The role of terrestrial isopods (Isopoda: Oniscidea) in the decomposition of aquatic macrophite detritus of Lake Balaton, Hungary

By

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Abstract. Terrestrial isopods were very abundant in the aquatic macrophyte detritus drifts washed ashore by wave action in Lake Balaton, Hungary. Repeated collecting trips yielded six species: *Porcellium collicola, Trachelipus rathkei, Armadillidium vulgare, A. zenckeri, A. versicolor quinqueseriatum, Hyloniscus* sp. The animals were especially abundant in drifts consisting of submerged aquatic plant detritus. In laboratory feeding experiments the animals consumed more detritus of submerged aquatic plants than emerged aquatic plants. Isopods lost weight when reed detritus was offered. The terrestrial isopods utilize detritus drifts as moist shelter and/or food source, thus contributing to the removal and decomposition of decaying aquatic plant material.

Several invertebrate groups are saprophagous, thus contributing to the decomposition of dead plant material. Most studies aiming to clarify their role in this process have been done in systems where both the decomposer organisms and their food source were of the same origin, aquatic or terrestrial. Freshwater streams are perhaps exception, since the fate of allochtonous plant material (mainly leaf litter) in these systems has been extensively studied (e.g. CUMMINS, 1973; KAUSHIK and HYNES, 1971; KOSTALOS and SEYMOUR, 1976; IVERSEN, 1974; ARSUFFI and SUBERKROPP, 1985). Much less is known about the reverse situation: the importance of aquatic detritus in the diet of terrestrial organisms.

Dead plant material can be washed ashore by waves building up drift belts. Depending on the moisture conditions determined by water level and wave action, these drifts still harbour some aquatic organisms while, at the same time, they are colonized by terrestrial animals. This special habitat is not stable. It can be washed back into the water, and to the shore again, and the cycle may continue for years (SEBESTYÉN, 1957).

The origin and fate of these drifts in the Lake Balaton, the largest lake in Central Europe, have been studied for many years (SEBESTYÉN, 1942, 1943, 1949, 1957; ENTZ et al., 1942). During the 1930-s and 40-s, when most of the field observations were carried out, detritus drifts were abundant in the supralittoral.

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Among the terrestrial organisms particularly abundant in detritus drifts are terrestrial isopods, especially if the plant material is sufficiently moist. Since this group is primarily saprophagous, they may utilize this special habitat as shelter, and/or as food source. I examined this possibility in laboratory experiments, and the results of this study are reported here.

Material and methods

Study site

A natural lakeshore area with large detritus drift patches was found on the southern shore of the Lake Balaton. An approximately 500 m long shore was chosen between the villages Balatonmária and Balatonberény. Here the detritus drifts are surrounded by reed and, on the higher regions, by a planted oak-poplar-pine forest stand.

Distribution of isopods

Isopods were collected by singling on several occasions during summer 1983. In September a brief survey was carried out to determine the pattern of local distribution of the animals. Two kinds of detritus patches could be distinguished on the study site: one consisting mainly of submerged aquatic vegetation (SAV hereafter) such as *Potamogeton* and *Myriophyllum;* the other consisting of emerged aquatic vegetation (EAV), mainly *Phragmites.* Three patches of the former and one of the latter type were chosen for the survey. Due to wave action and irregular flooding drift habitats are continuously changing. Therefore neither pitfall traps nor the quadrat method could be applied to assess isopod densities. I used BRERETON's method (BRERETON, 1957), in which animals were collected by singling for a certain time period. Each person spent fifteen minutes searching and collecting in each patch. The animals were later identified in the laboratory, and data of the separate collections were pooled. Obviously this method can be applied for estimating relative population density only. For identification of the isopods the monographs by GRUNER (1966), SCHMÖLZER (1965) and WÄCHTLER (1937) were used.

Feeding experiments

The two types of detritus (SAV and EAV) were sampled and offered to the isopods in laboratory feeding experiments. Four species, *Armadillidium vulgare* LATR., *A. versicolor* STEIN, *A. zenckeri* BRDT. and *Trachelipus rathkei* BRDT. were chosen for the experiments. They were collected on the study site during summer 1983. In the laboratory the animals were kept on a mixed diet. They were starved 48 hours prior to the experiment. *Armadillidium versicolor* received only SAV detritus, because the laboratory population died before experiment with EAV detritus were carried out.

The experiments were carried out in clay flower pots of 8 cm diameter. The pots were soaked in water until saturation before the previously weighed food and animals were placed into them. The pots were then covered with fine mesh-cloth and sunk into wet sand to maintain optimal moisture conditions (GERE, 1958). Further details of the experimental setup are summarized in Table 1. The temperature during the experiments was 17 ± 2°C. Five control pots were also set up to assess detritus weight loss due to microbial activity. At the end of experiments the feces were removed from the remaining food, which was then reweighed. The live weight of the isopods was also determined.

Table 1. The experimental setup for feeding experiments.
(Abbreviations: SAV: submerged aquatic vegetation, EAV: emerged aquatic vegetation)

Species	Live weight per animal (mean±SD) (mg)	Food	No. of isopods per pot	No. of. replicates	Duration of experiment (days)
T. rathkei	31.4±3.2	SAV	10	10	17
		EAV	10	10	17
A. vulgare	81.2±7.1	SAV	5	10	16
		EAV	4	10	17
A. zenckeri	20.8±2.5	SAV	10	10	17
		EAV	10	10	16
A. versicolor	19.3±2.3	SAV	15	10	16

To determine the moisture content of both the initial and the remaining food, plant detritus was dried on 105 C until constant weight. Consumption values are expressed in mg absolute dry weight food eaten/g live weight animals/day.

Food consumption (C) was calculated by using the REIMAN-formula (ZICSI and POBOZSNY, 1977):

$$C = \frac{(M-m)\,S}{M}, \text{ where}$$

S: initial weight of detritus, m: remaining weight of detritus in the feeding experiment, M=S*D, where D is the percentage weight of detritus remaining in the control.

Results

Species composition

The following terrestrial isopods were found in the lakeshore area:

Hyloniscus sp.

All 39 specimens collected were females; therefore exact identification was not possible. Members of this genus are known to be extremely sensitive to humidity and they occur in moist habitats.

Porcellium collicola VERHOEFF, 1907

Only one specimen was caught. The species is known to occur in a wide spectrum of plant communities and moisture conditions in Hungary (e.g. LOKSA, 1961, 1971; SZLÁVECZ, 1988; ALLSPACH and SZLÁVECZ, 1991).

Trachelipus rathkei (BRANDT, 1833)

This is a ubiquitous, very expansive species occurring in many different natural habitats. *Trachelipus rathkei* is also common around human settlements. In Hungary it has previously been reported from reed communities (LOKSA, 1973; SZLÁVECZ, 1991).

Table 2. Analysis of variance for the food consumption values of isopod species. (Abbrevations: SAV: submerged aquatic vegetation, EAV: emerged aquatic vegetation)

SAV detritus Source of variation	df	SS	MS	F	P
Between Groups	3	12962.36	4320.79	11.93	<0.001
Within Groups	27	9780.47	362.24		
Total	30	22742.83			
EAV detritus Source of variation	**df**	**SS**	**MS**	**F**	**P**
Between Groups	2	1322.23	661.11	5.80	<0.01
Within Groups	22	2506.32	113.92		
Total	24	3828.55			

Armadillidium vulgare (LATREILLE, 1804)

Armadillidium vulgare is a cosmopolitan, ubiquitous species, that occurs in many natural systems and human environments.

Armadillidium versicolor STEIN, 1859

This lakeshore population belongs to the northern variety of the species, *A. versicolor quinqueseriatum* (VERHOEFF, 1901). *Armadillidium versicolor quinqueseriatum* is reported to occur in loess terraces, under stones and treetrunks (WÄCHTLER, 1937). Otherwise nothing is known on the natural history of this species.

Armadillidium zenckeri BRANDT, 1833

Armadillidium zenckeri is one of the most frequently falsely identified pillbugs, therefore data on its distribution have to be treated cautiously (SCHMÖLZER, 1954). The generally accepted area of distribution of the species is northeastern Central Europe, and it is probably a boreo-alpine faunal element (WÄCHTLER, 1937). The species occurs in moist to very wet habitats, such as beach forests, alder-bogs, marshy meadows. It is capable of staying underwater for several days without drowning. *Armadillidium versicolor* and *A. zenckeri* are so similar to each other in appearance, that they could be clearly distinguished from each other only under microscope. I found the shape of the head lateral lobes to be the most useful character to separate live specimens.

Distribution of isopods

A total of 184 isopods were caught during the survey, a fairly large number considering that the search lasted only a short time. Both species composition and abundance (Fig. 1) varied in the different detritus patches ($\chi^2=118$, $P<0.001$). Only one or two species dominated each patch, the others were represented with very low numbers. *Hyloniscus* was the dominant isopod in the EAV patch. In the SAV detritus patches either *Armadillidium versicolor* or *A. zenckeri* was dominant, but these species did not occur together in equal abundances. Neither *Armadillidium vulgare*, nor

Porcellium collicola were abundant in the detritus drifts. Although we were able to collect *A. vulgare* in this habitat, it was clearly outnumbered by its two congenerics, *A. zenckeri* and *A. versicolor. A. vulgare* appeared to be more abundant in the oak-poplar forest stand that surrounds the study site (SZLÁVECZ, pers. obs.). *Trachelipus rathkei* seems to be more evenly distributed among the patches.

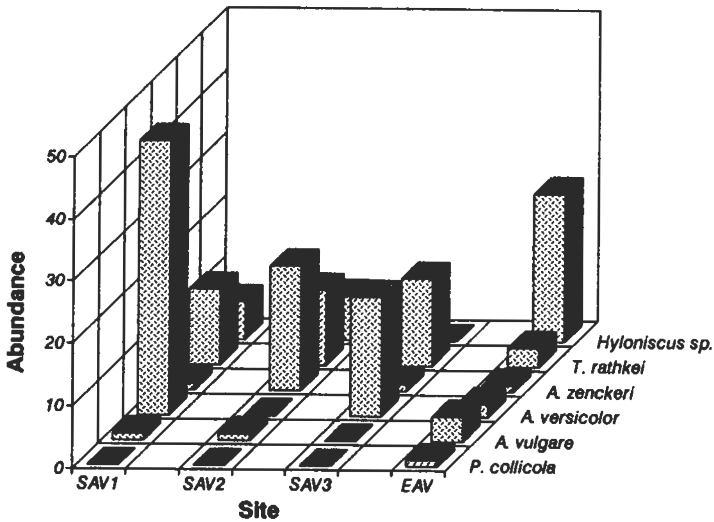

Fig. 1. Distibution of isopods in four detritus drift patches. On the vertical axis the number of isopods caught is shown. Abbreviations: SAV: submerged aquatic vegetation; EAV: emerged aquatic vegetation

Feeding experiments

Mortality was very low (usually less then one percent) during the experiments. Food intake varied, depending on the isopod species and the food type. *Armadillidium versicolor* has the highest consumption rate. *Armadillidium vulgare* and *A. zenckeri* consumed more SAV than EAV detritus. *Trachelipus rathkei* consumed both food types equally (Fig. 2).

The different species consumed different amounts of both food types (Tab 2). The multiple comparison test (Tab. 3) revealed, that for SAV detritus this is mainly due the two species (*Armadillidium versicolor* and *A. zenckeri*) with the highest consumption values. On EAV detritus *A. vulgare* behaved differently from the two other species. *Trachelipus rathkei* and *A. zenckeri* consumed equal amounts of this food type.

Isopods were able to grow on a diet of SAV detritus, on EAV detritus all three species lost weight (Fig. 3). Growth and food consumption were positively correlated (SPEARMAN rank correlation, r_s=0.79, P < 0.05).

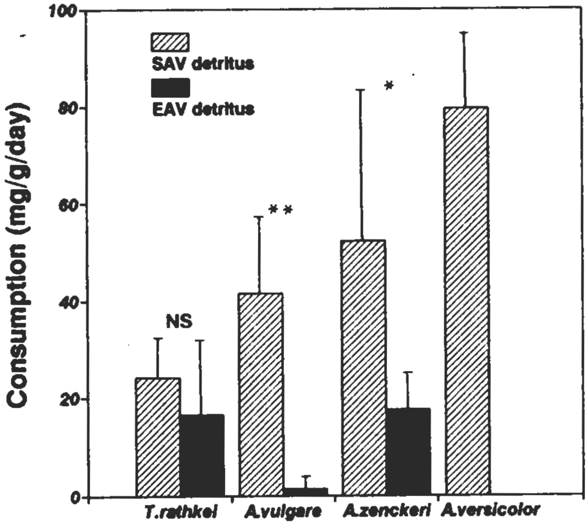

Fig. 2. Food consumption (mean ± SD) by four isopod species. To compare consumption values on the two food types STUDENT's t-test was used. **: P<0.001; *: P<0.05; NS: not significant

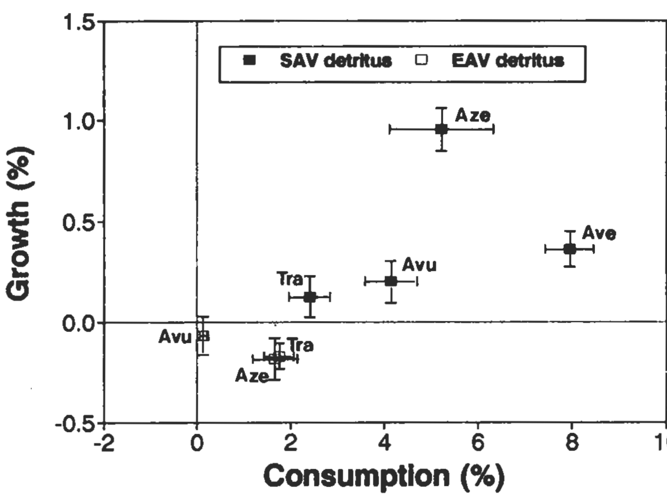

Fig. 3. Relationship between food intake and growth of isopods. Error bars indicate standard errors of the means. Both feeding and growth rates are expressed as a percentage of the live weight of one isopod per day. Abbreviations: Avu: *Armadillidium vulgare;* Ave: *A. versicolor;* Aze: *A. zenckeri;* Tra: *Trachelipus rathkei*

Table 3. Comparison among food consumption values of the isopods. Stars denote pairs of species with significantly different values at 0.05 level (multiple range test, Tukey's honestly significant method.) (Abbreviations: SAV: submerged aquatic detritus; EAV: emerged aquatic detritus; Tra: Trachelipus rathkei; Avu: Armadillidium vulgare; Aze: A. zenckeri; Ave: A. versicolor

	SAV detritus				EAV detritus		
	Tra	Avu	Aze	Ave	Tra	Avu	Aze
Tra							
Avu					•		
Aze	•					•	
Ave	•	•	•				

Discussion

Detritus drifts as habitats

A total of six species were found in the lakeshore detritus. Two of them (*A. vulgare, T. rathkei*) are ubiquitous, occurring in both natural and human environments. *P. collicola* also can be found in a wide range of habitats. The three remaining species are more restricted to moist conditions. The large number of animals we found in these detritus patches at any time of collection shows that this habitat is favoured by terrestrial isopods. Feeding experiments indicate that reed detritus seems to be a moist shelter rather than a food source, whereas SAV serves as both.

The population survey shows that isopods are patchily distributed not only due to habitat heterogeneity, but perhaps species interaction as well, indicated by clear differences in species composition among patches, especially distributions of *Armadillidium versicolor* and *A. zenckeri*. Naturally, this data set can be considered as preliminary, a more systematic survey is needed.

Detritus drifts as food source

Marine macrophytes and marcoalgae are of primary importance in the diet of many marine isopod species (NICOTRI, 1980; GROENENDIJK, 1984; ROBERTSON & MANN, 1980). Intertidal and supralittoral isopods also depend on this food source (ARRONTES, 1990; CAREFOOT, 1973; KOOP & FIELD, 1980; HAMNER et al., 1969). Terrestrial isopods are known to feed on a variety of woody and herbaceous litter material (see WARBURG, 1987, for review). Knowledge on the possible significance of terrestrial species in the decomposition of freshwater detritus, however, is very sparse. The present experiment demonstrated that detritus of submerged aquatic vegetation is a desirable food type for isopod species. Food intake was especially high for *Armadillidium zenckeri* and *A. versicolor quinqueseriatum*, the two species that are strongly associated with detritus drifts as habitat. It is important to point out, that the detritus itself is an extremely heterogenous material, consisting of not only the plant detritus itself, but microorganisms, algae, a wide array of live animals and animal remnants and inorganic particles (ENTZ et al, 1942; SEBESTYÉN, 1949, 1957; GELLÉRT & TAMÁS, 1959). Further studies are needed to clarify the exact role of these components in the nutrition of isopods.

POBOZSNY (1988) analyzed the main chemical components of aquatic macrophyte detritus. SAV drifts contained approximately five times more nitrogen (and crude protein) than EAV drifts. On the other hand, the cellulose content of the latter is almost ten times greater than that of the SAV. The total organic matter content of the former was also higher, and, due to differences in both the organic matter content and nitrogen content, the C/N ratio showed great differences between the two food types (21.0 and 166.5 for SAV and EAV detritus, respectively). Obviously SAV is a much better quality food, and this is reflected not only by the food consumption values, but, what is perhaps a better indicator, by the growth of the animals during the experiment. All isopod species lost weight while being fed EAV detritus regardless of the amount eaten. The case of *T. rathkei* is especially interesting. There was no significant difference between the two food consumption values of this species yet its growth was positive in the SAV experiments and negative in the EAV experiments. Differences in percentage growth clearly reflect different assimilation efficiencies on the two food types.

There is a millipede species, *Glomeris hexasticha*, in the study area. Its primary habitat is the forest stand, but in certain times of the year it becomes very abundant in the detritus-drifts (POBOZSNY, 1988). Food intake by this diplopod was also much higher on SAV than on EAV detritus. Consumption values by *Glomeris* (23—55 mg/g/day and 8.6—14.3 mg/g/day for SAV and EAV detritus, respectively) were within the range obtained for isopods (Fig. 1).

Conclusions

Aquatic plant detritus plays an important role in the ecology of terrestrial isopods inhabiting shore areas. The sand beach isopod, *Tylos punctatus*, is strictly nocturnal. After emerging from the sand the animals move seawards to search for food. In Baja California, Mexico, the most abundant food source of the species is the kelp *Macrocystis* washed ashore. The *Tylos* population there is capable of skeletonizing many meters long debris overnight (HAMNER et al., 1969). In the study of KOOP and FIELD (1980) kelp debris was also the major food source for the supralittoral isopod, *Ligia dilatata*. In Cape Peninsula, South Africa, the season of highest food availability coincided with highest growth rate of *Ligia*, and it was followed by the breeding period. Since physical environment is fairly uniform there, the result suggests that food availability is a major factor governing the life cycle of the isopods.

The detritus drifts at Lake Balaton also serve as moist habitat and/or food source for the animals. At the same time, by consuming large amounts of submerged aquatic detritus, terrestrial isopods contribute to the decomposition and humification of dead aquatic plant material. By being washed ashore, detritus drifts represent a large fraction of organic material removed from the lake. It is therefore very unfortunate, that a year after this study — similarly to most parts on the southern shore Lake Balaton — a dam of concrete blocks was built on our study site thus interrupting the exchange of material and energy between terrestial and aquatic systems.

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REFERENCES

1. ALLSPACH, A. & SZLÁVECZ, K. (1991): The terrestrial isopod (Isopoda, Oniscidea) fauna of the Bátorliget Nature Reserves. — In: MAHUNKA, S. (ed.): The Bátorliget Nature Reserve — after forty years. Studia Naturalia, 1. Hung. Nat. Hist. Mus., pp. 251—257.

2. ARRONTES, J. (1990): Diet, food preference and digestive efficiency in intertidal isopods inhabiting macroalgae. — J. Exp. Mar. Biol. Ecol., 139: 231—249.

3. ARSUFFI T. L. & SUBERKROPP, K. (1985): Selective feeding by stream caddisfly (Trichoptera) detritivores on leaves with fungal colonized patches. — Oikos, 45: 50—58.

4. BRERETON, J. G. (1957): The distribution of woodland isopods. — Oikos, 8: 85—106.

5. CAREFOOT, T. H. (1973): Feeding, food preference, and the uptake of food energy by the supralittoral isopod Ligia pallasii. — Mar. Biol., 18: 228—236.

6. CUMMINS, K. W. (1973): Trophic relations of aquatic insects. — Ann. Rev. Ent., 18: 183—206.

7. ENTZ, G., SEBESTYÉN, O. & SZABÓ, M. (1942): Studien über die Driften des Balatonsees. — Magy. Biol. Kut. Int. Munkái, 14: 10—82.

8. GELLÉRT, J. & TAMÁS, G. (1959): Ecological studies on the diatoms and ciliate infusorians in the detritus drifts along the shores of the Tihany Peninsula. — Acta Biol. Hung., 10: 117—125.

9. GERE, G. (1958): Methode zur Lebendhaltung und Zucht von Arthropoden der Waldböden. — Acta Zool. Hung., 3: 225—231.

10. GROENENDIJK, A. M. (1984): Consumption of eelgrass (Zostera marina L.) by the isopod Idotea chelipes (Pallas) in Lake Grevelingen, after the growing season. — Netherlands J. Sea Res., 18: 384—394.

11. GRUNER, H. (1966): Isopoda. In: Die Tierwelt Deutschlands, 53, 380 pp.

12. HAMNER, W. M., SMYTH, M. & MULFORD, E. D. (1968): The behaviour and life history of a sand beach isopod, Tylos punctatus. — Ecology, 50: 442—453.

13. IVERSEN, T. M. (1974): Ingestion and growth in Sericostoma personatum (Trichoptera) in relation to the nitrogen content of ingested leaves. — Oikos, 25: 278—282.

14. KAUSHIK, N. K. & HYNES, H. B. N. (1971): The fate of dead leaves that fall into streams. — Arch. Hydrobiol., 68: 465—515.

15. KOSTALOS, M. & SEYMOUR, L. R. (1976): Role of microbially enriched detritus in the nutrition of Gammarus minus. — Oikos, 27: 512—516.

16. KOPP, K. & FIELD, J. G. (1980): The influence of food availability on population dynamics of a supralittoral isopod, Ligia dilatata Brandt. — J. Exp. Mar. Biol. Ecol., 48: 61—72.

17. LOKSA, I. (1961): Quantitative Untersuchungen streuschichtbewohnender Arthropoden-Bevölkerungen in einigen ungarischen Waldbeständen. — Ann. Univ. Sci. Budapest, Sec. Biol., 4: 99—112.

18. LOKSA, I. (1971): Zoozönologische untersuchungen im nördlichen Bakony-Gebirge. — Ann. Univ. Sci. Budapest, Sec. Biol., 13: 301—314.

19. LOKSA, I. (1973): Bodenzoologische Untersuchungen in den Alkali-Waldsteppen von Margita, Ungarn. I. Untersuchungen der Arthropoden-Makrofauna, nebst Bemerkungen über die Oniscoidea-Arten. — Opusc. Zool. Budapest, 11: 79—93.

20. NICOTRI, M. E. (1980): Factors involved in herbivore food preference. — J. Exp. Mar. Biol. Ecol., 42: 13—26.

21. POBOZSNY, M. (1988): Die Bedeutung von Glomeris hexasticha (Diplopoda) beim Abbau von Detritus-Driften am Ufer des Balaton-Sees. — Opusc. Zool. Budapest, 23: 177—188.

22. ROBERTSON, A. I. & MANN, K. H. (1980): The role of isopods and amphipods in the initial fragmentation of eelgrass detritus in Nova Scotia, Canada. — Mar. Biol., 59: 63—69.

23. SCHMÖLZER, K. (1954): Beitrag zur Kenntnis der Gattung Armadillidium Latr. 1804 (Isopoda Terrestria). — Acta Zool. Fenn., 80: 1—64.

24. SCHMÖLZER, K. (1965): Ordnung Isopoda (Landasseln). — Bestimmungsbücher zur Bodenfauna Europas, 4—5: 1—468, Berlin.

25. SEBESTYÉN, O. (1942): A turzások jelentősége a Balaton életének megismerésében. — Állatt. Közlem., 39: 204—208.

26. SEBESTYÉN, O. (1943): A parti öv jelentősége a tó életében. — Magy. Biol. Kut. Int. Munkái, 15: 301—308.

27. SEBESTYÉN, O. (1949): Studies on detritus drifts in Lake Balaton. — Arch. Biol. Hung., 19: 49—64.

28. SEBESTYÉN, O. (1957): Parti tanulmány. — Annal. Biol. Tihany, 24: 165—182.

29. SZLÁVECZ, K. (1988): The isopod fauna of the Pilis Biosphere Reserve. I. Basaharc loess mine. — Opusc. Zool. Budapest, 23: 189—195.

30. SZLÁVECZ, K. (1991): The terrestrial isopod fauna of the Hortobágy National Park. — Miscell. Zool. Hung., 6: 61—66.

31. WÄCHTLER, W. (1937): Ordnung: Isopoda, Asseln. — In: BROHMER, P., P. EHRMANN & G. ULMER (eds): Die Tierwelt Mitteleuropas, 2: 224—317. Leipzig.

32. VERHOEFF, K. W. (1901): Über paläarktische Isopoden. — Zool. Anz., 24: 135—141.

33. WARBURG, M. R. (1987): Isopods and their terrestrial environments. — Adv. Ecol. Res., 17: 187—242.

34. ZICSI, A. & POBOZSNY, M. (1977): Einfluss des Zersetzungsverlaufes der Laubstreu auf die Konsumintensität einiger Lumbriciden-Arten. — In: PERSSON, T. & U. LOHM (eds.): Soil Organisms as Components of Ecosystems. Ecol. Bull. (Stockholm), 25: 229—239.