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How many larval instars do Raphidioptera have?

(Insecta, Neuropterida)

Axel Gruppe, Horst Aspöck & Ulrike Aspöck

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The development of two species of Raphidiidae occurring in Central Europe, *Raphidia mediterranea* H. Aspöck, U. Aspöck & Rausch, 1977, and *Ornatoraphidia flavilabris* (A. Costa, 1855) was studied by rearing them 'ab ovo' in order to clarify the number of larval instars and the length of the larval periods. *Raphidia mediterranea* represents Type I (pupation after the last hibernation and hatching of adults in spring of the second or third year), *Ornatoraphidia flavilabris* is a Type II species (pupation in summer or autumn before the last (usually second) hibernation and hatching of adults after overwintering of the pupa in spring of the third year).
We found a surprising variability of the numbers of larval instars in both species until pupation, 5 to 12 in *R. mediterranea* and 6 to 10 in *O. flavilabris*. There was also a considerable variability in the length of the larval period of *R. mediterranea*.
The enormous variability represents simultaneously a high intrinsic plasticity of the development of Raphidioptera and has been most probably an important precondition for snakeflies to overcome critical situations due to unfavourable environmental conditions.

Axel Gruppe (corresponding author), Chair of Zoology – Entomology group, Technical University of Munich (TUM), Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany; e-mail: gruppe@wzw.tum.de

Horst Aspöck, Institute of Specific Prophylaxis and Tropical Medicine, Medical Parasitology, Medical University of Vienna, Kinderspitalgasse 15, 1090 Vienna, Austria

Ulrike Aspöck, Natural History Museum Vienna (NHMV), Department of Entomology, Burgring 7, 1010 Vienna, Austria; and Unit for Integrative Zoology, Department of Evolutionary Biology, University of Vienna, Djerassiplatz 1, 1030 Vienna, Austria

Introduction

Duration of larval development of Raphidioptera was described for many species after breeding larvae 'ab ovo' in the lab (H. Aspöck et al. 1991). In contrast to most other insect taxa this period is highly variable and lasts two to three years, but one year as well as four to five (even up to seven) years larval development have been reported (H. Aspöck et al. 1974, 1975, 1991). In contrast to the well documented duration of the larval period, the number of larval instars was hardly studied in detail. According to the monograph of the Raphidioptera of the world (H. Aspöck et al. 1991) larvae exhibit around 10 instars, but numbers might be extended to 16 in lab cultures (H. Aspöck & U. Aspöck 1971).

Only in three Nearctic species of the genus *Agulla* Navás, 1914, the number of larval instars was studied (Kovarik et al. 1991, Woglum & McGregor 1958, 1959). These authors reared species of the genus *Agulla* in the lab and checked for exuviae in regular intervals. Woglum & McGregor (1958) studied

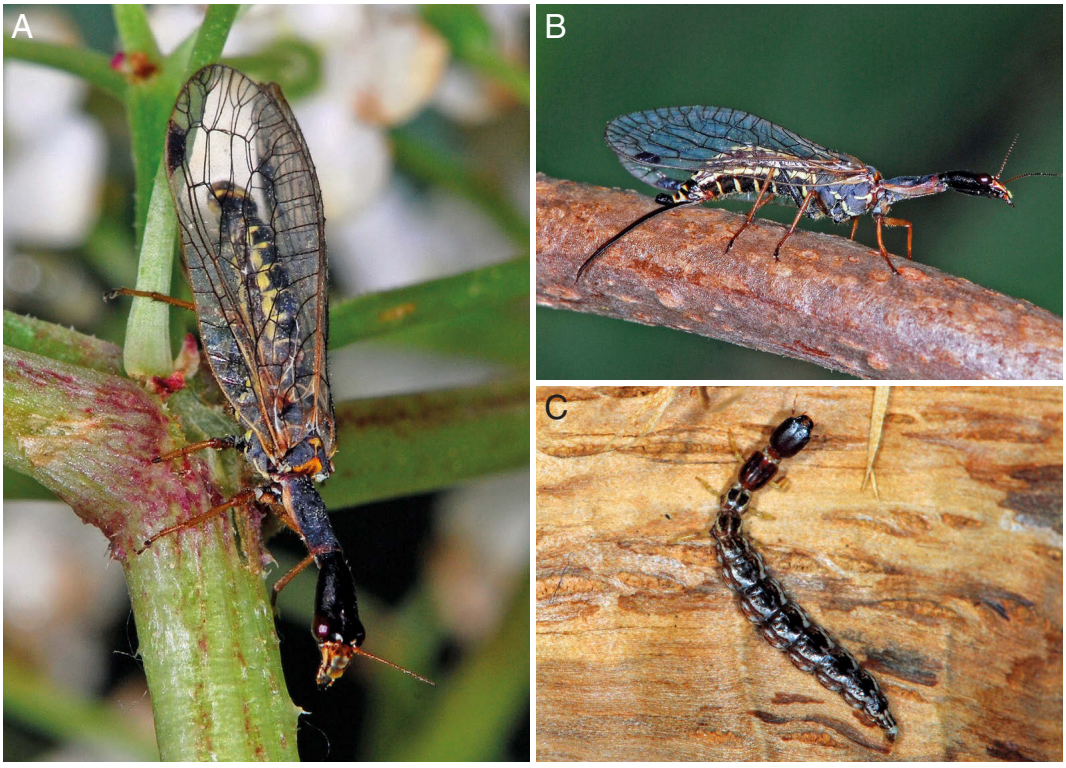

Fig. 1. A. *Raphidia mediterranea* (H. Aspöck, U. Aspöck & Rausch, 1977), ♂. Upper Austria, Pelmberg near Hellmonsödt, 3 July 2015, H. & U. Aspöck leg. (photo: H. Bruckner, photo archive NHMW and H. & U. Aspöck). **B.** *Raphidia mediterranea*, ♀. Upper Austria, Pelmberg near Hellmonsödt, 24 June 2014, H. & U. Aspöck leg. (photo: H. Bruckner, photo archive NHMW and H. & U. Aspöck). **C.** *Raphidia mediterranea*, last larval instar before pupation, 15 March 2016. Ex ovo from ♀ from Upper Austria, Pelmberg near Hellmonsödt, 24 June 2014, H. & U. Aspöck leg. (photo: H. Bruckner, photo archive NHMW and H. & U. Aspöck).

Agulla bractea Carpenter, 1936. From their tables the number of larval instars with 1-year development can be calculated as 7 (4.3 %), 8 (13.0 %), 9 (34.8 %), 10 (39.1 %) and 11 instars (8.7 %) (n = 23). For *Agulla astuta* (Banks, 1911) the same authors (Woglum & McGregor 1959) found fifty percent pupation both after 9 and 10 instars when larvae hibernated outdoors after one year of development (n = 16). In contrast, if larvae were kept at room temperature in the first winter and outdoors in the second winter they exhibited 9 (11.1 %), 11 (44.4 %), 12 (33.3 %) and 13 instars (11.1 %) (n = 9). Finally, Kovarik et al. (1991) applied the same technique (room temperature = 23 °C ± 3 °C, 58 % relative humidity) to rear *Agulla bicolor* (Albarda, 1891) and observed 75.6 % pupation at instar 10 and 24.4 % at instar 11 with 1-year development (n = 41). These results were obtained from cultures in artificial environments, i. e. in the lab, but temperature as a determining factor for the development of insects (Régnière et al. 2012) was not exactly recorded. Moreover, no chilling was applied to larvae in winter. However, we have demonstrated, that chilling period is an essential feature for pupation (Gruppe & Abbt 2018, H. Aspöck et al. 2018, H. Aspöck et al. 2019, Gruppe et al. 2020).

As the juvenile phase takes one to three or even more years, breeding experiments are very laborious and time consuming. A further obstacle in the breeding of Raphidioptera is mortality during juvenile phase which often exceeds 50 % (Kovarik et al. 1991, H. Aspöck & U. Aspöck 2009, Gruppe et al. 2020). Here we describe the larval development of two species of Raphidioptera, Raphidiidae, namely *Raphidia mediterranea* H. Aspöck, U. Aspöck & Rausch, 1977, and *Ornatoraphidia flavilabris* (A. Costa, 1855), which belong to different phylogenetic clades and are characterized by different modes of pupation (H. Aspöck 2002).

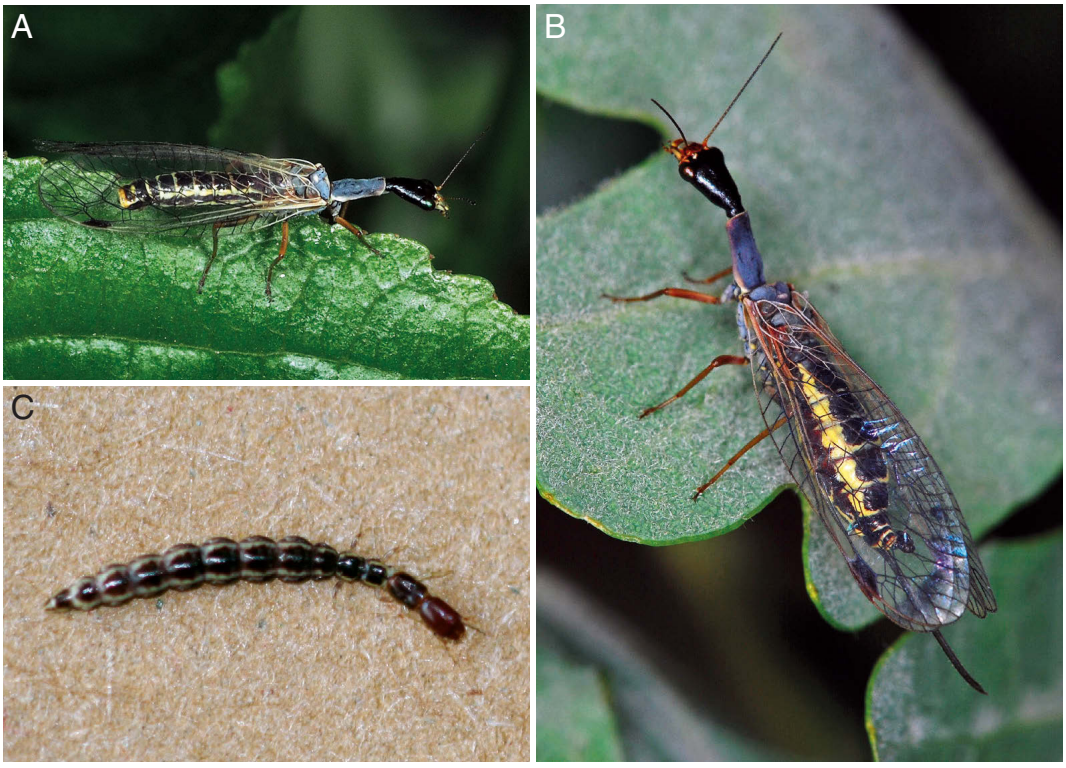

Fig. 2. A. *Ornatoraphidia flavilabris* (A. Costa, 1855), ♂. Lower Austria, Eichkogel, 10 May 2021, H. & U. Aspöck leg. (photo: H. Bruckner, photo archive NHMW and H. & U. Aspöck). **B.** *Ornatoraphidia flavilabris*, ♀. Lower Austria, Eichkogel, 10 May 2022, H. & U. Aspöck leg. (photo: H. Bruckner, photo archive NHMW and H. & U. Aspöck). **C.** *Ornatoraphidia flavilabris*, last larval instar before pupation, 26 October 2007. Ex ovo from ♀ from Italy, Calabria, Camigliatello, May 2006, H. & U. Aspöck leg. (photo: F. Anderle, photo archive H. & U. Aspöck).

Material and methods

Females of the two studied species were collected in the field in May and July 2018. Individuals of *Raphidia mediterranea* H. Aspöck, U. Aspöck & Rausch, 1977 (Fig. 1A–C) were obtained from the well described population at Pelmberg (Hellmonsödt, Oberösterreich, 48.41° N, 14.32° E, 800 m a. s. l. Austria) (Rausch et al. 2016, H. Aspöck et al. 2017, Gruppe et al. 2017). Nine females were caged for oviposition in plastic vials as described by H. Aspöck & U. Aspöck (2009) and kept in a thermostat cabinet at 20 °C (60–70 % rh, 16 h light, 8 h dark). They were supplied with pieces of mealworms every other day. Thirty-eight neonate larvae were separated in individual cages fitted with a sandwich of two small discs of filter paper on July 5th. All cages were checked weekly and supplied with fresh pieces of mealworms. This was applied until larvae became prepupae (Gruppe & Abbt 2018). From November to March each year larvae were moved to a cabinet with constant 4 °C without light (rh not adjusted). Larvae were checked once a month and a piece of mealworm was put in each cage during this period. *Raphidia mediterranea* belongs to the Type I of development, i. e., mature larvae hibernate, and pupation happens in spring (H. Aspöck 2002).

Two females of *Ornatoraphidia flavilabris* (A. Costa, 1855) (Fig. 2A–C) were collected at the nature reserve Eichkogel (Mödling, Niederösterreich, 48.06° N, 16.29° E 360 m a. s. l., Austria) in May 2018. Adults were handled and kept as described above. Neonate larvae were observed between May 16th and 18th 2018. Second instar larvae were separated on June 28th. One batch of 35 individuals was kept at 20 °C and a second batch of 37 individuals at 25 °C. Hibernation at 4 °C happened between November 2018 and March 2019. As we did not observe significant differences in the development at the two temperatures, all larvae were kept at 20 °C in the second year and results were calculated together. *Ornatoraphidia flavilabris* belongs to the Type II of development, i. e., prepupae occur in late summer, prepupae or pupae hibernate, and adults emerge in spring (H. Aspöck 2002). Only occasionally mature larvae hibernate, and pupation happens in spring, followed by an immediate hatch of adults like in Type I development.

Table 1. Appearance of prepupae of *R. mediterranea* after one or two hibernations (n = 36) (calendar week 2_16 = 15.–21.04.2019; calendar week 3_14 = 30.03.–06.04.2020).

	2nd year (1 hibernation)						3rd year (2 hibernations)			
calendar week	2_16	2_17	2_18	2_19	...	2_22	3_14	3_15	...	3_28
n prepupae	2	5	7	4		1	9	7		1
% of prepupae	5.6	13.9	19.4	11.1		2.8	25.0	19.4		2.8

During the weekly check of the larvae exuviae as an indication of a moult were removed. Because larvae might feed on the less sclerotized parts of the exuvia special attention was paid to the detection of the strongly sclerotized head capsule and prothorax. The first moult was assigned to second larval instar. Consequently, we calculated the number of larval instars as observed moults plus 1. As mortality strongly increased during pupation and adult hatch, we assessed the appearance of the prepupa as a sign of pupation (Gruppe et al. 2020). For documentation of the development, moults, i. e., appearance of a larval instar, were assigned to calendar week of the corresponding year. Results are given as percentages of pupated individuals, i. e., 36 for *R. mediterranea* and 38 for *O. flavilabris*. Specimens are deposited in the collection of the first author.

Results

Raphidia mediterranea

In spring of the second year, i. e., 1-year development, 44.6 % of specimens had reached prepupa, and 50.0 % in spring of the third year (2-years development). Only two larvae (5.4 %) did not pupate but died as larvae in summer of the third year. Prepupae appeared between week 16 (2_16 = mid of April) and week 22 (2_22 = end of May) in the second year and between week 14 (3_14 = beginning of April) and 16 (3_15 = mid of April) in the third year (Table 1). Three larvae moulted once after hibernation before pupation, one larva after 1st and two larvae after 2nd hibernation.

Specimens exhibited 5 to 9 instars with1-year development, 5 to 12 instars with 2-years development and 9 instars with 3-years development (Fig. 3). Regarding larva exhibiting a 2-years development first hibernation happened in the 3rd to 8th instar followed by 2 to 6 instars in the second year (Table 2). One larva hibernated three times exhibiting 7 instars in the first year, 1 additional instar in the second and another instar in the 3rd year resulting in 9 instars.

There was a very high variation in the occurrence of larval instars within the offspring of individual females. The first moult of a larva to fourth instar within the offspring of female 4 happened in week 33 but the last in week 37 of the first year; the first moult to sixth instar in week 38 of the first year, but the last one in week 17 of the second year. On the other hand, instars three to five were present at week 34 in the first year (Fig. 4).

Table 2. Numbers of *R. mediterranea* larvae (2-year development) with their number of instars in the first (rows) and second (columns) year of development (n = 16). For example: 1 larva passed through 3 instars in the 1st year and 2 instars in the 2nd, resulting in 5 instars (left column, first row).

		number of larval instars in 2nd year				
		2	3	4	5	6
number of larval instars in 1st year	3	1	1			
	4		1			
	5	1	3	3	1	
	6			2		1
	7		1			
	8		1			

Ornatoraphidia flavilabris

At the end of second year 38 larvae had reached prepupa (Table 3). One larva survived second hibernation and was alive until summer of the third year without pupation but died during third hibernation. Prepupae appeared between week 32 (beginning of August) and 39 (end of September) with the highest number of prepupae at week 36 of the second year (Table 3).

Individuals had reached instars 6 to 10 in that time with more than 50 % 8 instars (n = 38) (Fig. 5).

There was a high variation in the occurrence of larval instars within the offspring of one female. The first moult of a larva to fifth instar, for example within the offspring of female 2, happened in week 32 of the first year, but the last one in week 22 of the second year (Table 4). On the other hand, instars three to seven were present at week 18 in the second year (Fig. 6).

Discussion

Rearing Raphidioptera 'ab ovo' in the lab resulted in an unexpected high variability of larval development. This was demonstrated for two species, *Raphidia mediterranea* H. Aspöck, U. Aspöck & Rausch, 1977, and *Ornatoraphidia flavilabris* (A. Costa, 1855), which represent biologically different clades and exhibit different modes of development (H. Aspöck 2002). It is well known that larval development of Raphidioptera is variable and might last one to several years (H. Aspöck et al. 1974, U. Aspöck H. Aspöck 2005a) and the number of larval instars is around 10 (H. Aspöck et al. 1991, U. Aspöck & H. Aspöck 2005a). However, detailed studies on the number of larval instars are lacking except for three Nearctic species: *Agulla bractea* Carpenter, 1936, with 7 to 11 instars (Woglum & McGregor 1958), *Agulla astuta* (Banks, 1911) with 9 to 13 instars (Woglum & McGregor 1959) and *Agulla bicolor* (Albarda, 1891) with 10 to 11 instars (Kovarik et al. 1991). However, these results were generated without adjusted temperature scenarios.

In our experiments under defined temperature and day length most larvae pupated 2 or 3 years after oviposition and reached larval instar five to twelve (*R. mediterranea*) or six to ten (*O. flavilabris*) in that time. We observed a tendency of more instars during 3-years development in *R. mediterranea*. Although physiological regulation of moulting and metamorphosis is consistant in insects (Nijhout 1981, Rolff et al. 2019) and number of instars is constant in most insects, intraspecific variability is well documented in some species, both hemi- and holometabolous (Esperk et al. 2007). Most insect taxa have three to eight instars with some phylogenetically older taxa which have more than ten, up to 34 in Ephemeroptera (Clifford et al. 1979). This applies to Raphidioptera which are among the oldest holometabolous taxa (Misof et al. 2014). Raphidioptera is the sistergroup of Megaloptera + Neuroptera. Megaloptera have 7 to 12 larval instars (New & Theischinger 1993, U. Aspöck & H. Aspöck 2005b), Neuroptera, however, with few exceptions (Ithonidae, Dilaridae) have constantly three larval instars (New 1989). Ithonidae have 5 to 9 larval instars, in Dilaridae up to 10 larval instars have been found under experimental conditions (U. Aspöck & H. Aspöck 2005c). However, there is no recent paper summarizing intraspecific variability in the number of larval instars in insect taxa (Esperk et al. 2007).

Snakeflies have an extraordinarily high variability in the number of larval instars. *Raphidia mediterranea* represents Type I development, i.e., mature larvae hibernate, and pupation happens in spring followed by adult hatch after two to three weeks (H. Aspöck 2002). Until pupation larvae pass five to nine instars within one year or 6 to 12 instars within two years. The same was observed in *O. flavilabris*, a species representing Type II development, i.e., mature larvae pupate or become prepupae in late summer or autumn and hatch in spring after hibernation. Rarely a second hibernation occurs in the larval stage and pupation takes place in spring of the following year (H. Aspöck et al. 1991, H. Aspöck 2002). In our experiments all individuals of this species pupated at the end of the year, thus behaved like Type II and number of instars span from six to ten. Variability in the number of instars, in the length of a particular instar or in the time of development appeared under identical environmental conditions and occurred not only intraspecifically but also full siblings had 1- and 2-years-development and five to ten larval instars.

Intraspecific variability in the number of larval instars is known to occur under standardized environmental conditions in some insect taxa but it was not shown within siblings. In most insect species intraspecific variability is low and spans 1 to 3 instars. Environmental factors known to modulate the number of instars are temperature, humidity or food quantity and quality (Esperk et al. 2007). All these

Table 3. Appearance of prepupae of *O. flavilabris* in the 2nd year of development (n = 38) (calendar week 2_32 = 05.–11.08.2019; calendar week 2_39 = 23.–29.09.2019).

calendar week	n prepupae	% of prepupae
2_32	3	7.9
2_33	–	–
2_34	1	2.6
2_35	14	36.8
2_36	18	47.4
2_37	1	2.6
2_38	–	–
2_39	1	2.6

Table 4. Numbers of *O. flavilabris* larvae with their number of instars in the first (rows) and second (columns) year of development (n = 38). For example: 2 larvae passed through 4 instars in the 1st year and 2 instars in the 2nd, resulting in 6 instars in total (left column).

		number of larval instars in 2nd year			
		2	3	4	5
number of larval instars in 1st year	4	2	6	6	1
	5		16	3	
	6		1	1	

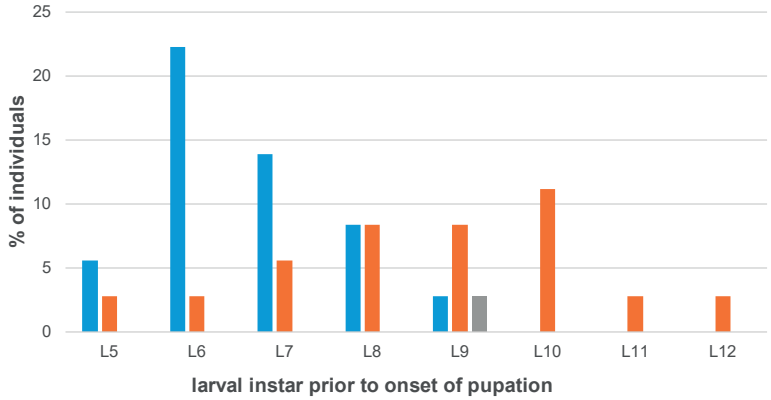

Fig. 3. Larval instars of *R. mediterranea* before pupation after one (■, n = 19), two (■, n = 16) or three (■, n = 1) years of development.

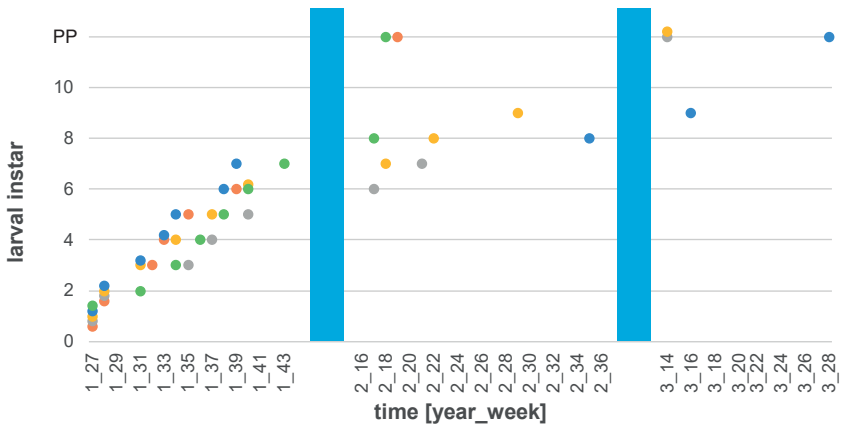

Fig. 4. Times of moulting of five individual *R. mediterranea* larvae (●, ●, ●, ●, ●) (offspring of female 4, n = 5). Vertical blue boxes indicate hibernation; PP = prepupa. Note: two specimens (●, ●) moulted once in the year of pupation.

factors remained identical for all individuals in our experiments, thus it is unlikely that they represent essential cues for variability.

The adaptive value of variability in instar number and time of development in Raphidioptera is unknown. It can be hypothesized that this mechanism ensures survival in periods of adverse conditions. Since some Raphidioptera live in regions with harsh climatic conditions like Central Asia and mountain areas they are well adapted to extreme temperature conditions. On the other hand, adverse conditions might also be shortage of food. Even at high temperature larvae survived for several months without food. Larvae of all Raphidioptera are zoophagous and feed on any dead, soft skinned or squeezed arthropod, at least in captivity. However, the natural food resource has not been studied jet and no direct observation in nature has been published. We never observed that moving insects like bark beetle larvae or big aphids were attacked by Raphidioptera larvae in captivity. In contrast, motionless aphids, dead bark beetle larvae or cut mealworms are suitable food. We also observed cannibalism. Larvae frequently attacked moulting conspecifics.

Variability in the number of larval instars of Raphidioptera is an interesting phenomenon that seems to be closely related to their biology and current distribution on Earth (U. Aspöck et al. 2012). It might be speculated that it was one essential feature that ensured the survival of some species out of the previously rich Raphidioptera fauna after the K/T impact 66 million years ago (H. Aspöck 1998). Biology of Raphidioptera can therefore be seen as an example of how insects might survive rapid climate change. In other words: Raphidioptera are survivalists par excellence!

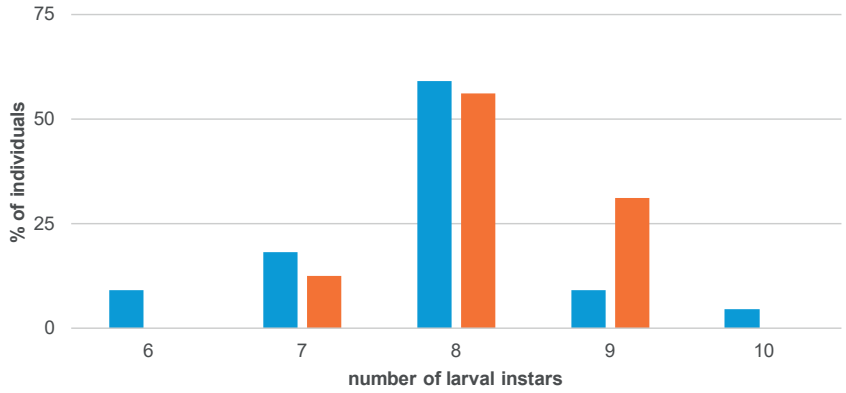

Fig. 5. Larval instars of *O. flavilabris* at 20 °C (■, n = 22) and 25 °C (■, n = 16) in the first year and 20 °C in the second year. Percentages were calculated separately for the temperature treatments in the first year.

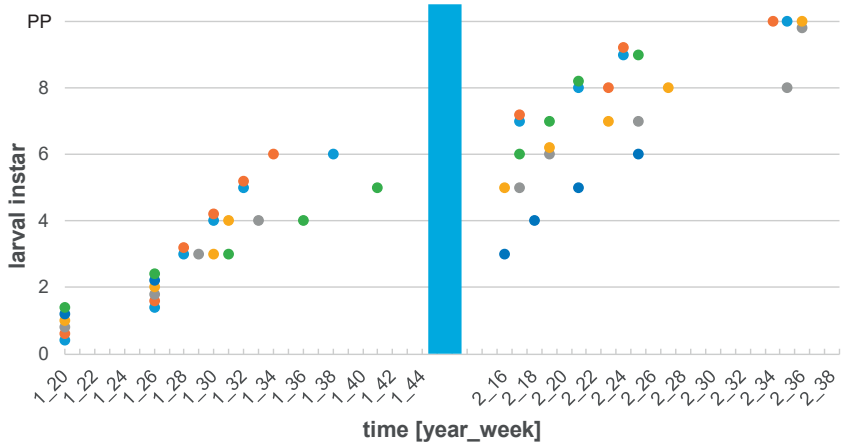

Fig. 6. Times of moulting of six individual *O. flavilabris* larvae (●, ●, ●, ●, ●, ●) (offspring of female 2, 6 out of 25 individuals are shown). Vertical blue boxes indicate hibernation; PP = prepupa.

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