STRUCTURE OF ANT ASSEMBLAGES IN PLANTED POPLAR (POPULUS ALBA) FORESTS AND THE EFFECT OF THE COMMON MILKWEED (ASCLEPIAS SYRIACA)

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Besides changes in vegetation during succession, the regular disturbance can be also responsible for the alteration of arthropod assemblages in planted forests, especially when the disturbance allows the establishment of non-native plant species. In our study, we investigated the structure of ant assemblages in plantations of different aged poplar forests (*Populus alba*) infested with the invasive common milkweed (*Asclepias syriaca*). Our results showed that the dispersion pattern of colonies was mostly regular with higher interspecific neighbour distances in the younger forests and higher intraspecific neighbour distances in the older forests. In the younger forests, most colonies nested in milkweed stems, while in the older forests colonies used more types of nesting sites and were mostly found in the soil and litter. These findings suggest that depending on whether suitable sites for nesting are limited or not, the importance of intra- and interspecific competition may vary among the different aged forests. The high abundances of milkweed thus can lead to the significant alteration of local ant assemblages, especially in the earlier successional stages of the forests.

Keywords: dispersion pattern, inter-nest distances, invasive species, plantation, succession.

INTRODUCTION

Poplar forests (with *Populus alba* and its natural hybrid *Populus canescens*) are common types of planted forests on calcareous sandy sites in the Danube–Tisza region of Hungary (Rédei 2000). In the absence of natural forests, planted forests can still act as shelters for some forest dwelling species (Carnus *et al.* 2006, Brockerhoff *et al.* 2008, Bremer & Farley 2010). For example, the endangered ground beetle, *Holcaspis brevicula*, a locally endemic species in New Zealand, is thought to depend on a forest plantation, as its only remaining habitat (Brockerhoff *et al.* 2005). However, the management in planted forests can be much more intense (e.g. intensive logging) than in natural regenerative forests (Noble & Dirzo 1997). This regular disturbance allows the establishment of non-native species (e.g. plants) (Gordon 1998, Gallé *et al.*

2015, Gallé *et al.* 2016), which can induce negative changes in ground-dwelling arthropod assemblages (Schirmel *et al.* 2011, Gallé *et al.* 2015), usually by altering habitat structure (Hejda *et al.* 2009). Other consequences of habitat disturbance can be the reduction in the number of habitat specialists (Okland *et al.* 2003), or increase in the number of generalist or open habitat specialist species (Riley & Browne 2011, Gallé *et al.* 2016). In the older planted forests, however, native forest species can settle due to the well-developed soil layer and associated fungal flora, and the increased dead wood on the forest floor (Brockerhoff *et al.* 2008).

Another factor responsible for the alteration of arthropod assemblages is the on-going change of forest vegetation throughout the succession (Gallé et al. 2016). From the ants' perspective, forests can differ markedly in many characteristics (e.g. vegetation structure, litter coverage, number of fallen twigs and rotten trunks), which can substantially alter local ant assemblages (Gallé et al. 1998, ALVARADO et al. 2000, HOLEC et al. 2006). Therefore, the alteration of these characteristics may lead to changes in the relative and absolute frequencies of different ant species (GALLÉ 1991), influencing also their foraging behaviour, dispersion, colonising potential and competitive interactions (Puntilla & Haila 1996, Vepsäläinen et al. 2000). Competition is usually considered to have a great effect in shaping ant communities (Savolainen & Vepsäläinen 1988, Braschler & Baur 2003), although other types of interactions can also be important, e.g. predation or social parasitism (Сzесноwsкі & Markó 2005, Cerdá et al. 2013, Gallé et al. 2016). The heterogeneity of a given habitat, however, can favour the co-occurrence of several ant species on the same location by decreasing the overlap in resource requirements (Coelho & Riberio 2006) and/or by increasing the amount of available nesting sites (Brockerhoff et al. 2008).

Ants represent a diverse and locally very abundant group of omnivorous forest arthropods (Hölldbeler & Wilson 1990). Since they are keystone species in several ecological processes that can be sensitive to environmental changes, they can provide substantial information about the ecological and functional implications of disturbances (Hoffman & Andersen 2003, Ribas *et al.* 2012). The quality of a given habitat is determined primarily by the variability and quantity of available nesting sites and food resources (Braschler & Baur 2003), but it can also be influenced by the presence of other ant species, especially by those with similar needs (Levings & Traniello 1981, Andersen 1991, Davidson 1998).

In our study, we investigated the structure and composition of ant assemblages in plantations of different aged poplar forests infested with the invasive common milkweed (*Asclepias syriaca*) by using nest mapping. We expected that there would be differences (1) in the dispersion pattern and internest distances of colonies, (2) in the types of nesting sites and proportion of

each nesting site used, and (3) in the influence of the milkweed cover on the nesting habits of ants among the different aged forest stands.

MATERIAL AND METHODS

Study site – Our field work was carried out near Bugacpusztaháza village (in the southern Great Plain region of Hungary) in June 2012. This region has a characteristic semi-desert climate, therefore, local plant assemblages usually develop on large granulous sandy soil (Kertész *et al.* 2011), but a chernozem or a chernozem-like sandy soil is also present in several parts of the region (Biró 2006). The mean annual precipitation is between 550–600 mm, and the mean temperature varies between 10.2°C and 10.8°C (Török *et al.* 2003).

We investigated four mixed deciduous forest stands, which were mainly formed by *P. alba* (at least 70%), with at least 10 years between their age. For nest mapping, we choose a 10-year-old (ca. 11 ha, further FA), a 26-year-old (ca. 3.2 ha, further FB), a 36-year-old (ca. 5 ha, further FC), and a 46-year-old (ca. 3.35 ha, further FD) forest. The smallest distance between the forests was 800 m.

Asclepias syriaca, the common milkweed is a native to the eastern part of North America (Bhowmik & Baden 1976), but it is considered an invasive species in Hungary. The species was repeatedly introduced to Hungary over the past few centuries, and as a successful invader, it has recently spread rapidly, especially on sandy soils, infesting forest plantations, field crops, vineyards, orchards and other habitats under anthropogenic influence (Balogh et al. 2007, Bagi 2008). According to the study of Gallé et al. (2015), the common milkweed has mixed (i.e. negative but also positive) effects on local invertebrate assemblages. Aphids that feed on common milkweed are usually tended by ants for their honeydew (Smith et al. 2008, Molnár et al. 2010, Abdala-Roberts et al. 2012, Gallé et al.

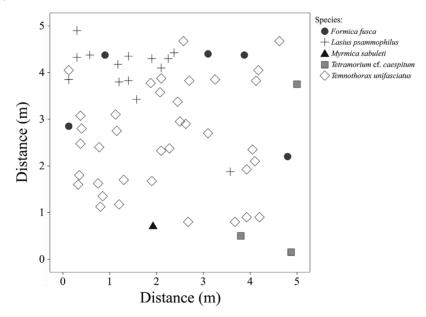


Fig. 1. An example of 5 m × 5 m sampling plot (FB1) from the 26-year-old forest (FB)

 Table 1. Number of colonies found in the eight sampling plots of the four different aged forests (FA: 10-year-old, FB: 26-year-old,

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Species	FA1	FA2	FB1	FB2	FC1	FC2	FD1	FD2	Total
Formica fusca Linnaeus, 1758	5	Ŋ	5	9	4	17	3	8	53
Lasius flavus (Fabricius, 1782)	I	I	I	I	I	I	I	1	1
Lasius psammophilus Seifert, 1992	I	I	14	I	I	I	I	I	14
Myrmica sabuleti Meinert, 1861	2	гO	1	10	15	10	20	20	83
Solenopsis fugax (Latreille, 1798)	I	I	I	2	I	I	I	I	2
Tapinoma madeirense Forel, 1895	I	1	I	I	I	I	1	1	3
Temnothorax crassispinus (Karavaiev, 1926)	I	2	I	I	9	18	П	2	29
T. interruptus (Schenck, 1852)	I	I	I	I	I	I	I	1	1
T. unifasciatus (Latreille, 1798)	30	36	37	27	20	27	24	18	219
Tetramorium cf. caespitum	1	I	3	1	1	I	I	1	3
Total	37	49	09	45	45	72	49	51	408

2015), and hollow milkweed stems can serve as potential nesting sites for many ant species (ALLOWAY 1979, STUART 1992).

Study methods - In order to survey local ant assemblages, we selected two 5 m × 5 m plots with at least 50 m distance between them in each forest type. In each plot we surveyed the upper soil surface, leaf litter, snail shells, fallen twigs and stems serving as potential nesting sites for ants. We recorded only those nesting sites that were actually used by an ant colony. To determine the exact distance between individual colonies, the nesting sites were accurately mapped with the help of a grid of 0.2 m × 0.2 m. Together with colony mapping, the type of nesting sites (i.e. in the soil, twigs, etc.) was also recorded. For species identification, we took a sample of at least three workers from each nest. Ants were determined using the keys of Czechowski et al. (2002, 2012). In each forest site, the cover of milkweed was estimated in three 1 m × 1 m plots within a few meters distance from the 5 m \times 5 m plots. In each case, the average of the cover estimates was calculated for the analyses.

Statistical analysis. Dispersion pattern and inter-nest distances of colonies – Using the maps with the coordinates of ant colonies (Fig. 1) we estimated both the dispersion pattern of colonies and their nearest intraspecific and interspecific neighbour distances (further intraspecific distances, respectively).

The dispersion pattern of colonies was determined using Clark and Evans' (1954) nearest neighbour method. This was carried out both for all colonies mapped in a

given sampling plot and for individual species if the number of their colonies was at least 9 per plot. The differences among the different aged forests regarding the intraspecific (N = 398) and interspecific (N = 405) distances were analysed with GLMMs. In the model, the forest age was included as a fixed factor, while plot ID as a random factor. Since the data was overdispersed, negative binomial error term was used in the model. GLMMs were performed using the *glmer* function from the *lme4* package (BATES *et al.* 2015). The relevel function was used to carry out post hoc sequential comparisons among factor levels. We applied a table-wide sequential Bonferroni-Holm correction to reveal the exact significance levels. The within-forest type comparisons of the intraspecific and interspecific distances of colonies were compared with paired Wilcoxon signed rank tests. These pairwise comparisons were also carried out separately for species with 9 or more colonies per plot (as in the analysis of dispersion patterns).

Types of nesting sites and the effect of milkweed – The differences between the older (FC and FD) and younger (FA and FB) forests regarding the number of colonies found in milkweed stems and in other nesting sites were analysed using Fisher's exact tests for count data. This was also carried out separately for *Temnothorax unifasciatus*, since this species was the only one that was found in each sampling plot. The same statistical analysis was used to test whether there are differences in the relative frequencies of different nesting types and milkweed nests among the different aged forest stands. Relative frequencies of the different types of nesting sites in the different aged forest stands were calculated by dividing the number of colonies occupying that type of nesting site with the total number of colonies mapped.

The correlation between the age of forest stands and the total number of colonies (with and without taking into account the nests in milkweed stems) found inside the stands was calculated with Spearman rank correlation. The same test was used for analysing the relation between the estimates of milkweed cover and the number of nests in milkweed stems from the different aged forests. In these tests, the average of the two plots per forest stand was used.

All statistical analyses were carried out using R statistical environment (R Development Core Team 2014).

RESULTS

Altogether, a total of 408 colonies belonging to 10 ant species were found in the eight sampling plots (Table 1). Three species, *Formica fusca, Myrmica sabuleti* and *T. unifasciatus* were those that occurred in all plots, while other species were found only in one or a few plots. Overall, more than half of the colonies mapped belonged to *T. unifasciatus* (FA: 77% of all colonies, FB: 60.5%, FC: 48 % FD: 40%), which nested mainly in milkweed stems.

Dispersion pattern and inter-nest distances of colonies

Overall, a total of 12 different types of nesting sites were recorded and distinguished during nest mapping (Table 2). In most cases, the dispersion pattern of colonies was regular, although the colonies of the most frequent

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Nesting site	FA	FB	FC	FD
soil	0.15	0.21	0.25	0.40
soil & leaf litter	0.01	0.00	0.03	0.03
soil & twig	0.00	0.02	0.04	0.04
soil & milkweed stem	0.01	0.00	0.00	0.00
snail house	0.00	0.00	0.03	0.02
milkweed stem	0.80	0.71	0.50	0.35
twig	0.00	0.02	0.06	0.03
leaf litter	0.02	0.01	0.05	0.11
under stone	0.00	0.02	0.03	0.00
soil & under stone	0.00	0.00	0.09	0.00
litter & twig	0.00	0.00	0.00	0.10
soil & moss	0.00	0.00	0.00	0.02

Table 2. Relative frequencies of nesting site types in the four different aged forests (FA: 10-year-old, FB: 26-year-old, FC: 36-year-old, FD: 46-year-old). Relative frequencies over 0.10 are highlighted in bold.

species, *T. unifasciatus* showed all three types of dispersion patterns (Table 3). The dispersion pattern of the colonies of *M. sabuleti*, the second most frequent species, also proved to be mostly regular ($R \ge 1.44$, p < 0.01), except in one of the FC plots, where it exhibited a random dispersion pattern (R = 0.82, *NS*). The colonies of *Lasius psammophilus* were present in higher numbers only in one of the FB plots, where they showed an aggregated dispersion (R = 0.73, P < 0.05). The colonies of *F. fusca* and *Temnothorax crassispinus*, which were found in higher numbers only in the FC2 plot, were also regularly dispersed (R = 1.56, P < 0.001, and R = 1.49, P < 0.001, respectively).

When comparing the age categories of forest stands, we found no significant differences among them concerning the intraspecific distances (GLMM 2.1 > z > -1.16, N = 398, NS). There were, however, significant differences between the younger (FA and FB) and older forests (FC and FD) in respect of interspecific distances (GLMM z = -3.62, N = 405, p < 0.001), while the differences between the two younger (FA vs FB) and the two older forests (FC vs FD) were not significant (z = -0.09, NS and z = 1.09, NS, respectively).

In the older forests (FC and FD), the intraspecific distances were significantly higher than the interspecific distances (paired Wilcoxon z = -6.70, p < 0.001 and z = -5.78, p < 0.001, respectively), while in the younger forests (FA and FB) the opposite pattern was found (z = -2.24, p < 0.05 and z = -1.99, p < 0.05, respectively) (Fig. 2). From among species, only *T. unifasciatus* had enough (9 or more) colonies in each plot to compare the intraspecific and in-

Table 3. Density and dispersion pattern of all colonies summed and the colonies of the most frequent species in the sampling plots of the different aged forests (FA = 10-year-old, FB = 26-year-old, FC = 36-year-old, FD = 46-year-old). N = number of colonies per plot, R = Clark and Evans' (1954) dispersion index.

Plot	Species	N	Density (colony/m²)	R	Dispersion pattern
FA1	T. unifasciatus	30	1.20	1.28**	regular
	all colonies	37	1.48	1.18**	regular
FA2	T. unifasciatus	36	1.44	0.79*	aggregated
	all colonies	49	1.96	1.28***	regular
FB1	T. unifasciatus	37	1.48	0.91 NS	random
	all colonies	60	2.40	1.41***	regular
FB2	T. unifasciatus	27	1.10	1.08 NS	random
	M. sabuleti	10	0.40	1.71***	regular
	all colonies	45	1.80	1.20**	regular
FC1	T. unifasciatus	20	0.80	1.40***	regular
	M. sabuleti	15	0.60	1.61***	regular
	all colonies	46	1.80	1.33***	regular
FC2	T. unifasciatus	27	1.08	1.58***	regular
	M. sabuleti	9	0.36	0.82 NS	random
	all colonies	71	2.80	1.15**	regular
FD1	T. unifasciatus	25	0.96	0.92 NS	random
	M. sabuleti	20	0.80	1.44***	regular
	all colonies	50	1.96	1.19**	regular
FD2	T. unifasciatus	19	0.76	1.27*	regular
	M. sabuleti	20	0.80	1.40***	regular
	all colonies	52	2.40	1.05 NS	random

t-test: NS 0.05 < p; * 0.01 ; ** <math>0.001 ; *** <math>p < 0.001

terspecific distances of its colonies. In the younger forests (FA and FB), the interspecific distances (paired Wilcoxon z = -4.98, p < 0.001 and z = -4.51, p < 0.001, respectively), while in the older forests (FC and FD) the intraspecific distances were significantly higher (z = -2.10, p < 0.05 and z = -2.04, p < 0.05, respectively).

Types of nesting sites and the effect of milkweed

In the two younger forests (FA and FB), colonies found in milkweed stems belonged to seven species (F. fusca, L. psammophilus, M. sabuleti, Tapinoma

madeirense, T. crassispinus, T temnothorax interruptus, T. unifasciatus), while in the two older forests (FC and FD) only the colonies of T. unifasciatus occupied these nesting sites. In each forest type, significantly more colonies of T. unifasciatus were found in milkweed stems than in any other types of nesting sites summed (Fisher exact test, p < 0.01). In the older forests, the total number of colonies of other species in milkweed stems was significantly lower than that of colonies in other types of nesting sites (Fisher exact test, p < 0.01), while in the younger forests the difference was not significant (Fisher exact test, p = 0.08).

Ants used slightly more types of nesting sites in the older forests than in the younger ones (FA: 5, FB: 6, FC: 7, FD: 9). With the growing age of the forests, the relative frequencies of colonies in milkweed stems decreased, while the relative frequencies of other types of nesting sites increased (FA: 5:1, FB: 7:2, FC: 2:1, FD: 1:1). From among all nesting sites, three (soil, leaf litter and milkweed stems) were used by ants in all forest stands (Table 2).

The mean cover of milkweed was 36% in FA, 13% in FB, 5% in FC and 9% in FD. The percent of milkweed cover was significantly correlated with the total number of colonies found in milkweed stems (Spearman rho = 0.85, p = 0.01). There was, however, no significant correlation between the age of forests and the total number of colonies per forest type (Spearman rho = 0.49, p = 0.21), although, if colonies in milkweed stems were not taken into account, the correlation became significant (Spearman rho = 0.92, p < 0.001).

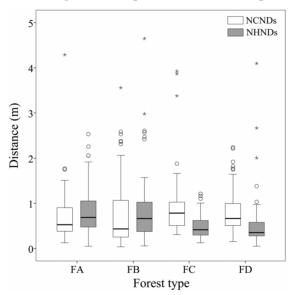


Fig. 2. The nearest intraspecific (white boxes) and interspecific neighbour distances (grey boxes) in the four different aged forests: FA: 10-year-old, FB: 26-year-old, FC: 36-year-old, FD: 46-year-old (median, quartiles, minimum and maximum values, outliers)

DISCUSSION

Dispersion pattern and inter-nest distances of colonies

According to the nearest neighbour method, the dispersion pattern of all colonies found in a given sampling plot was mostly regular, which suggests that competition has an important effect in shaping ant communities in these planted poplar forests. This result is in concordance with many previous findings obtained in other forest habitats (e.g. Levings & Traniello 1981, Ryti & Case 1986, Gotelli & Ellison 2002, Czechowski & Markó 2005), even if other factors, such as forest age, can mask the overall effect of competition (GALLÉ et al. 2016). Competition can have a significant influence on the dispersion of colonies by shifting them to a more regular (overdispersed) spatial arrangement (Herbers 1989, Soares & Schoereder 2001), but it can also cause the exclusion of some species from optimal habitats, forcing them to live under suboptimal conditions (Savalainen & Vepsäläinen 1988, Andersen & Patel 1994, Cerdá et al. 1997, Sanders & Gordon 2000). In our study, the colonies of individual species also showed a regular dispersion pattern in most cases, indicating the existence of strong intraspecific competition. Regular dispersion seems to be typical when the density of colonies is high, and as a result, the overlap in foraging areas and territories can be reduced (Levings & Traniello 1981, Ryti & Case 1984, 1986, Cushman et al. 1988). Contrary to these, the colonies of *L. psammophilus* were aggregated in the FB1 plots, which can be the result of polydomy (i.e. when a colony occupies several nesting sites), as was observed in other Lasius species (Brian et al. 1965, Traniello & Levings 1986, LŐRINCZI 2011). The aggregation of colonies may be not only the result of polydomy, but also of various interspecific interactions (e.g. mutualism) or habitat heterogeneity (Ryti & Case 1984, Herbers 1989, Soares & Schoereder 2001).

Based on our results it seems that the types of nesting sites used were mostly determined by interspecific competition in the younger forests. In these habitats, suitable nesting sites seem to be limited, which was also demonstrated by the nesting of most colonies in milkweed stems. On the contrary, more suitable nesting sites were available in the older forests, so the dispersion pattern of colonies may have been determined mostly by intraspecific competition. This was also supported by the comparison of the nearest intraand interspecific neighbour distances.

Types of nesting sites and the effect of milkweed

During succession, changes in plant diversity are accompanied by changes in habitat variables and by an increase in structural diversity, which can promote the settlement of newcomer ant species and the coexistence of resident ones (Doncaster 1981, Coelho & Riberio 2006). One can expect that ant species richness will increase during succession in response to an increase in structural diversity and forest age (Gallé *et al.* 2016), but this is not always the case. For instance, Osorio-Perez *et al.* (2007) found that the 25–35 years old Puerto Rican forests had the highest ant species richness, since these forests combine the advantageous properties of both the younger (0–5 years) and older (over 60 years) forests.

Early colonizing (pioneer) species have lesser habitat requirements, so they can colonise at the beginning of forest formation, but since they are weaker competitors and react more sensitively to the changes of microclimatic properties, they get easily excluded under stronger competitive pressure (Connell & Slatyer 1977, Soares 2013). On the other hand, poplar forests do not form a closed canopy; moreover, an older forest can even open up (Borhidi 2003), so the appearance of species that are early colonisers, or occur on open, sandy habitats (e.g. *Tetramorium* cf. *caespitum* or *L. psammophilus*) is not surprising, which is supported also by our results. Furthermore, the presence of these species in the younger forest can be explained by the fact that there are still opened sandy patches on the forest floor (Gallé 1991).

Our results indicate that milkweed cover has a significant influence on the nesting habits of some ant species. In the younger forests, where potential nesting sites were scarce, several species and not just typical cavity-dwellers made their nests in milkweed stems, such as T. crassispinus, T. interruptus, L. psammophilus, M. sabuleti and F. fusca. In the older forests, however, these species tended to use other types of nesting sites, except T. unifasciatus, which nested almost exclusively in milkweed stems, independently from the age of forests. In the older forests, more colonies were found in the soil and in decaying wood than in the younger stands. The reason of this may be that during succession, the forest soil becomes firm enough for nest construction (contrary to the sandy soils of younger forests) (Brockerhoff et al. 2008), and the number of fallen branches and rotten trees increases, which can serve as suitable nesting sites for many ant species (ALVARADO et al. 2000, BROCKERHOFF et al. 2008). Our findings support these observations, since we found less species nesting in milkweed stems, and more species that used other types of nesting sites, despite the presence of milkweed stems. Nevertheless, the high abundances of milkweed, especially in the earlier successional stages of the forests, can lead to the significant alteration of local ant assemblages. In the early stages, it can affect the availability of food by hosting several species of aphids, whose honeydew can serve as a stable food source even for laterappearing ant species (Alloway 1979, Stuart 1992, Molnár et al. 2010). More importantly, in the presence of milkweed, the nesting habits of some ants can be altered, since dried milkweed stems can offer nesting possibilities for many

opportunistic, disturbance tolerant ant species. On the other hand, some species that have more developed habitat requirements (characteristic for later successional stages) can also find suitable nesting sites in the early stages, resulting in the homogenization of local ant assemblages through the different successional stages. The appearance of these species in the early stages in higher abundances due to changes induced by *A. syriaca* in the habitat structure (see e.g. Riley & Browne 2011) can lead to the competitive exclusion of other, mainly habitat specialist species, leading to a decrease in local species diversity (Okland *et al.* 2003).

In conclusion, with the growing age of the forests, many changes take place that can markedly affect, among others, the nesting habits of ants and thereby influence the composition and structure of their assemblages. Furthermore, the regular disturbance regime of planted forests can promote the appearance and fast spread of invasive plants, such as *A. syriaca*, which can further alter the nesting habits of many ant species by providing potential nesting sites. This can lead to a homogenization of the different aged stands in respect of local ant assemblages, resulting in considerable differences only between the younger and older forests.

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A Magyar Természettudományi Múzeum gyászbogártípusainak (Tenebrionidae) katalógusa Type catalogue of darkling beetles (Tenebrionidae) preserved in the Hungarian Natural History Museum

by Ottó Merkl, Aranka Grabant & Zoltán Soltész

The Hungarian Natural History Museum (HNHM) houses one of the largest and most complete Tenebrionidae collections of the world, thanks to Zoltán Kaszab (1915–1986), the Museum's former General Director and the most prominent figure of Hungarian coleopterology. The book is a commemoration of the centenary of his birthday.

The introduction summarises the history of the Hungarian Natural History Museum, its Coleoptera Collection and the scientific activity of Zoltán Kaszab.

Type specimens constitute the scientifically most valuable assets of the collection. The catalogue contains types of all the species, subspecies, variations and aberrations which have ever been described in the family Tenebrioni-



dae, and kept in the HNHM, including those already assigned to other families, as well as those which were described in different families but are now members of Tenebrionidae. A total of 21,313 type specimens belonging to 5,941 names are listed herein, including 1,222 holotypes, 4 neotypes, 88 lectotypes, 4,914 syntypes, 86 allotypes, 248 paralectotypes and 14,751 paratypes. The list of the names is followed by a complete list of the 1,212 publications containing the original descriptions.

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