Evolutionary aspects of host plant specialisation – a study on bruchids (Coleoptera: Bruchidae)

Tibor Jermy and Árpád Szentesi

Jermy, T. and Szentesi, Á. 2003. Evolutionary aspects of host plant specialisation – a study on bruchids (Coleoptera: Bruchidae). – Oikos 101: 196–204.

We have studied the relationship of bruchids and their legume hosts by extensive field sampling throughout Hungary over 17 years and by rearing the beetles from the samples in the laboratory. The value of the system lies in the accuracy of host affiliations. A total of 138 species and subspecies of plants were sampled, representing approximately 87% of the Leguminosae in Hungary. Only 51 legume species (37.0%) harboured bruchids (12 *Bruchus* spp. and 15 *Bruchidius* spp). Bruchids occurred in 38.3% of the host plant samples. Thirty-seven plant species congeneric with bruchid host species were unoccupied by bruchids.

The degree of host specificity ranged from monophagy (at least ecological monophagy) to oligophagy. On the basis of presence/absence data we tested the null hypothesis assuming that plant taxa and seed consuming bruchid species form congruent phyletic relations at the species level. We argue that the case for coevolution between the beetles and their hosts is weak. A comparison of the available taxonomic relationships (and presumed phylogenies) best fits a case of sequential evolution, with stronger phylogenetic conservatism in *Bruchus* species than in *Bruchidius* species. Bruchid and host plant taxa showed rough congruence only at the tribe level. We suggest that host shifts are best explained by the changes in the bruchids' chemosensory system that determines the females' host selection behaviour.

T. Jermy and Á. Szentesi, Plant Protection Inst. of the Hungarian Academy of Sciences, P.O. Box 102, H-1525 Budapest, Hungary. Present address of Á.S.: Loránd Eötvös Univ., Faculty of Natural Sciences, Dept of Systematic Zoology and Ecology, P.O. Box 120, H-1518 Budapest, Hungary (szentesi@cerberus.elte.hu).

Following Ehrlich and Raven's (1964) seminal paper, there have been numerous studies on evolutionary aspects of insect-plant associations including, to date, over twenty comparisons of insect and host-plant phylogenies. In some cases there is striking species-to-species congruence between the two, while in others there is remarkable lack of congruence at the species level. Tight congruence of phylogenies has been regarded as a proof of coevolution (Farrell and Mitter 1990, 1998), while in case of incongruence the lack of coevolution has been supposed (Futuyma and McCafferty 1990, Menken et al. 1992, Wahlberg 2001). A major problem with many of the related studies is, however, the reliability of host plant data. In a critical review of the literature on ecological characters and phylogeny,

Miller and Wenzel (1995 p. 403) concluded that for studying host-plant evolution in phytophagous insects "plant-association characters should be derived from highly corroborated field reports rather than laboratory experiments, but host records for phytophagous insects are notoriously poor. Published plant and insect species identifications are often incorrect. An insect's repertoire may include additional host plants that have not been recorded simply because of insufficient field work.... In summary, the quality of such characters as host plants strongly depends on the quality of data on which they are based, and the potential for error is great."

To meet the above requirements of reliable host plant data for a group of phytophagous insects that can serve as a basis for estimating phyletic relations, we have

chosen the bruchids (seed beetles) because the adults can be reared from the fruits (pods, heads) of their host plants collected in nature, thus unequivocal data on host affiliation can be obtained. Earlier work on bruchids has only rarely been based on rearing (Birch et al. 1989), therefore the majority of host plant data contained in the European studies that deal primarily with bruchid taxonomy (Hoffmann 1945, Lukjanovitsh and Ter-Minassian 1957, Kaszab 1970, Strejček, 1990) are unreliable. Already Zacher (1952a) pointed out that collecting adult bruchids from plants in nature resulted in erroneous host plant data, because the adults may feed on the pollen of various plant species other than their hosts. The reliability of data is biased also by uncertainties in the earlier identification of bruchids, as the taxonomy of several European species has been worked out quite recently (see below). Finally, no information exists on what part of the local flora is occupied by the local bruchid species. As far as we are aware, this is the first study on insect-plant associations based on rearing the insects from plant samples that were collected repeatedly over several years on the territory of a whole country.

To characterise the bruchid-plant relationship we focus on the following questions:

1. Presence or absence of bruchid species in the legume species of the local flora?
2. How broad are the host plant ranges of bruchid species?
3. Are closely related bruchid species specialised on closely related plant species?

Methods

Sampling

In this paper an independent sample means the amount of fruits (pods, heads) taken from a plant stand at a location, or in different years from the same location. During 17 years we collected ripe, or almost ripe, fruits of legume species from natural and semi-natural habitats (nature reserve areas and national parks) at 239 locations situated on the territories of 175 municipalities (towns, villages) scattered all over Hungary. The number of samples collected per year ranged from 53 to 165. We considered two locations as distinct, if they were at least 1 km apart, even if they represented the same type of habitat. Cultivated plants were sampled only occasionally. Repeated sampling at the same location over years increased the probability of revealing the presence of a bruchid species on a plant species in case of very low bruchid densities. The number of samples given in Table 1–3 represent independent samples. The differences between the total number of samples and the number of locations shown in the tables indicate repeated sampling.

Each sample contained as many pods or heads as were available at the location when, due to extreme weather conditions, the amount of available fruiting plant individuals was very low. In such cases only a dozen or so seeds were in the sample. In most cases, however, the samples contained several hundred or several thousand seeds. The samples were put in paper bags and transferred to the laboratory where they were placed into glass jars covered with linen. The jars were kept at room temperature until autumn and afterwards in an open-air insectary over winter. The jars were rechecked at one or two monthly intervals until late autumn, and after over-wintering at least twice a year for emerging adults that were collected and preserved for identification. Afterwards, all seeds per small sample or at least 100 seeds per large sample were examined, and those showing unopened operculum were boiled in distilled water to extract the unhatched adults.

Data

The analysis is restricted to qualitative data, i.e., to the presence or absence of bruchids in plant species. Even a single bruchid adult emerging from a sample was considered as presence and the lack of any sign of infestation as absence. Repeated sampling enabled us to estimate the variation in the rate of seed infestation by bruchids. The quantitative data (rate of bruchid infestation per sample, change of infestation over time, etc.) will be reported elsewhere.

Bruchid and plant taxonomy and nomenclature

Although several entomologists have dealt with the taxonomy of European bruchids during the last six decades (Hoffmann 1945, Lukjanovitsh and Ter-Minassian 1957, Kaszab 1970, Borowiec 1988, Strejček 1990) the synonymy of some species groups has been worked out satisfactorily only recently (Anton 1998a, 2001). The bruchids were identified by the first author, however, specimens of all species were sent for taxonomical confirmation to Dipl.-Biol. K.-W. Anton (Emmendingen, Germany), who is an authority in European bruchid taxonomy. (In order to avoid confusion of species' affiliation to genera due to the abbreviated names, we use *Bu.* instead of *Bruchus*, and *Bi.* instead of *Bruchidius*.)

Here we use the names of *Bruchus* species according to Lukjanovitsh and Ter-Minassian (1957) with two exceptions: (1) *Bu. libanensis* Zampetti (1993) the specimens of which have been identified by Anton (2001). It had been considered earlier as *Bu. rufipes* Herbst (Szentesi and Jermy 1995, Szentesi et al. 1996). (2) Anton (2001) found that *Bu. sibiricus occidentalis* Lukj. et Ter-Min. is a good species, so its valid name is *Bruchus occidentalis* Lukj. et Ter-Min.

Table 1. The host plants of *Bruchus* spp. in Hungary.

Bruchus spp.	No. of adults reared	Host plant species	Samples total no. (loc.)[1]	Samples infest. no. (%)	References[2]
affinis Fröl.	>100	*Lathyrus latifolius*	27(10)	13(48)	F, Z,
	11	*L. pratensis*	56(33)	1(2)	H, K, Z,
	>100	*L. sylvestris*	33(13)	15(45)	F, H, K, L, Z
	>100	*L. tuberosus*	54(20)	12(22)	H, Z
atomarius (L.)	2	*Lathyrus latifolius*	27(10)	1(4)	
	51	*L. niger*	26(15)	5(19)	
	6	*L. pannonicus*	8(3)	4(50)	
	8	*L. sylvestris*	33(23)	1(3)	
	>100	*L. vernus*	8(3)	6(75)	L, Z
	8	*Vicia cassubica*	28(19)	3(11)	
	18	*V. pisiformis*	13(11)	4(31)	K, L
	>100	*V. sepium*	35(18)	13(37)	H, K, L, Z
	>100	*V. sparsiflora*	8(3)	3(38)	
brachialis Fåhr.	4	*Vicia tenuifolia*	90(31)	4(4)	
	88	*V. villosa*	23(19)	8(35)	A, B, H, K, L, Z
libanensis Zampetti	57	*Vicia cracca*	50(29)	7(14)	
	>100	*V. tenuifolia*	90(31)	44(49)	
loti Payk.	6	*Lathyrus nissolia*	9(5)	2(22)	
	30	*L. pratensis*	56(33)	5(9)	H, K, L, S, Z
luteicornis Illig.	>100	*Vicia angustifolia*	116(43)	65(56)	A, K, L, Z
	>100	*V. grandiflora*	25(19)	14(56)	
pisorum (L.)	>100	*Pisum sativum*	12(4)	5(42)	A, B, H, K, L, S, Z
rufimanus Boh.	60	*Vicia pannonica.* ssp. *pannonica*	12(8)	8(67)	
	>100	*V. p.* ssp. *striata*	6(3)	5(83)	
occidentalis Luk. & T.-M.	>100	*Vicia cracca*	50(29)	10(20)	
	>100	*V. tenuifolia*	90(31)	30(34)	S
tristiculus Fåhr.	31	*Lathyrus hirsutus*	8(6)	4(50)	Z
	7	*L. odoratus*	2(2)	2(100)	H, K, Z
venustus Fåhr.	63	*Vicia cracca*	50(29)	2(4)	
	>100	*V. tenuifolia*	90(31)	61(68)	
viciae Ol.	17	*Lathyrus niger*	26(15)	4(15)	K, L
	5	*L. pannonicus*	8(3)	3(38)	
	6	*L. pratensis*	56(33)	2(4)	

[1] Number of locations.
[2] Only publications are referred to that report on the same host plant species. Publications mentioning only plant genera (e.g. "*Vicia* spp.") have not been considered. A = Anton 1998b; B = Borowiec 1988; F = Fabres and Reymonet 1991; H = Hoffmann 1945; K = Kaszab 1970; L = Lukjanovitsh and Ter-Minassian 1957; S = Strejček 1990; Z = Zacher 1952b.

The names of *Bruchidius* species correspond to the literature sources cited: *lividimanus, pusillus, seminarius, villosus* (Anton 1998a); *glycyrhizae* (Anton 1998b); *picipes* (Borowiec 1987); *dispar, imbricornis, marginalis, martinezi, pauper, sericatus, varius* (Lukjanovitsh and Ter-Minassian 1957); *poupillieri* (Anton 2001) and *varipes* (Anton pers. comm.). Several specimens of each bruchid species reared during this study are deposited in the collections of the Hungarian National History Museum, Budapest. All above listed *Bruchus* and *Bruchidius* species are considered autochthonous or have invaded the Carpathian Basin long ago as *Bruchus pisorum*. *Acanthoscelides pallidipennis* and *A. obtectus* are not dealt with below as they were introduced to Hungary only during the 20th century (Wendt 1981, Jermy and Balázs 1990).

According to the recent taxonomy of European bruchids (Borowiec 1988, Strejček 1990) the genera *Bruchus* and *Bruchidius* are well separated as they belong to different tribes of the subfamily of Bruchinae: *Bruchus* to *Bruchini* and *Bruchidius* to *Acanthoscelidini*.

The names of higher plant taxa agree with the nomenclature by Polhill and Raven (1981). The species names follow Tutin et al. (1978) with the exception of *Vicia angustifolia* which is regarded by the latter authors as a synonym of *Vicia sativa* ssp. *nigra*, while it appears as a distinct species in the Central European botanical literature (Jávorka 1925, Soó and Kárpáti 1968, Hanelt and Mettin 1989).

Results

Number of samples

For over 17 years we have collected samples of pods and/or heads of 138 species and subspecies of Leguminosae amounting to approximately 87% of the native and introduced legumes known to occur in Hungary (Soó and Kárpáti 1968). The remaining species are either very rare, recently disappeared, or protected by law. The number of samples taken from each bruchid

Table 2. Host plants of *Bruchidius* spp. in Hungary.

Bruchidius spp.	No. of adults reared	Host plant species	Samples		References[2]
			total no. (loc.)[1]	infest. no. (%)	
dispar (Gyll.)	1	*Trifolium pratense*	16(10)	1(6)	
	13	*T. striatum*	6(4)	3(50)	
glycyrhizae (Gyll.)	>100	*Glycyrrhiza echinata*	4(4)	4(100)	A, L
imbricornis (Panz.)	>100	*Galega officinalis*	6(5)	5(83)	B, K, L, Z
lividimanus (Gyll.)	>100	*Cytisus scoparius*	3(3)	1(33)	H, Z
marginalis (F.)	>100	*Astragalus glycyphyllos*	62(29)	24(39)	B, H, K, L, S, Z
martinezi (All.)	11	*Trifolium fragiferum*	3(3)	2(67)	
pauper (Boh.)	11	*Coronilla coronata*	2/(1)	1(50)	
picipes (Germ.)	>100	*Trifolium striatum*	6(4)	2(33)	
poupillieri (All.)	2	*Anthyllis vulneraria* ssp. *polyphylla*	26(15)	2(8)	
	1	*Onobrychis arenaria*	6(4)	1(17)	
pusillus (Germ.)	>100	*Coronilla varia*	82(30)	33(40)	
seminarius (L.)	>100	*Tetragonolobus maritimus*	10(7)	5(50)	S
sericatus (Germ.)	34	*Trifolium rubens*	17(9)	1(6)	
varipes (Boh.).	9	*Astragalus asper*	3(2)	1(33)	
	88	*A. onobrychis*	20(19)	7(35)	
	1	*A. varius*	2(2)	1(50)	
	10	*A. vesicarius*	3(3)	1(33)	
	15	*Oxytropis pilosa*	7(3)	2(29)	
varius (Ol.)	>100	*Trifolium alpestre*	11(7)	5(45)	
	4	*T. diffusum*	1(1)	1(100)	
	7	*T. medium*	22(19)	2(9)	
	74	*T. pratense*	16(10)	9(56)	B, KT
	27	*T. rubens*	17(9)	5(29)	
villosus (F.)	20	*Chamaecytisus hirsutus*	6(5)	2(33)	
	10	*Ch. supinus*	10(6)	1(10)	
	13	*Cytisus scoparius*	3(3)	3(100)	AP, S, Z
	19	*C. sessilifolius*	2(2)	2(100)	Z
	8	*Genista pilosa*	4(1)	2(50)	
	3	*G. tinctoria*	52(29)	2(4)	Z
	>100	*Laburnum anagyroides*	8(7)	2(25)	Z
	7	*Petteria ramentacea*	5(2)	5(100)	Z
	15	*Spartium junceum*	8(4)	4(50)	Z

[1] Number of locations.
[2] Only publications are referred to that report on the same host plant species. Publications mentioning only plant genera (e.g. "*Trifolium* spp.") have not been considered. A = Anton 1998b; B = Borowiec 1988; AP = Aldridge and Pope 1986; H = Hoffmann 1945; K = Kaszab 1970; KT = Kruess and Tscharntke 1994; L = Lukjanovitsh and Ter-Minassian 1957; S = Strejček 1990; Z = Zacher 1952b.

host plant species and their congeneric plant species are given in Tables 1–3, roughly reflecting the frequency of the plant species' occurrence.

Frequency of bruchid presence

Bruchids were found in 51 plant species (37.0% of all plant species sampled) with 12 *Bruchus* and 15 *Bruchidius* species (Table 1 and 2, Fig. 1 and 2). Of the 51 bruchid host plant species, 40 (78.4%) were attacked by a single bruchid species, eight (15.7%) by two, two (3.9%) by three, and only one (2.0%), *Vicia tenuifolia*, by four species, although one of the latter, *Bruchus brachialis*, occurred very sporadically in that plant (Table 1). Moreover, 37 plant species that are congeneric with bruchid host species were uninfested (Table 3). Bruchids occurred in 38.3% of the host plant samples.

Host specificity

Most bruchid species reared from the plant samples were found to be highly host specific (Table 1 and 2, Fig. 1 and 2). Considering only those species that were reared from 4 or more samples of a plant species, the following exemplify monophagy or at least ecological monophagy (Fox and Morrow 1981): *Bruchus pisorum* on *Pisum sativum*, *Bruchidius glycyrhizae* on *Glycyrrhiza echinata*, *Bi. imbricornis* on *Galega officinalis*, *Bi. marginalis* on *Astragalus glycyphyllos*, *Bi. pusillus* on *Coronilla varia*, and *Bi. seminarius* on *Tetragonolobus maritimus*. Very narrow oligophagy (restricted to one plant genus) was found in *Bruchidius varius* associated only with *Trifolium* spp. (Table 2, Fig. 2). *Bruchus* spp. (Table 1, Fig. 1) occurred only in either *Lathyrus* or *Vicia* species, except for *Bu. atomarius* that infested species of both genera. However, *Bu. atomarius* occurred only in *Vicia* spp. not attacked by *Bu. brachialis*,

Bu. libanensis, *Bu. luteicornis*, *Bu. rufimanus*, *Bu. occidentalis* or *Bu. venustus*. *Bruchidius villosus* showed the broadest host range by occurring in species of 5 genera that, however, belong to a single tribe, Genisteae. Even this case represents narrow oligophagy.

Discussion

Presence/absence of bruchids in legume species

The literature on bruchid host plants often refers to plant genera only (Hoffmann 1945, Lukjanovitsh and Ter-Minassian 1957, Kaszab 1970, Borowiec 1988, Strejček 1990) suggesting the null hypothesis that bruchid species are specialised on plant genera rather than on plant species. According to our data, however, only 37% of the sampled legume species harboured bruchids leaving 37 congeneric species (27% of all species sampled) unoccupied (Table 3). As several of the latter species are mentioned in the literature as bruchid host plants, our negative results may mean that very low infestation rate prevented detection or that the literature data do not hold for the local ecological scenario or that they are incorrect. Thus, almost 2/3 of the legume species represent resources not used by bruchids ("empty" or "vacant niches", Strong et al. 1984). This strongly supports Price's (1983) opinion that in nature the species are "more like sardines in an ocean than sardines in a tin, with much ecological space
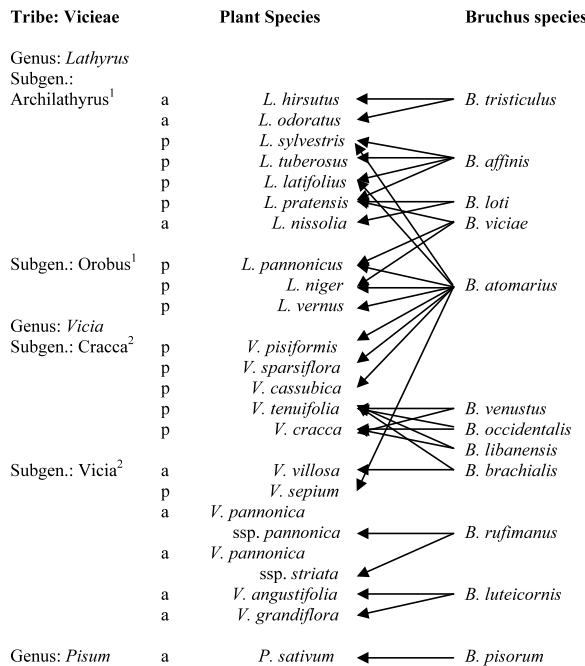

Fig. 1. The host plant relations of *Bruchus* species. 1 = subgenus names after Jávorka (1925); 2 = subgenus names after Hanelt and Mettin (1989); a = annual; p = perennial.
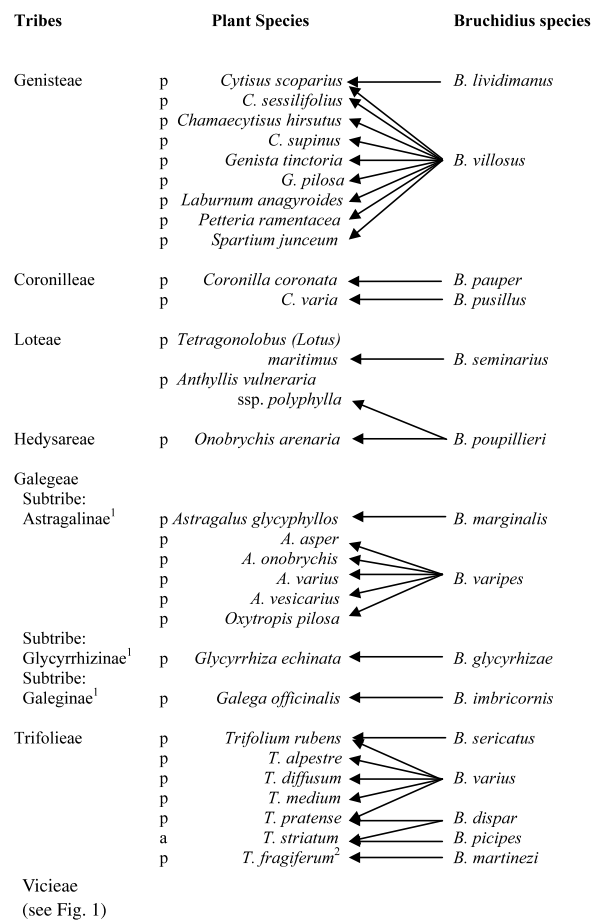

Fig. 2. The host plant relations of *Bruchidius* species. 1 = subtribe names after Sanderson and Liston (1995); 2 = *Trifolium fragiferum* belongs to the subgenus *Lotoidea*, the other *Trifolium* species belong to the subgenus *Trifolium* (Tutin et al. 1978); a = annual; p = perennial.

between species." This, and the fact that 78.4% (!) of the host plant species harboured only a single bruchid species, also indicate that the likelihood of interspecific competition in bruchids must be very low. So, it is highly unlikely that the extant pattern of host affiliation (Table 1–3) represents niche partitioning that resulted from competition.

Comparison of bruchid and host plant phylogenies

Unfortunately, no phylogeny of bruchid species is available so far. For a phylogenetic comparison with the host plants only taxonomic relations can be used. The genera *Bruchus* and *Bruchidius* are clearly distinct, as they belong to well-defined separate tribes of the subfamily Bruchinae (see above). Thus, recent bruchid taxonomy can be considered roughly reflecting phylogenetic relations at least above the species level.

Table 3. List of uninfested plant species congeneric with the species from which *Bruchus* or *Bruchidius* spp. were reared.

Plant tribes and species	No. of samples (locations)
Tribe Genisteae	
Chamaecytisus albus	2(2)
Ch. austriacus	17(12)
Chamaespartium (Genista) sagittale	2(2)
Genista germanica	2(2)
Laburnum alpinum	1(1)
Lembotropis (Cytisus) nigricans	30(21)
Tribe Coronilleae	
Coronilla emerus	3(2)
Tribe Loteae	
Lotus tenuis	3(2)
L. corniculatus	75(45)
Tribe Hedysareae	
Onobrychis viciifolia	7(6)
Tribe Galegeae	
Astragalus austriacus	4(4)
A. cicer	28(23)
A. dasyanthus	1(1)
A. exscapus	4(4)
Glycyrrhiza glabra	1(1)
Tribe Trifolieae	
Trifolium angulatum	1(1)
T. arvense	3(3)
T. aureum	20(11)
T. campestre	4(4)
T. hybridum	6(6)
T. incarnatum	3(3)
T. montanum	6(6)
T. ochroleucon	4(4)
T. pallidum	1(1)
T. pannonicum	4(4)
T. repens	12(8)
T. retusum	1(1)
Tribe Vicieae	
Lathyrus aphaca	3(2)
L. sativus	7(3)
L. sphaericus	2(2)
Vicia dumetorum	7(7)
V. faba	3(2)
V. hirsuta	22(18)
V. lathyroides	3(3)
V. narbonensis	2(2)
V. sativa ssp. *sativa*	3(3)
V. tetrasperma	10(9)

At present no unified, detailed phylogenies are available for all legume genera (J. H. Kirkbride, Jr. pers. comm.). Yet, a recent comparison of the available data has shown good agreement between molecular and morphological phylogenies at various taxonomic levels (Crisp and Doyle 1995, Doyle 1995) Molecular studies indicate also that Genisteae, Coronilleae and Loteae form one related group, while Hedysareae, Galegeae, Trifolieae and Vicieae comprise another one (Liston 1995). Furthermore, Sanderson and Liston (1995) have defined the subtribes of Galegeae by analysing the chloroplast genome. That means that legume taxonomy, as summarised by Polhill and Raven (1981), practically reflects phylogeny at least at the tribal level. In Fig. 1 and 2 we use Liston's (1995) grouping of the tribes.

Though no phylogenies have been worked out for bruchids so far, the genera *Bruchus* and *Bruchidius* are well separated as they belong to two different tribes, so they can be considered as distinct phyletic units. Therefore, their relation to legume taxa may reflect phyletic relations, so we can conclude from Fig. 1 and 2 that phyletic congruence is lacking at the species-to-species level. However, bruchid genera (representing two separate tribes) show rough congruence with legume tribes. Specifically, *Bruchus* species live in species of a single tribe (Vicieae), while *Bruchidius* species live in legume species of 7 tribes! Thus, *Bruchus* species seem phylogenetically more conservative than *Bruchidius* species. It is also noteworthy that the 7 legume tribes share no *Bruchidius* species among them except *Bruchidius poupillieri* occurring in both Loteae and Hedysareae. Furthermore, in the tribe Galegeae each subtribe harbours different bruchid species. This picture is very similar to the affiliation of the clades of *Ophraella* leaf beetle species to their hosts that also belong to different tribes of Asteraceae (Futuyma et al. 1995).

Evolution of bruchid-plant association

Following Ehrlich and Raven's (1964) paper many authors suppose that extant insect-plant associations resulted from coevolution. Assumptions are made at two levels: (1) At the species level it is assumed that insects select the plants for resistance traits (e.g. toxic chemicals), and that the plants select the insects for counteradaptations (e.g. detoxifying mechanisms) resulting in an "arms race" between the partners (Bell 1981, Rosenthal 1981, 1983, Berenbaum 1983, 2001, Mitter et al. 1991). (2) At the macroevolutionary level it is assumed that reciprocal selection resulted in cospeciation exemplified by congruent insect-plant phylogenies (Berenbaum 1983, 2001, Farrell and Mitter 1990, Mitter et al. 1991). It should be kept in mind, however, that any association of organisms can be regarded as a result of coevolution, if there is evidence for reciprocal selection between the partners (Thompson 1994). Yet, presently it seems as Thompson (1999) rightly states that "we do not have even a single study demonstrating actual reciprocal selection on herbivores and plants and its dynamics over multiple generations within a local community." Thus, it is not surprising that Johnson (1990) concluded in his review that "all of the literature on bruchid-host plant coevolutionary studies is correlative" and that coevolution is equivocal. In fact, there is no evidence whatever for a reciprocal selection between bruchids and legumes and for assuming that speciation in legumes and bruchids resulted or was influenced by coevolution.

Considering our data, the evolution of bruchid/plant associations can be envisaged as follows. At the species level: Though there is no experimental evidence for the

selection of legume plant traits (e.g. concentration of secondary seed chemicals) by bruchids, its possibility can not be excluded. It is, however, unknown to what extent (if at all) the chemical composition of the legume species has been affected by earlier attacks of the bruchid species presently associated with them? As Janzen (1981) pointed out, "we can never know with which animal a plant trait coevolved, if it did at all." The legumes, however, most likely selected the bruchids for adaptation to their host's chemistry, phenology, etc., therefore, selection acting also presently in bruchid/plant associations must be highly asymmetric.

As regards the macroevolutionary level, the lack of evidence of tight reciprocal selective interactions between plants and bruchids, as well as the lack of a species-to-species phyletic congruence that has been regarded as a proof for coevolution, negate the assumption of bruchid-plant coevolution. Likewise, Futuyma and McCafferty (1990) found no evidence for coevolution in the case of *Ophraella* leaf beetle species that show a host plant pattern very similar to that of bruchids. An alternative explanation is sequential evolution (Jermy 1984; sequential colonisation, Brooks and McLennan 1991) proposing that legumes have evolved into the extant species, while bruchids switched and adapted to them without affecting the macroevolution of legumes.

As for the possible mechanism of host switches, i.e. of sequential evolution, it should be considered that according to behavioural studies on bruchids (Szentesi 1976, Jermy and Szentesi 1978, Pouzat 1981) and on other herbivorous insects (Wiklund 1975), host specificity is based primarily on the females' oviposition behaviour. Therefore, it is very likely that the evolution of host specialisation in bruchids resulted primarily from the evolution of the nervous system (especially chemoreception) that determines host selection behaviour, as has been propounded by several authors for herbivorous insects in general (Jermy 1984, 1993, Dethier 1987, Menken and Roessingh 1998). As Chapman (1999) pointed out: "It's all in the neurones." According to Bernays (2001), in non-orthopteroid insects "small changes in a receptor or synapse may have a large impact on behaviour," therefore, these insects "may evolve detection and discrimination mechanisms relatively rapidly and so are able to track plant chemical evolution..." Thus, the evolution of the neural mechanisms resulting in specific plant recognition may be the leading process in host switches, followed by selection through various ecological and physiological agents, such as enemies (Bernays and Graham 1988), competition with other herbivores, nutritional value or toxicity of the new host, its phenology, etc. acting at particular places and times (Jermy 1993, Schoonhoven et al. 1998). The nature of genetic changes affecting host selection behaviour may explain the host patterns shown in Fig. 1 and 2, as well as the absence of

bruchids in 37 legumes congeneric with the host species (Table 3) and their absence in further 50 species from all sampled species.

It is regrettable that the plant chemicals that evoke specific oviposition behaviour in bruchids have not been studied so far. There is a vast literature on the secondary chemicals of ripe seeds. However, all bruchid species dealt with here oviposit on unripe pods, or into flowering heads, so it is unlikely that the same chemicals represent specific sign stimuli for the females.

Narrow host specificity, however, may result also via "host race" formation (Bush 1975, Diehl and Bush 1989, Feder 1998, Nosil et al. 2002). How far this process was involved in the evolution of bruchid-plant associations is difficult to estimate. It would be important to check, however, whether association with phenologically and morphologically diverse species of 6 plant genera also results in genetic differences among populations of the broadly oligophagous *Bruchidius villosus*.

In conclusion, host switches presumably had different courses in the two bruchid genera resulting in host affiliations that show more evolutionary conservatism in *Bruchus* than in *Bruchidius* species. The resulting host patterns may mirror also different genetic constraints on this evolutionary process, as has been emphasised by Futuyma et al. (1995) for the evolution of host affiliation in phytophagous insects in general. It also strongly supports Futuyma's (1991) view: "Such cases challenge us to ask whether the evolutionary events can be understood or predicted at all."

References

Aldridge, R. J. W. and Pope, R. D. 1986. The British species of *Bruchidius* Schilsky (Coleoptera: Bruchidae). – Entomol. Gaz. 37: 181–193.

Anton, K.-W. 1998a. Revision of the genus *Bruchidius*. Part I: the *B. seminarius* group (Coleoptera: Bruchidae). – Stuttgart. Beitr. Naturkde Ser. A 573: 1–13.

Anton, K.-W. 1998b. Results of the Czechoslovak-Iranian entomological expeditions to Iran 1970, 1973 and 1977. Coleoptera: Bruchidae. – Casopis Národního muzea. Rada prirodovedn 167: 73–90.

Anton, K.-W. 2001. Bemerkungen zur Faunistik und Taxonomie mitteleuropäischer Samenkäfer (Coleoptera: Bruchidae). – Folia Entomol. Hung. 62: 43–49.

Bell, E. A. 1981. Non-protein amino acids in the Leguminosae. – In: Polhill, R. M. and Raven, P. H. (eds), Advances in legume systematics. R. Bot. Gardens, Kew, England, pp. 489–499.

Berenbaum, M. R. 1983. Coumarines and caterpillars. A case in coevolution. – Evolution 37: 163–179.

Berenbaum, M. R. 2001. Chemical mediation of coevolution: phylogenetic evidence for Apiaceae and associates. – Ann. Missouri Bot. Gard. 88: 45–59.

Bernays, E. A. 2001. Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. – Annu. Rev. Entomol. 46: 703–727.

Bernays, E. and Graham, M. 1988. On the evolution of host specificity in phytophagous arthropods. – Ecology 69: 886–892.

Birch, A. N. E., Simmonds, M. S. J. and Blaney, W. M. 1989. Chemical interactions between bruchids and legumes. – In: Stirton, C. H. and Zarucchi, J. L.(eds), Advances in legume biology. Monogr. Syst. Bot. Mo. Bot. Gard., St. Louis, Missouri 29: 781–809.

Borowiec, L. 1987. The type-material of *Bruchus pusillus* Germar and *B. picipes* Germar (Coleoptera, Bruchidae). – Polskie Pismo Entomol. 57: 591–592.

Borowiec, L. 1988. Bruchidae-Strakowce (Insecta: Coleoptera). Fauna Polski-Fauna Poloniae, Tom. 11. – Panstwowe Wydawnictwo Naukowe, Warszawa.

Brooks, D. R. and McLennan, D. A. 1991. Phylogeny, ecology, and behavior. – The Univ. of Chicago Press.

Bush, G. L. 1975. Modes of animal speciation. – Annu. Rev. Ecol. Syst. 6: 339–364.

Chapman, R. F. 1999. It's all in the neurones. – Entomol. Exp. Appl. 91: 259–265.

Crisp, M. D. and Doyle, J. J. 1995. Advances in legume systematics. Part 7. Phylogeny. – The R. Bot. Gardens, Kew, England.

Dethier, V. G. 1987. Analyzing proximate causes of behavior. – In: Huettel, M. D. (ed.), Evolutionary genetics of invertebrate behavior. Plenum Press, pp. 319–328.

Diehl, S. R. and Bush, G. L. 1989. The role of habitat preference in adaptation and speciation. – In: Otte, D. and Endler, J. A. (eds), Speciation and its consequences. Sinauer, pp. 345–365.

Doyle, J. J. 1995. DNA data and legume phylogeny: a progress report. – In: Crisp, M. D. and Doyle, J. J. (eds), Advances in legume systematics. Part 7. Phylogeny. The R. Bot. Gardens, Kew, England, pp. 11–30.

Ehrlich, P. R. and Raven, P. H. 1964. Butterflies and plants: a study in coevolution. – Evolution 18: 586–608.

Fabres, G. and Reymonet, C. 1991. L'induction maternelle de la diapause larvaire chez *Dinarmus acutus* (Hym.: Pteromalidae). – Entomophaga 36: 121–129.

Farrell, B. D. and Mitter, C. 1990. Phylogenies of insect-plant interactions: have *Phyllobrotica* leaf beetles (Chrysomelidae) and the Lamiales diversified in parallel? – Evolution 44: 1389–1403.

Farrell, B. D. and Mitter, C. 1998. The timing of insect/plant diversification: might *Tetraopes* (Coleoptera: Cerambycidae) and *Asclepias* (Asclepiadaceae) have co-evolved? – Biol. J. Linn. Soc. 63: 553–577.

Feder, J. L. 1998. The apple maggot fly, *Rhagoletis pomonella*. Flies in the face of conventional wisdom about speciation? – In: Howard, D. J. and Berlocher, S. H. (eds), Endless forms, species and speciation. Oxford Univ. Press, pp. 130–144.

Fox, L. R. and Morrow, P. A. 1981. Specialization: species property or local phenomenon? – Science 211: 887–893.

Futuyma, D. J. 1991. Evolution of host specificity in herbivorous insects: genetic, ecological, and phylogenetic aspects. – In: Price, P. W., Lewinsohn, T. M., Wilson Fernandes, G. and Benson, W. W. (eds), Plant-animal interactions: evolutionary ecology in tropical and temperate regions. J. Wiley & Sons, pp. 431–454.

Futuyma, D. J. and McCafferty, S. J. 1990. Phylogeny and the evolution of host associations in the leaf beetle genus *Ophraella* (Coleoptera, Chrysomelidae). – Evolution 44: 1885–1913.

Futuyma, D. J., Keese, M. C. and Funk, D. J. 1995. Genetic constraints on macroevolution: the evolution of host affiliation in the leaf beetle genus *Ophraella*. – Evolution 49: 797–809.

Hanelt, P. and Mettin, D. 1989. Biosystematics of the genus *Vicia* L. (Leguminosae). – Annu. Rev. Ecol. Syst. 20: 199–223.

Hoffmann A. 1945. Coléoptères Bruchides et Anthribides. Faune de France. – Paul Lechevalier, Paris 44: 1–184.

Janzen, D. H. 1981. The defenses of legumes against herbivores. – In: Polhill, R. M. and Raven, P. H. (eds), Advances in legume systematics. R. Bot. Gardens, Kew, England, pp. 951–977.

Jávorka, S. 1925. Flora Hungarica. – Studium, Budapest.

Jermy, T. 1984. Evolution of insect/host plant relationships. – Am. Nat. 124: 609–630.

Jermy, T. 1993. Evolution of insect-plant relationships – a devil's advocate approach. – Entomol. Exp. Appl. 66: 3–12.

Jermy, T. and Balázs, K. (eds) 1990. A növényvédelmi állattan kézikönyve. 3. köt. [Handbook of agricultural entomology, Vol. 3] – Akadémiai Kiadó, Budapest. (in Hungarian)

Jermy, T. and Szentesi, Á. 1978. The role of inhibitory stimuli in the choice of oviposition site by phytophagous insects. – Entomol. Exp. Appl. 24: 458–471.

Johnson, C. D. 1990. Coevolution of Bruchidae and their hosts: evidence, conjecture, and conclusions. – In: Fujii, K., Gatehouse, A. M., Johnson, C. D. et al. (eds), Bruchids and legumes: economics, ecology and coevolution. Dr. W. Junk Publishers, pp. 181–188.

Kaszab, Z. 1970. Bruchidae-Zsizsikfélék. Fauna Hungariae. – Akadémiai Kiadó, Budapest 9: 1–34.

Kruess, A. and Tscharntke, T. 1994. Habitat fragmentation, species loss, and biological control. – Science 264: 1581–1584.

Liston, A. 1995. Use of polymerase chain reaction to survey for the loss of the inverted repeat in the legume chloroplast genome. – In: Crisp, M. D. and Doyle, J. J. (eds), Advances in legume systematics. Part 7. Phylogeny. The R. Bot. Gardens, Kew, England, pp. 31–40.

Lukjanovitsh, F. K. and Ter-Minassian, M. E. 1957. Zhestkokrylie. Zhuki-zernovki (Bruchidae). – Izdatelstvo Akademii Nauk SSSR, Moskva. Fauna SSSR, XXIV, 1: 1–209.

Menken, B. J. and Roessingh, P. 1998. Evolution of insect-plant associations. – In: Howard, D. J. and Berlocher, S. H. (eds), Endless forms, species and speciation. Oxford Univ. Press, pp. 145–156.

Menken, S. B. J., Herrebout, W. M. and Wiebes, J. T. 1992. Small ermine moths (*Yponomeuta*): their host relations and evolution. – Annu. Rev. Entomol. 37: 41–88.

Miller, J. S. and Wenzel, J. W. 1995. Ecological characters and phylogeny. – Annu. Rev. Entomol. 40: 389–415.

Mitter, C., Farrell, B. and Futuyma, D. J. 1991. Phylogenetic studies of insect-plant interactions: insights into the genesis of diversity. – Trends Ecol. Evol. 6: 290–293.

Nosil, P., Crespi, B. J. and Sandovar, C. P. 2002. Host-plant adaptation drives the parallel evolution of reproductive isolation. – Nature 417: 440–443.

Polhill, R. M. and Raven, P. H. (eds) 1981. Advances in legume systematics. – R. Bot. Gardens, Kew, England.

Pouzat, J. 1981. The role of sense organs in the relations between bruchids and their host plants. – In: Labeyrie, V. (ed.), The ecology of bruchids attacking legumes (pulses). Dr. W. Junk Publishers, pp. 61–72.

Price, P. W. 1983. Hypotheses on organization and evolution in herbivorous insect communities. – In: Denno, R. F. and McClure, M. S. (eds), Variable plants and herbivores in natural and managed systems. Academic Press, pp. 559–596.

Rosenthal, G. A. 1981. Role of allelochemics in the specialisation of trophic relations between bruchids and legumes. – In: Labeyrie, V. (ed.), The ecology of bruchids attacking legumes (pulses). Dr. W. Junk Publishers, pp. 97–100.

Rosenthal, G. A. 1983. The adaptation of a beetle to a poisonous plant. – Sci. Am. 249: 164–171.

Sanderson, M. J. and Liston, A. 1995. Molecular phylogenetic systematics of Galegeae, with special reference to *Astragalus*. – In: Crisp, M. D. and Doyle, J. J. (eds), Advances in legume systematics. Part 7. Phylogeny. The R. Bot. Gardens, Kew, England, pp. 331–350.

Schoonhoven, L. M., Jermy, T. and van Loon, J. J. A. 1998. Insect-plant biology. From physiology to evolution. – Chapman and Hall.

Soó, R. and Kárpáti, Z. 1968. Növényhatározó. (Handbook of the Hungarian Flora.) Vol. II. – Tankönyv Kiadó, Budapest. (in Hungarian.)

Strejček, J. 1990. Brouci čeledi, Bruchidae, Urodonidae a Anthribidae. – Academia, Praha.

Strong, D. R., Lawton, J. H. and Southwood, Sir Richard 1984. Insects on Plants. – Blackwell.

Szentesi, Á. 1976. The effect of the amputation of head appendages on the oviposition of the bean weevil, *Acanthoscelides obtectus* Say (Coleoptera: Bruchidae). – Symp. Biol. Hung. 16: 275–281.

Szentesi, Á. and Jermy, T. 1995. Predispersal seed predation in leguminous species; seed morphology and bruchid distribution. – Oikos 73: 23–32.

Szentesi, Á., Jermy, T. and Takács, V. 1996. Niche relations in *Vicia*-inhabiting *Bruchus* spp. – Entomol. Exp. Appl. 80: 152–155.

Thompson, J. N. 1994. The coevolutionary process. – Univ. of Chicago Press.

Thompson, J. N. 1999. What we know and do not know about coevolution: insect herbivores and plants as a test case. – In: Olff, H., Brown, V. K. and Drent, R. H. (eds), Herbivores: between plants and predators. Blackwell Science.

Tutin, T. G., Heywood, V. H., Burges, N. A. et al. (eds), 1978. Flora Europaea. Vol. 2. Rosaceae to Umbelliferae. – Cambridge Univ. Press.

Wahlberg, N. 2001. The phylogenetics and biochemistry of host-plant specialization in melitaeine butterflies (Lepidoptera: Nymphalidae). – Evolution 55: 522–537.

Wendt, H. 1981. Eine für Südost-Europa neue Samenkäfer-Art (Coleoptera: Bruchidae). – Folia Entomol. Hung. 34: 223–226.

Wiklund, C. 1975. The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. – Oecologia 18: 186–197.

Zacher, F. 1952a. Die Nährpflanzen der Samenkäfer. – Z. Angew. Entomol. 33: 210–217.

Zacher, F. 1952b. Die Nährpflanzen der Samenkäfer. – Z. Angew. Entomol. 33: 460–480.

Zampetti, M. F. 1993. Una nuova specie di *Bruchus* del Libano (Coleoptera, Bruchidae). – Fragm. Entomol., Roma 24: 215–218.