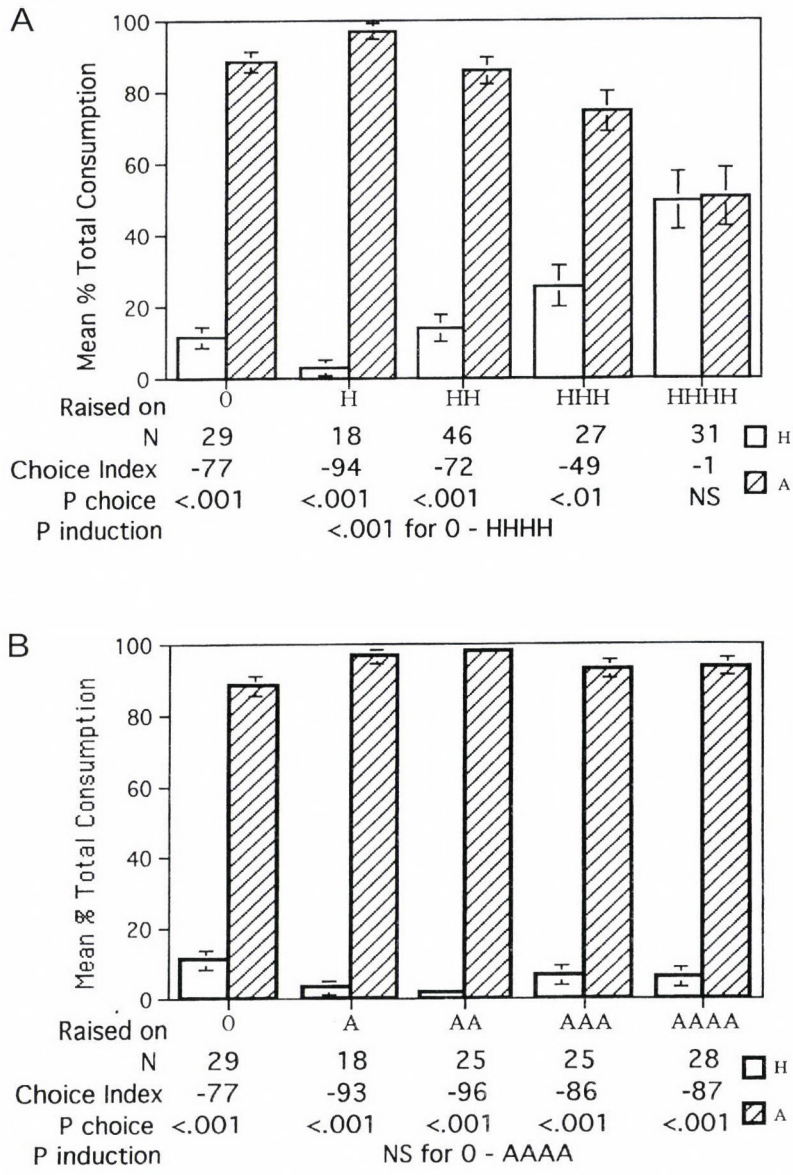

Fig. 2. Strength of induction depends on the number of instars of feeding on inducing plant. Larvae were tested after rearing on one plant for the indicated number of instars (0 = neonates tested; H = fed for one instar on H and tested in early second; HH = fed for two instars on H and tested in early third, etc.). Legend as in Fig. 1; also, P induction = significance of difference in feeding preference between the indicated cohorts (0 vs. HHHH, or 0 vs. AAAA). (2a) Note that the preference for H increases with the number of instars reared on H. (2b) Since A is already maximally preferred by neonates, the preference for A could not be increased further

Table 2. P-induction for five cohorts of larvae that were switched from host plant #1 to host plant #2 at first, second, third or fourth instars and tested in the fifth instar

Tested on	H:A		H:A		H:Z
Raised on	1=H, 2=A	1=A, 2=H	1=A, 2=Z	1=Z, 2=A	1=Z, 2=H
1111:2111	ns	ns	ns	ns	ns
2111:2211	ns	ns	ns	ns	ns
2211:2221	ns	ns	ns	ns	ns
2221:2222	<.001	<.001	<.001	<.001	ns

presumably because *Z* was so much preferred to *H* in the test that very little *H* was selected.

Is there a critical time window for induction? This question was answered by substituting a second plant during one instar only, but varying the instar in which the substitution occurred. Results show that the larvae preferred the plant species they consumed in the fourth instar; switching to an alternate plant during one of the other instars had no discernible effect (Fig. 4*a, b*).

Is the important induction factor the total amount of inducing food, or the most recent food? The above data show that stronger induction is seen in later instars when most of the larval feeding occurs, but do not distinguish between the quantity of inducing food vs. the most recent food prior to the test. To attempt to discriminate between these two alternatives, larvae were reared for four instars in the normal fashion and thus had consumed a large quantity of inducing food. Early in the fifth instar just prior to testing, they were fed an additional small amount (four leaf discs) of either their inducing plant or the paired plant. The amount fed, four discs of the type offered in the test, is a small fraction of the quantity of food

Table 3. Amount vs. recency of feeding as important factors in induction. For each of three pairs of plants, the first control cohorts of larvae were fed only on plant #1, including four discs in the fifth instar just prior to testing. In contrast, the first experimental cohorts were reared on plant #1 for four instars and then fed four discs of plant #2 just prior to testing. The procedure was then reversed for the second control and experimental cohorts. Note that slight but significant induction occurred in most plant pair comparisons

Tested on	H:A				H:Z				A:Z			
Raised on	H(4h)	H(4a)	A(4a)	A(4h)	H(4h)	H(4z)	Z(4z)	Z(4h)	A(4a)	A(4z)	Z(4z)	Z(4a)
Number	40	36	39	40	28	7	17	21	39	40	41	39
Choice index	13	–11	13	39	37	26	–51	–4	62	30	–39	8
P choice	ns	ns	ns	<.001	<.001	ns	<.005	ns	<.001	<.001	<.001	ns
Induct. index	24		26		11		47		32		47	
P induction	.05		.07		ns		<.02		<.005		<.002	

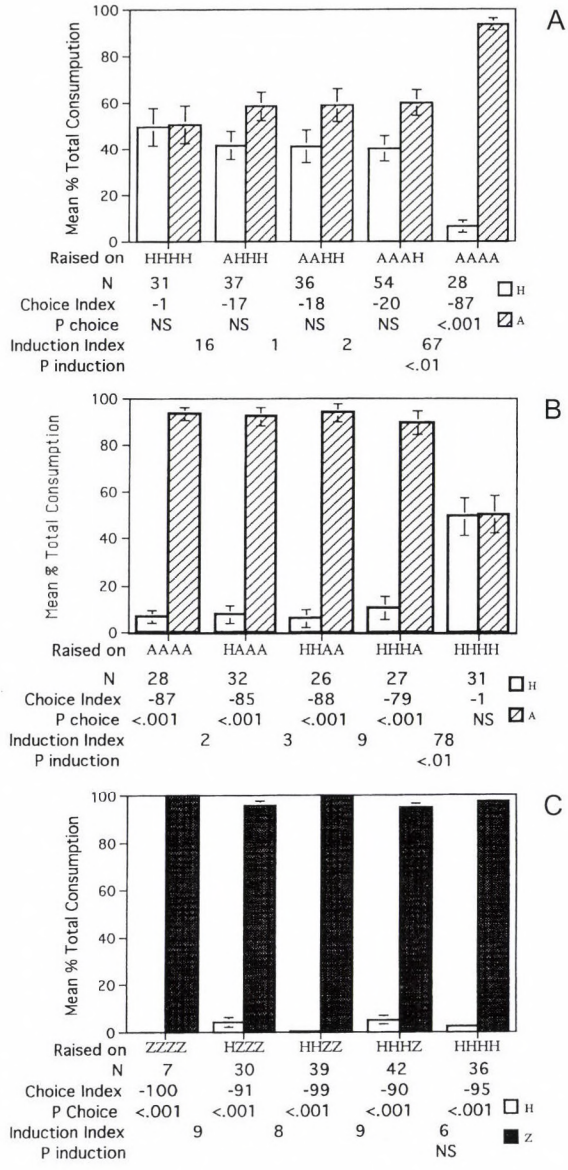

Fig. 3. Host plant switching. Animals were reared on plant #1 for a variable number of instars, then switched to plant #2 until tested in early fifth instar. Legend as in Fig. 2; also, Induction Index (range: 0 to 200) is the absolute value of the difference between choice indices of the above two cohorts, and P induction is the significance of that induction index. (3a, 3b) Note that the plant on which the animal fed during its fourth instar is the plant the animal prefers when tested in the fifth. (3c) Induction is not manifested when one plant, Z, is so highly preferred that little or no feeding occurs on the other plant, H, in the test

they had consumed during their first four instars. The results show that this amount of feeding on the paired plant just prior to the test does indeed produce a slight but significant increase in preference for it in most cases (see Fig. 5 for *A:Z*; other plant pairs are reported in Table 3). This suggests that recency of feeding on a different species may also be a factor in determining preference.

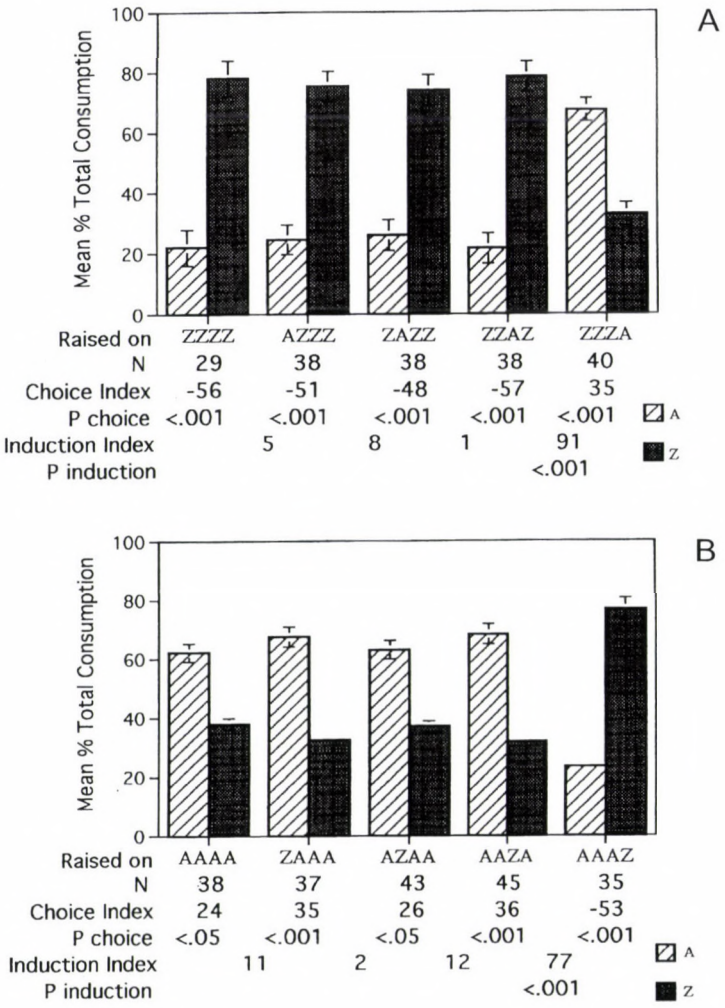

Fig. 4. Critical time window for induction. (4a) Animals were reared on Z except for one (variable) instar on A and tested in early fifth instar on A and Z. (4b) Same as 4a, but the plants were reversed. Legend as in Fig. 3, except that the Induction Index and P induction always compare responses of the indicated cohort against those of the first cohort. Note that the larvae always prefer the plant they fed on during the fourth instar

DISCUSSION

A classic induction of feeding preference was clearly demonstrated for most of the tested plant pairs by larvae of the nymphalid butterfly, *Chlosyne lacinia*. Preference for a plant is significantly increased by feeding on that plant. Most reports in the literature also show an increased preference for the rearing plant, although a few studies report reverse induction (e.g., WASSERMAN 1982, PORTILLO *et al.* 1996) or failures on certain plant pairs (e.g., JERMY *et al.* 1968, HANSON 1976, CHEW 1980). An explanation for failure has been suggested by DEBOER and HANSON (1984), namely that the two members of the experimental plant pair are too close taxonomically and thus chemically too similar. In his review of the role of experience in host selection, JERMY (1987) lists 21 lepidopteran species in which this phenomenon was shown, and others have since been added (e.g., *Spodoptera frugiperda* and *S. latifascia* by PORTILLO *et al.* 1996). Induction has been seen in other orders as well (JERMY 1987, LU & LOGAN 1993). A phenomenon this widespread must be important for insects and deserves the attention of experimental and evolutionary biologists to provide a basic understanding of its proximate and ultimate mechanisms.

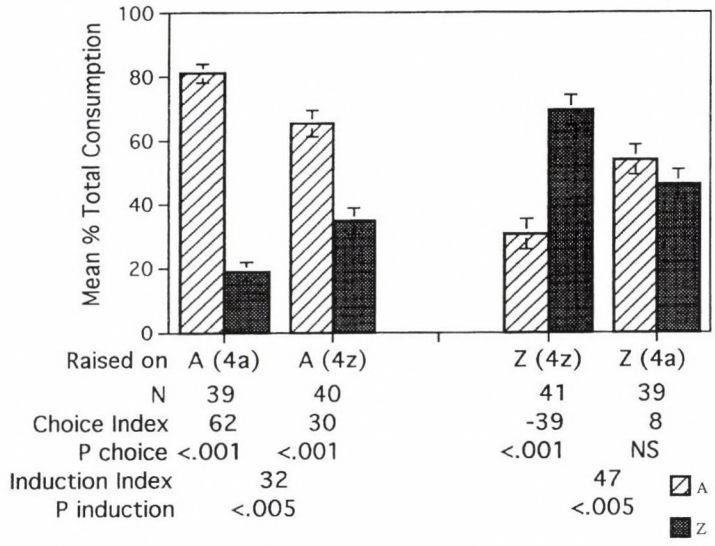

Fig. 5. Recency and amount of feeding affects preference. Larvae were reared on plant #1 for four entire instars; in the fifth instar just prior to testing, the control larvae were fed four more discs of the same plant (first pair of columns) whereas the experimental larvae were fed four discs of plant #2 (second pair of columns). Legend as in Fig. 2. Note that a slight but significant increase in preference results from recent feeding on plant #2

One of the characteristics of induction is that it begins early in the larval stage. Tests on *C. lacinia* in the beginning of the third instar show that highly significant induction has already taken place due to feeding in the first two instars. This supports the observations of WIKLUND (1973) who reported that larvae of *Papilio machaon* developed a preference for their rearing plants by the third instar. Larvae of the gypsy moth, *Lymantria dispar*, have been shown to have experience-dependent preference changes by the second instar that intensify with further feeding (BARBOSA *et al.* 1979). Our experiments on *C. lacinia* also show a comparable increase in the strength of induction with each instar of feeding on the inducing plant (Fig. 2). A similar result was reported in *Manduca sexta* by YAMAMOTO (1974) using a different bioassay (attraction test).

The host plant switching experiments patterned after the classic studies cited earlier showed that preferences induced in *C. lacinia* are moderately labile. Literature reports indicate that even though a strong preference can be demonstrated in a choice test, most species are still capable of switching to another host plant. Exceptions are noted by MA (1972) who reported that after induction, *Pieris brassicae* could not be successfully switched to certain other host plants, and HANSON (1983) who reported a similar result for the promethia moth, *Callosamia promethea*. Presumably, as yet undiscovered incompatible switches exist for other insect species as well.

In the present paper, the host plant switching experiments on *C. lacinia* provided an example of an inconsistency sometimes encountered in these types of experiments: inductions successfully demonstrated at one time fails at another. For example, larvae show significant induction on *H:Z* in Tables 1 and 3, but clearly not in Fig. 3*c* and Table 2. Perhaps the explanation for this anomaly is that the plants vary due to season or may have had an unseen contaminant or disease. Our experimental protocol sought to minimize such problems by scheduling trials of one experiment within as narrow a time window as possible, and we place more confidence in comparisons within than across experiments.

The question arises as to whether there is a critical time window for induction in *C. lacinia* as there is, for example, in newborn vertebrates that imprint on moving or sound-producing objects during their first day of life. Such an early critical window was hypothesized by YAMAMOTO (1974) to explain his observations that in the attraction test *Manduca sexta* became less polyphagous because of foods eaten in the first instar. Using a different assay (disc test), DEBOER and HANSON (1984) found no evidence of a critical window in *M. sexta*. Likewise in the present study there is no evidence for an early critical window in *C. lacinia* (Fig. 4). The importance of the fourth instar could be construed to be a late critical window, although an alternate interpretation (below) appears to be more plausible. In all of

the above studies, however, subtle differences may not have been detected due to the crudeness of the behavioural bioassay. With the discovery of a host specific phytochemical that appears to modify chemoreceptors (DEL CAMPO *et al.* 2001), this question may need to be reinvestigated using more sensitive assays.

The experimental results show that induction, when present, is determined by the plant species eaten in the instar just prior to testing. Thus recency of feeding may be an important factor. Alternatively, the total amount of the inducing food consumed may be the important factor, as would be the case if the operative mechanisms involved a cumulative effect. Many studies have shown that larvae eat more in any given instar than in all the previous instars combined, so in our plant switching experiments the total amount consumed would have been greatest in the fourth instar. Since this is just prior to testing in the fifth instar, however, recency of feeding may be confounded with amount of feeding. Further experiments (Fig. 5) indicated that recency of feeding may indeed play a role: Four (but not two) leaf discs of the second plant are enough to change the preference slightly but significantly with some plant pairs. Thus it is likely that both factors play a role and that they interact. Similarly, JERMY *et al.* (1968) found that the most recent 24 hours of feeding on a second plant could change the preferences of *Helicoverpa zea*, and MA (1972) found that the most recent four (but not two) hours of feeding on *Tropaeolum majus* would change the preference of *Pieris brassicae*.

Perhaps the ultimate importance of induction of preference is that it may contribute to the formation of biological races, which are groups of insects occurring in the same locality but having different food preferences (i.e., host races for phytophagous insects). DETHIER (1954) speculated that the formation of biological races may be an early step in the process of speciation. When feeding preferences of races differ and they establish on different hosts, spatial isolation and selection could result in genetically different races if gene interchange were sufficiently restricted. Host shifts by insects must have occurred many times in the past, and reports of this have surfaced in the literature since the beginning of the last century (SCHRODER 1903, PICTET 1911). The mechanism often proposed is a mutation in the insect sensory system that permits feeding and oviposition on a formerly unacceptable plant, perhaps after the population has gone through a genetic bottleneck (PICTET 1911). Alternatively, some adaptability in food choice behaviour may be present that increases the acceptability of the new plant after prolonged exposure to it. This alternative raises questions about the degree of adaptability of feeding preference that is present in a normal population (i.e., one without stringent selection). Adaptability includes plasticity of preferences, which in the pre-JERMY era had been thought to be absent in insects. Plasticity is, however, alive and well, as the induction of preference data show.

Whether the changes brought by induction are sufficiently strong to affect host race formation is not clear. From our current vantage point induction appears to be less of an ultimate and more of a proximate mechanism, such as restricting the insect to the plant on which it is currently feeding. When a larva switches plants, new detoxifying enzymes may need to be induced, and this has its metabolic cost. If these enzymes are not produced quickly, mortality may follow. As an example, induction of preference protects *Callosamia promethea* reared on sassafras (*Sassafras albidum*) or spicebush (*Lindera benzoin*); larvae induced on either of these will generally not switch to wild cherry (*Prunus serotina*), another host plant. Those that do eat cherry will die, presumably from the cyanogens in the cherry leaves which they can no longer detoxify (HANSON 1983). Similarly, *Pieris brassicae* larvae reared on *Brassicae oleracea* do not survive the switch to *Tropaeolum major*, which is otherwise a good host plant for *Pieris* when reared on it from the first instar (MA 1972).

To conclude, the induction of preference, a concept pioneered by TIBOR JERMY, has been examined in larvae of a nymphalid lepidopteran, the patch butterfly, *Chlosyne lacinia*. Our studies have illuminated some of the factors involved in induction and changes in preference following host plant switching. But to fully understand the basis of preference change will require further investigations into the physiological mechanisms of feeding decisions. This is stated more eloquently by TIBOR JERMY: "...the insect receives very detailed information from the plant; this information is in some way stored in the nervous system and is used as reference information for the decision to be made by the insect at subsequent encounters with plants. At present the neural basis of these processes is largely unknown..." (JERMY 1987). Indeed, it is still largely unknown, but thanks to pioneers like TIBOR JERMY the veil of ignorance about these feeding decisions and other insect-plant interactions is beginning to lift.

*

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PERIMETER TRAPPING: A NEW MEANS OF MASS TRAPPING WITH SEX ATTRACTANT OF ANOMALA SCARABS

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Two mass trapping trials were undertaken with traps baited with the sex-attractant of *Anomala vitis* FABR. and *A. dubia* SCOP. (Coleoptera: Scarabaeidae, Melolonthinae), one in a young sour cherry plantation and the other in mature peach orchard. Traps in the 1st and 2nd perimeter rows of the trap grid caught many more beetles on an average than traps in the 3rd or 4th rows. In the mature peach orchard trial, fruit damage was estimated to have been lowered to ca. 5%, a level acceptable for the farmers. The results suggests that the majority of the beetles did not develop from pupae within the plantation but had flown in from neighbouring areas to feed on the fresh leaves or fruit; consequently mass trapping of *Anomala* spp. using perimeter traps might be a viable alternative to insecticides for the control of these pests. In contrast to mass trapping trials with moths, it is the adult stage of these scarab beetles which is economically important and which are caught in these traps, so damage should be reduced in proportion to the population trapped.

Key words: *Anomala vitis*, *A. dubia*, Coleoptera, Scarabaeidae, Melolonthinae, mass trapping, sex attractant

INTRODUCTION

In Hungary, adults of the scarabs *Anomala vitis* FABRICIUS and *A. dubia* SCOPOLI (Coleoptera, Scarabaeidae, Melolonthinae) are known to cause significant leaf damage during outbreaks. The former species is especially important on grapes; although both species feed on many orchard trees and shrubs (JABLONOWSKI 1912, HOMONNAY & HOMONNAYNÉ-CSEHI 1990). Damage caused by these two species has been reported with increasing frequency and importance, not only in vineyards but also in several orchard crops (VOIGT *et al.* 2000, VOIGT & TÓTH 2000). Damage is predominantly caused by adult beetles feeding on either the leaves or fruit or both. When leaf damage occurs in a young orchard or nursery, the growth of the young trees is reduced and they may even be killed. In older orchards, especially in peaches, the beetles prefer to feed on ripening fruits, resulting in low quality fruit, which may be impossible to market.

Damage by these beetles is difficult to prevent as both species have a long flight period, in some years starting towards the end of May and lasting until early August. Because of this long flight period, preventive control can be achieved only

by repeated insecticide sprays. These are both costly and leave hazardous residues, so that applications during harvest are unacceptable.

Some years ago, the synthetic compound (2*E*)-2-nonenol was found to be a highly effective sex attractant for males of both *Anomala* species (TÓTH *et al.* 1994). More recently, a high capacity funnel trap has been developed by the Plant Protection Institute, Budapest (TÓTH *et al.* unpubl.) which has proved to be excellent for capturing these two pests in large numbers (VOIGT *et al.* 2000).

In the present paper, we describe preliminary trials for controlling these two *Anomala* species by mass trapping with traps baited with the above sex attractant. The use of these traps could be an excellent alternative control method, as it might reduce damage to below an economically acceptable threshold and, at the same time, is non-toxic, posing no health or environmental risks, and so can be used throughout the harvest period.

MATERIALS AND METHODS

The traps and baits used were standard *Anomala* funnel traps (CSALOMON® VARb2) produced by the Plant Protection Institute, Hungarian Academy of Sciences, Budapest, Hungary. Each trap consisted of a plastic funnel (top opening inner diameter of 16 cm, funnel hole diameter 3 cm, height of funnel 19 cm), beneath which was held a round, transparent, plastic catch container (ca. 1 litre in volume) which, in turn, was held in place by a rubber band. The bait dispenser was attached onto the inner wall in the middle of the funnel opening.

Two trials were carried out during the summer of 2000, one in a young sour cherry orchard and the other in a mature peach orchard. The trial in the sour-cherry orchard was carried out in a young plantation planted in 1998 at Vetter Kft., Csengele (Csongrád county, Hungary). Here the traps were placed on tree branches at a height of ca 1.5–2.0 m on May 31, in an 18×15 m grid covering the total area (2.5 ha) of the plantation.

The trial in ripening peaches was performed in an orchard at the Bóka-Mangó family farm, Zákányszék (Csongrád county, Hungary; cultivars: Red June, Early Redhaven, Flavortop). Here the traps were set out at a height of 1.8–2.0 m in the crown of the trees on June 14, in a 15×20 m grid, covering 1.4 ha of the total orchard area of 2.4 ha. At this time, it was observed that the neighbouring orchards with early-ripening cultivars (i.e., Springcrest, etc.) already had large numbers of both *Anomala* spp.

In both trials, the traps were inspected at fortnightly intervals and the number of captured beetles was recorded.

The capture data were transformed to $(x+0.5)^{1/2}$ and were analysed by ANOVA. Treatment means were separated by the Games-Howell-test. All statistical procedures used the software packages StatView® v4.01 and SuperANOVA® v1.11 (Abacus Concepts, Inc., Berkeley, USA).

Damage assessment in the peach orchard was by observing 100 randomly selected fruits per tree at the time of harvest.

RESULTS AND DISCUSSION

In the young sour-cherry plantation, leaf damage was negligible, suggesting a low overall pest density. Despite the relatively low numbers of beetles captured, the same trends were observed at all inspection dates: the traps at the perimeter usually captured more *Anomala* than those within the plantation (Fig. 1). Thus, of the total of 285 beetles caught, 94% were in the traps in the 1st and 2nd rows of the grid (1st row: 63%; 2nd row 31%), significantly more than was caught in the 3rd or 4th rows (Fig. 3). These results suggest that the majority of the beetles were not emerging from pupae within the plantation, but were flying in from neighbouring areas to feed on the fresh leaves of the young sour-cherry trees. If so, traps placed at the perimeter of plantations might be able to reduce the damage by trapping out a significant percentage of immigrating beetles.

In the peach orchard, the trends were similar to those in the sour-cherry plantation, with the traps at the perimeter catching more than those inside the grid (Fig. 2). Thus, of the total of 3754 beetles caught, 92% were in the traps in the 1st and 2nd rows of the grid (1st row: 65%; 2nd row 27%), again significantly more than catches in the 3rd or 4th rows (Fig. 3). The level of fruit damage was assessed at not

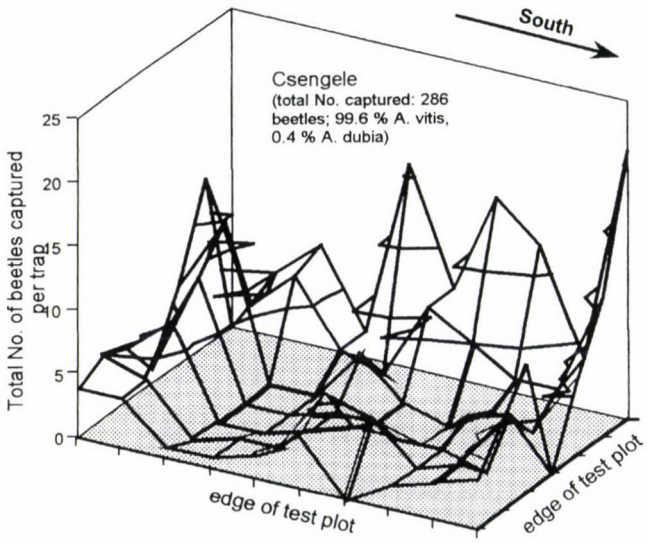

Fig. 1. Distribution of catches in the test orchard at Csengele. Surface graph shows total catches of *A. vitis* and *A. dubia* at the position of each trap

more than ca. 5% at harvest, a level acceptable to the farmer. Although no direct comparison of damage levels was made with orchards without traps, neighbouring farmers were complaining of ca. 20% damage, despite of insecticide sprays.

Although the present results are preliminary and only cover a single season, they suggest that mass trapping of *Anomala* spp. using perimeter traps might be a viable alternative to insecticides in the control of these pests. When using these traps, the methodologies will vary depending on whether the aim is to reduce damage to the leaf (as in sour-cherry plantation) or to the fruit (as in the peach orchard). When attempting to reduce leaf damage, the traps should be set out before the flight period starts (usually late May in Hungary), and should then be left out until the end of flight period (end of July in Hungary). As the longevity of the sex attractant bait in the trap exceeds this period and, since the CSALOMON® VARb2 funnel traps have a catch capacity of ca. 3–4000 beetles/trap, it is unlikely that there will be a need to replace traps within the season.

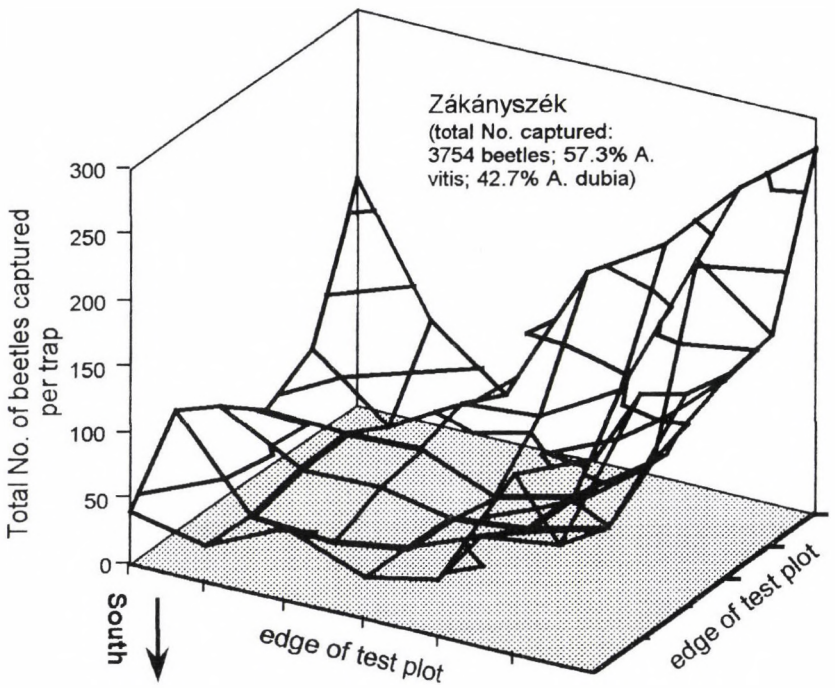

Fig. 2. Distribution of catches in the test orchard at Zákányszék. Surface graph shows total catches of *A. vitis* and *A. dubia* at the position of each trap

On the other hand, when attempting to reduce fruit damage, it is sufficient to set out the traps about 10 days before the ripening period of the cultivar in question. Our results suggest that placing the traps around the perimeter of orchards not larger than 3–4 ha may give sufficient protection. In this case, the traps should be positioned sufficiently high in the crown of trees where most damage would be expected. However, care must be taken to hang the traps from branches with little or no fruit, because those beetles which fail to enter the traps can congregate nearby, feeding on any available fruit or leaves (VOIGT & TÓTH unpubl.).

With Lepidoptera, reduction of pest populations through mass trapping with attractant-baited traps has been conducted with variable success (see reviews by BAKKE & LIE 1989, LANIER 1990). However, in the case of moths, it is the adult stage which is removed through mass trapping and this is not usually the life stage that causes the damage, so that the main benefits to be obtained by a removal of the individuals trapped is a reduction in the reproductive potential of the population. In contrast, it is the noxious stage of the *Anomala* spp. itself, which is removed by trapping, and thus the damage will be reduced in proportion to the percentage of the population trapped out.

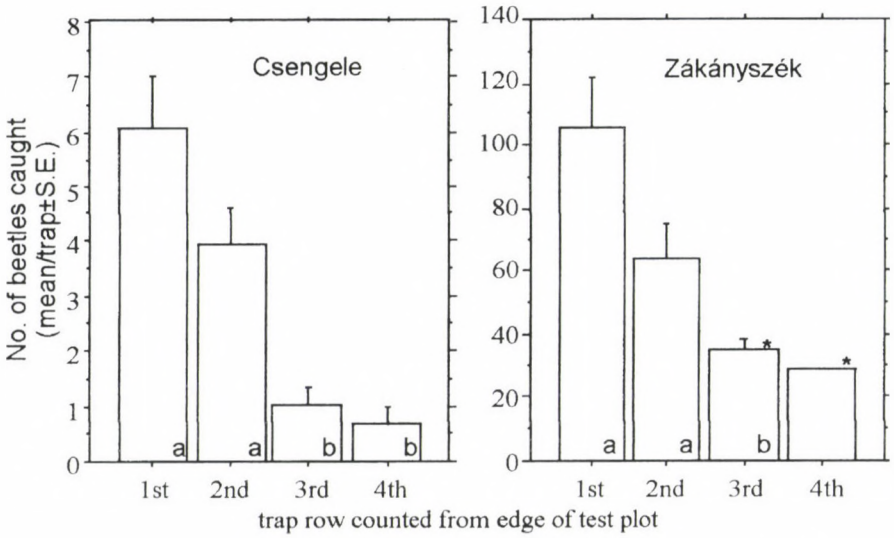

Fig. 3. Numbers of *A. vitis* and *A. dubia* caught at each trap position in the sour-cherry orchard at Csengele and Zákányszék. Columns with same letter within one diagram are not significantly different at P=5% by ANOVA followed by Games-Howell-test. At Zákányszék, the columns with an asterisk do not differ significantly from the catch in a single trap in the 4th row (29 beetles) by one-sample *t*-test

However, one difficulty could be that the bait used is attractive only towards males (TÓTH *et al.* 1994), leaving the females unaffected. No study on the actual sex ratio of the *Anomala* populations was attempted at our test sites in this study. The method could be made more efficient by introducing supplementary attractants capable of also attracting the females. Efforts to chemically define such an attractant for the two *Anomala* spp. are underway. Plant-derived attractant substances are already described for a number of scarabs (see for review LEAL *et al.* 1994). For example, with the Japanese beetle (*Popillia japonica* NEWMAN), a close relative, the synthetic sex pheromone attracted only males but, when applied together with a mixture of the food lure phenethyl propionate, eugenol and geraniol, catches of both sexes were maximized (LADD & KLEIN 1986). With regard to *Anomala* spp., there was a clear synergistic effect with *Anomala rufocuprea* MOTSCHULSKY when the food-type lure methyl anthranilate was combined with the synthetic pheromone (IMAI *et al.* 1997), while a combination of synthetic pheromone plus a mixture of food-plant derived volatile compounds significantly increased captures of *Anomala octiescostata* BURMEISTER as compared to the pheromone alone (LEAL *et al.* 1994).

Mass trapping of scarab pests has been successful in some species. Traps for mass trapping the Japanese beetle are marketed commercially and are frequently seen on urban properties in the U.S. Three years of mass trapping on Nantucket Island, MA, was reported to have reduced the *P. japonica* population by 50% (HAMILTON *et al.* 1971).

In Japan, traps baited with the floral lure 2-phenylethanol (IMAI pers. comm., cited in LEAL 1999) are used for reducing the population of *Hoplia communis* F. on golf courts. Adults of this species, which normally feed on whitish flowers, are highly attracted to any whitish surfaces, especially T-shirts of golf players, and become a nuisance in the main flight period in May.

Apart from the Carpathian Basin, *A. vitis* is present in almost all temperate and Mediterranean regions of Europe, from Spain to the Black See, while *A. dubia* is even more widespread, from England to the Caucasus and from south Scandinavia to Italy (HURPIN 1962). Attempts for reducing their numbers through perimeter trapping as suggested in the present study may be useful also in these areas.

*

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