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THE BIOLOGY OF RAPHIDIOPTERA: A REVIEW OF PRESENT KNOWLEDGE

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Basic information on the systematics and distribution of the order Raphidioptera is provided, followed by details of the biology of snakeflies with respect to habitats, substrates upon which they develop, food of adults, food of larvae, life cycles, prothetely, mating and oviposition, parasites and parasitoids, hyperparasites, possible economic importance, and rearing methods.

Key words: Raphidioptera, biology, systematics, distribution, parasites, parasitoids, rearing methods

INTRODUCTION

Raphidioptera were among the most poorly investigated insects before 1960, and there was very little information on the biology of snakeflies. During the past 40 years, however, both families of the order – Raphidiidae and Inocelliidae – have been the subjects of intensive research in all major parts of the world where snakeflies occur. The number of known species has increased considerably, from 62 in 1960 to 206 species, which means that about 70% of the known species have been discovered within this period. Almost all of these have been studied alive, partly as adults but mainly as larvae in the field, and particularly in the laboratory during rearing of immature stages.

The aim of this review is to summarize what we know and what we do not know, and to outline open questions of particular significance, also in the context of a possible role of snakeflies in integrated pest control.

BASIC SYSTEMATIC FEATURES

The order Raphidioptera is a relic systematic group of "living fossils" (Aspöck 1998*b*, 2000), that comprises two extant families, Raphidiidae (with 185 described valid species) and Inocelliidae (with 21 species). The estimated total of extant snakeflies is about 260 species. The Raphidiidae are assigned to 25 recognised genera that comprise 7 (probably monophyletic) species groups* (group I, II,

* For the former group V see footnote to Table 1.

III, IV, VI, VII, VIII), while the Inocelliidae include 6 genera (ASPÖCK *et al.* 1991, 1998). A computerized cladistic analysis, including molecular biological data, is presently being carried out. The extant snakeflies are the remaining – and apparently far distant – twigs of many more branches of earlier geological periods: the Mesozoic biodiversity of the Raphidioptera was indeed much richer (ASPÖCK 1998, 2000).

DISTRIBUTION

Extant Raphidioptera are confined to the Northern Hemisphere and, moreover, almost exclusively to the Holarctic region. In Central America the southernmost records are from high altitudes at the Mexican–Guatemalan border. In Africa they have only been found in arboreal regions (*i.e.* in mountains) north of the Sahara, and in Asia the southernmost records are from altitudes above 900 m in transition areas from the Palaearctic to the Oriental Region in Northern India, Myanmar and Northern Thailand. It is of particular interest that the northern and eastern parts of North America lack snakeflies. Moreover, there is no genus or species with a Holarctic distribution, and almost all species are restricted to very limited areas of a refugial nature, sometimes even being restricted to a certain mountain range. Only three species manifest the Eurosiberian type of distribution throughout Northern Asia to Northern and Central Europe. A few species with Mediterranean distribution centres in Europe have expanded their distribution to extramediterranean parts of Europe, while a few species in North America with distribution centres in the southwest, succeeded in reaching the south of Canada after the last glacial period.

HABITATS

Snakeflies are confined to arboreal habitats, although in the broadest sense including all types of forests, macchias and even biotops with scattered shrubs. In the northern temperate zones they occur from sea level up to the timberline. In the warmer (temperate) zones (*e.g.* the Mediterranean, the Middle East, Central and Eastern Asia and Central America), they are confined to higher altitudes, occurring particularly between 1000 and 2000 m, but even reaching 3000 m in some parts.

In Europe they are typical inhabitants of coniferous as well as of deciduous forests, in Mediterranean regions a few species even occur above the treeline where there are only single bushes. In Central Asia they are characteristic insects of rocky slopes with single trees or shrubs (see illustrations in ASPÖCK *et al.* 1999) and in Eastern Asia as well as in Central America they inhabit the pine forests in particular but also forests with decidous trees.

SUBSTRATES OF DEVELOPMENT

Since the first detection of a larva of a snakefly about 200 years ago by LATREILLE (ASPÖCK 1998*a*), and throughout the whole 19th and until the second half of the 20th century it was believed that larvae of Raphidioptera live exclusively under bark. The presence of a long ovipositor in all snakeflies, very suitable for laying eggs deeply under the bark, seemed to be a convincing confirmation of this assumption. We now know that all Inocelliidae, but only a part (probably even the smaller part) of Raphidiidae probably develop under bark. The majority of Raphidiidae have larvae that live in superficial layers of soil, particularly in the detritus around the roots of shrubs, possibly sometimes even in crevices of rocks (Table 1).

Table 1. Biology of Raphidioptera: development of larvae under bark (corticolous) or in superficial layers of soil/detritus at the base of shrubs, trees etc. (terricolous)

Family, genus-group, genus, subgenus	Number of species			
	corticolous	terricolous	corticolous and terricolous	unclarified
RAPHIDIIDAE				
Group I.				
Phaeostigma NAVÁS s. l.	13	13	9	6
Phaeostigma NAVÁS s. str.	6			
Graecoraphidia H. A. et U. A.			3	
Crassoraphidia H. A. et U. A.		1	2	
Magnoraphidia H. A. et U. A.	5			1
Pontoraphidia H. A. et U. A.		4		
Aegeoraphidia H. A., U. A. et R.		4	3	1
Caucasoraphidia H. A. et U. A.	2			
Superboraphidia H. A. et U. A.		3	1	1
Miroraphidia H. A. et U. A.		1		
Species not assigned to a subgenus				3
Dichrostigma NAVÁS		3		1
Tjederiraphidia H. A., U. A. et R.	1			

Table 1 (continued)

Family, genus-group, genus, subgenus	Number of species			
	corticolous	terricolous	corticolous and terricolous	unclarified
Turcoraphidia H. A. et U. A.		4		1
Iranoraphidia H. A. et U. A.				1
Tauroraphidia H. A., U. A. et R.	2			
Subilla NAVÁS	9			
Ornatoraphidia H. A. et U. A.		2		
Xanthostigma NAVÁS	1	1		3
Parvoraphidia H. A. et U. A.	3			
Ulrike H. A.				2
Raphidia L. s. l.	3	4	7	1
Raphidia L. s. str.	3	2	6	1
Aserbeidshanoraphidia H. A. et U. A.		1		
Nigroraphidia H. A. et U. A.		1	1	
Group II				
Atlantoraphidia H. A. et U. A.			1	
Harraphidia STEINMANN		2		
Hispanoraphidia H. A. et U. A.		1		
Africoraphidia U. A. et H. A.		1		
Ohmella H. A. & U. A.		4		
Italoraphidia H. A. et U. A.		1		
Puncha NAVÁS	1			
Group III				
Venustoraphidia H. A. et U. A.	2			
Mauroraphidia H. A., U. A. et R.	1			
Group IV				
Tadshikoraphidia H. A. et U. A.				2
Group VI*				
Mongoloraphidia H. A. et U. A. s. l.	9	16	1	29
Japanoraphidia H. A., U. A. et R.				1
Formosoraphidia H. A. et U. A.				3
Kirgisoraphidia H. A. et U. A.	2		1	
Mongoloraphidia H. A. et U. A. s. str.	3			9
Hissaroraphidia H. A., U. A. et R.				7
Ferganoraphidia H. A. et U. A.		1		

* Group V (*Usbekoraphidia*) has turned out to be a senior synonym of *Bureschiella* and is now (still) regarded as a subgenus of *Mongoloraphidia* (ASPÖCK *et al.* 1998).

Table 1 (continued)

Family, genus-group, genus, subgenus	Number of species			
	corticolous	terricolous	corticolous and terricolous	unclarified
Usbekoraphidia H. A. et U. A.	3			
Kasachoraphidia H. A. et U. A.				1
Neomartynoviella H. A. et U. A.		2		
Alatauoraphidia H. A. et U. A.		1		5
Species not asigned to a subgenus	1	12		3
Group VII				
Agulla NAVÁS, s. l.	4(?)	1(?)	1(?)	11
Agulla NAVÁS s. str.	4(?)	1(?)	1(?)	5
Glavia NAVÁS				4
Franciscoraphida H.A., U.A. et R.				1
Californoraphidia H. A., U. A. et R.				1
Group VIII				
Alena NAVÁS s. l.	3			5
Alena NAVÁS s. str.				1
*Mexicoraphidi*a U. A. et H. A.	1			
*Aztekoraphidi*a U. A. et H. A.	2			4
INOCELLIIDAE				
Fibla NAVÁS s. l.	4			
Fibla NAVÁS s. str.	3			
Reisserella H. A. et U. A.	1			
*Parainocelli*a H. A. et U. A. s. l.	4			1
Parainocellia H. A. et U. A. s. str.	4			
Amurinocellia H. A. et U. A.				1
Inocellia SCHNEIDER	6			
*Indianoinocelli*a U. A. et H. A.	2			
Negha NAVÁS	3(?)			
Sininocellia YANG				1
TOTAL	71	53	19	62

FOOD OF ADULTS

As far as we know, the adults of all species of Raphidiidae are entomophagous with a distinct preference for aphids and other Sternorrhycha. In captivity they may be fed with any arthropods, even strongly sclerotized species, if these are injured.

Adult snakeflies have repeatedly been observed to feed on pollen, and pollen is sometimes found in the gut when imagoes are dissected. Whether pollen is necessary, or whether it improves the condition (or prolongs the lifespan), is not known.

The natural food of Inocelliidae is virtually unknown. We have never observed any inocelliid feeding on an insect; however, this need not be necessarily conclusive. In captivity they take an artificial diet. Pollen has very rarely been found in the gut of adult inocelliids, but no special investigations have been carried out.

FOOD OF LARVAE

All stages of the larvae of all species of both families are entomophagous, feeding on a great variety of (preferably soft-bodied) arthropods. Virtually no special field studies have, however, been carried out to investigate the question of food under natural conditions. Potential prey may include eggs and larvae of any insects, particularly Lepidoptera, Hymenoptera, Coleoptera, larvae and adults of Psocoptera, Auchenorrhyncha and Sternorrhyncha, and also Collembola, mites and spiders (ASPÖCK *et al*. 1991, KOVARIK *et al*. 1991). It is suggested (but not really proven) that corticolous larvae may hunt for prey on the bark at night, which would be of great importance with respect to the selection of food. It is also not known how far they may move during the night (if they really migrate).

There is no doubt that the spectrum of prey must be considerably different in corticolous larvae on one hand and in larvae living in the soil on the other. Again, no field studies have been done. Under experimental conditions bark-dwelling and soil-dwelling larvae do not show any differences in their feeding behaviour.

LIFE CYCLES

During the past three decades several thousand larvae of a considerable number of species of Raphidioptera have been kept in captivity and largely reared to the adult stage. Many observations have consequently been recorded (ASPÖCK *et al.* 1974*a*, *b*, 1975, 1991, ASPÖCK *et al.* 1992, 1994*a, b,* 1995, KOVARIK *et al*. 1991, RAUSCH & ASPÖCK 1992, SUNTRUP 1990). The number of larval instars is not fixed, it varies around 10–11, but may reach 15 or even more (ASPÖCK *et al*. 1991, KOVARIK *et al*. 1991).

The egg stage lasts, probably in all species without exception, a few days up to three weeks only.

The larval period lasts at least (in few species of Raphidiidae of group I and of *Agulla*) one year, in most species two or three years and, at least under experimental conditions, in some individuals of some species several (up to six) years. The prepupal stage is always a short period of a few days duration only.

The duration of the pupal stage depends on the time of pupation. In the majority (most genera of group I except *Tjederiraphidia* and *Ornatoraphidia*; genera of groups III, IV, and VII; most Inocelliidae) pupation (usually) takes place in spring and lasts a few days up to about three weeks (life cycle type I).

In some (or all) species of a few genera of Raphidiidae (life cycle type II: *Tjederiraphidia, Ornatoraphidia, Atlantoraphidia, Harraphidia, Hispanoraphidia, Africoraphidia, Ohmella*) pupation (usually) takes place in summer or autumn, and the pupal stage lasts several (up to 10!) months. In very few species (genus *Alena*, Mexican inocelliid species) pupation takes place in summer and after a pupal stage of a few weeks the adults hatch in late summer (life cycle type III).

Hibernating stages may thus be the last larval stage (usually type I), penultimate (or even an earlier) larval stage (type III, rarely probably also in type I) or pupa (type II), but never egg, prepupa or adult. Figure 1 shows the three main types of life cycles known in Raphidioptera.

It is of interest that single individuals of species belonging to type II may sometimes behave like species of type I, *i.e.* they pupate after hibernation of the last larval stage.

As far as we know all snakeflies need a period of low temperature (probably around 0°C) to induce pupation (type I) or hatching of the imago (type II). In type III the low temperature is probably important for the mature larvae to pupate in (late) summer after one or two moults after winter. KOVARIK *et al.* (1991), who studied the American snakefly *Agulla bicolor* (type I) stated that "chilling was not necessary to initiate pupation". This finding needs further confirmation, and it will have to be determined whether this can be reproduced in a larger number of specimens. It is possible that in some species only a slight decrease of temperature may be sufficient.

PROTHETELY

Larvae that are continuously kept at room temperature will usually not pupate, but may live several years with several additional moults thus reaching up to 15 instars. Most of these larvae become prothetelous, *i.e.* they develop pupal or imaginal characters, *e.g.* compound eyes, wing pads, and appendages on the abdo-

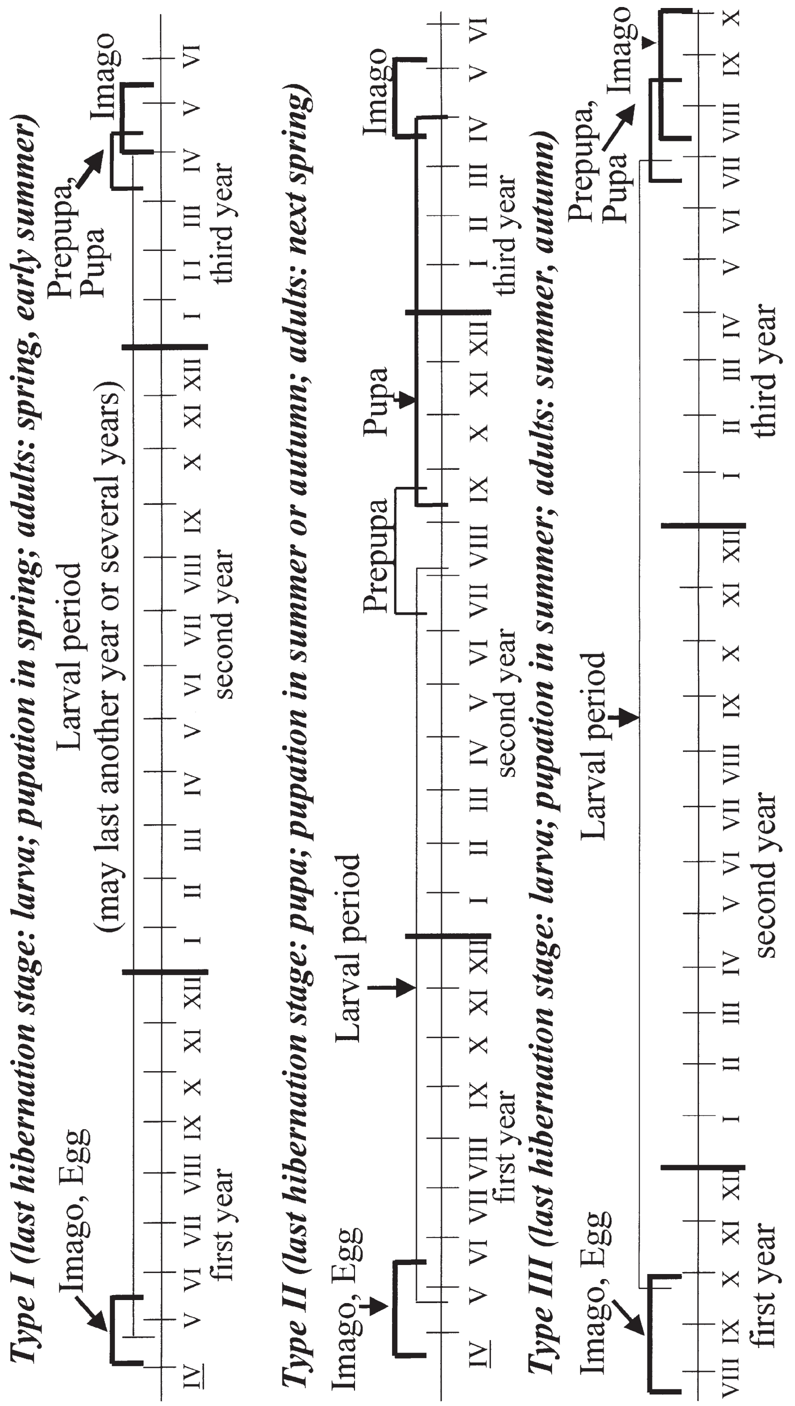

Fig. 1. Life cycles of Raphidioptera

men. The prothetelous larvae may live for further months, even years, but eventually, they usually die. Pupation may be achieved only in very rare cases, and in even rarer cases an adult will hatch with various abnormalities.

MATING AND OVIPOSITION

Courtship behaviour and mating have been repeatedly observed and described (ASPÖCK *et al.* 1991, KOVARIK *et al.* 1991, ASPÖCK *et al.*1995). Two positions of copulation have been found; a "wrecking position", in which the male hangs head first from the female and being carried by her, and a "tandem position", in which the male crawls under the female attaching his head in fixed connection to the fifth sternite of the female. The "wrecking position" is the usual position found in all Raphidiidae examined (with some differences in *Alena*). The "tandem position" has been observed in Inocelliidae only and is probably typical for the whole family. So far it has not been revealed how the male fixes his head to the ventral side of the female. There are eversible sacs near the bases of the antennae and these are apparently (how?) attached to the fifth sternite of the female.

Copulation lasts a few minutes to 1½ hours in Raphidiidae, but is much longer, up to three hours in Inocelliidae.

PARASITES AND PARASITOIDS

Table 2 provides a list of the species known to parasitise Raphidioptera.

The Gregarinida are apparently non-pathogenic. Mermithids usually kill their hosts, but they are extremely rare in snakeflies. Erythraeid mites are sometimes found on adults, but are not life-threatening and, moreover, rare.

Hymenoptera are of considerable significance as parasitoids of larvae. Species of genus *Nemeritis* (Ichneumonidae) of the subfamily Campopleginae are by far the most important parasitoids. They probably comprise 90–95% of all parasitoids in snakefly larvae, at least in the Palaearctic. Two species are particularly frequent in Western Palaearctic Raphidioptera: *Nemeritis caudatula* and *N. specularis*. Both species are widely distributed from Morocco and Spain in the west throughout Europe to Eastern Anatolia. Both have been found in many species of both families, Raphidiidae as well as Inocelliidae, and they comprise 70–80% of all parasitised larvae.

Other ichneumonids, braconids and chalcidids contribute to about 1% of the parasitised larvae. In the Palaearctic 5–15% of a population are usually parasitised,

Table 2. Parasites (P) and parasitoids (Pd) in Raphidioptera (R = Raphidiidae, I = Inocelliidae). See also ASPÖCK *et al*. (1991), HORSTMANN (1993, 1994), SUNTRUP (1990)

Parasite (P), parasitoid (Pd)	Raphidiopteran hosts recorded	Parasit-ised stage	Other hosts
Protozoa: Apicomplexa: Eugregarinida Gregarinidae			
P *Gregarina raphidiae* ACHTELIG	R: *Phaeostigma* s.l. (2 spp.)	Larva	–
	Raphidia s.str. (1 sp.)	Larva	
Nematoda: Trichosyringida			
Mermithoidea: Mermithidae			
P Mermithidae gen. sp.	I: *Fibla* (1 sp.)	Larva	?
Acari: Trombidiformes: Erythraeidae			
P Erythraeidae gen. sp.	R: *Xanthostigma* (1 sp.)	Imago	?
Hymenoptera:			
Ichneumonidae: Campopleginae			
Pd *Nemeritis caudatula* THOMSON	R: *Phaeostigma* s.l. (10 spp.)	Larva	–
	Subilla (3 spp.)	Larva	
	Xanthostigma (1 sp.)	Larva	
	Raphidia s.str. (2 sp.)	Larva	
	Puncha (1 sp.)	Larva	
	Venustoraphidia (1 sp.)	Larva	
	Mauroraphidia (1 sp.)	Larva	
	I: *Fibla* s.str. (3 spp.)	Larva	
	Parainocellia (1 sp.)	Larva	
Pd *Nemeritis scaposa* HORSTMANN	R: *Raphidia* s.l. (5 spp.)	Larva	–
Pd *Nemeritis specularis specularis* HORSTMANN	R: *Phaeostigma* s.l. (11 spp.)	Larva	–
	Tauroraphidia (2 spp.)	Larva	
	Subilla (5 spp.)	Larva	
	Ornatoraphidia (1 sp)	Larva	
	Raphida s.str. (1 sp.)	Larva	
	Puncha (1 sp.)	Larva	
	Venustoraphidia (1 sp.)	Larva	
	I: *Fibla* (1 sp.)	Larva	
	Parainocellia s.str. (2 spp.)	Larva	
Pd *Nemeritis specularis anatolica* HORSTMANN	R: *Phaeostigma* s.l. (4 spp.)	Larva	–
	Tauroraphidia (1 sp.)	Larva	

Table 2 (continued)

Parasite (P), parasitoid (Pd)	Raphidiopteran hosts recorded	Parasit-ised stage	Other hosts
Pd *Nemeritis specularis anatolica* HORSTMANN	*Raphidia* s.l. (3 spp.)	Larva	
Pd *Nemeritis specularis indica* HORSTMANN	I: *Inocellia* (1 sp.)	Larva	–
Pd *Nemeritis elegans* (SZÉPLIGETI)	R: *Dichrostigma* (1 sp.)	Larva	–
Pd *Nemeritis colossea* HORSTMANN	R: *Subilla* (1 sp.)	Larva	–
Pd *Nemeritis silvicola* HORSTMANN	R: *Phaeostigma* s.l. (2 spp.)	Larva	–
Pd *Nemeritis* sp. B (near *silvicola* and *graeca*)	R: Raphidiidae gen.sp. (1 sp.)	Larva	–
Pd *Nemeritis canaliculata* HORSTMANN	R: *Phaeostigma* s.l. (1 sp.)	Larva	–
Pd *Nemeritis* sp. C (near *canaliculata*)	R: *Phaeostigma* (1 sp.)	Larva	–
Pd *Nemeritis graeca* HORSTMANN	R: *Phaeostigma* s.l. (3 spp.)	Larva	–
Pd *Nemeritis similis* HORSTMANN	R: *Phaeostigma* s.l. (3 spp.)	Larva	–
	Raphidia s.str. (1 sp.)	Larva	–
Pd *Nemeritis* sp. D (near *similis*)	R: *Phaeostigma* s.l. (1 sp.)	Larva	–
Pd *Nemeritis* sp. E (near *similis*)	R: *Phaeostigma* s.l. (2 spp.)	Larva	–
Pd *Nemeritis* sp. F	R: *Subilla* (1 sp.)	Larva	–
Ichneumonidae: Cryptinae			
Pd *Tropistes falcatus* (THOMSON)	R: *Phaeostigma* (1 sp.)	Larva	?
	Puncha (1 sp.)	Larva	
Pd *Tropistes nitidipennis* (GRAVENHORST)	R: *Puncha* (1 sp.)	Larva	?
Ichneumonidae: Pimplinae			
Pd *Itoplectis alternans* (GRAVENHORST)	Raphidiidae gen. sp	Larva	Broad host spectrum compris-ing Lep., Col., Dipt. & Hym.
Hymenoptera: Braconidae: Euphorinae			
Pd *Meteorus pachypus* (SCHMIEDEKNECHT)	R: *Xanthostigma* (1 sp.)	Larva	?
Pd *Meteorus punctifrons* THOMSON	R: *Hispanoraphidia* (1 sp.)	Larva	?
Hymenoptera: Chalcidiodea: Perilampidae			
Pd *Perilampus maceki* BOUČEK	I: *Inocellia* sp	Larva	?

Table 3. Hyperparasites in Raphidioptera

Hyperparasite	Raphidiopteran hosts (larvae) parasitized by Ichneumonidae	Other hosts
Hymenoptera: Chalcidoidea: Perilampidae		
Perilampus polypori BOUČEK	Raphidiidae:	?
	Phaeostigma s.l. (6 spp.)	
	Subilla (2 spp.)	
	Puncha (1 sp.)	
	Venustoraphidia (1 sp.)	
	Inocelliidae:	
	Parainocellia s.str. (1 sp.)	
Perilampus cephalotes BOUČEK	Raphidiidae:	?
	Phaeostigma s.l. or	
	Raphidia s.str. (1 sp.)	
	Puncha (1 sp.)	

but in a few populations more than 50% of the larvae of a species were parasitised. It is, however, of interest that among some hundred larvae of several species collected in Mexico (under bark of pines) none was found to be parasitised.

Hyperparasites so far recorded (only Chalcidoidea: Perilampidae) are listed in Table 3.

ECONOMIC IMPORTANCE

Snakeflies are effective predators. All larval stages of all species of both families, and at least the adults of the Raphidiidae feed on (mainly soft-bodied) arthropods (see above) so that the question arises as to whether they could play a significant role in integrated pest control.

Three basic facts should be considered (ASPÖCK 1991, ASPÖCK *et al*. 1991):

1. Because of historical/zoogeographical but not for ecological factors, large parts of our planet lack snakeflies: including the north and east of North America and the whole southern hemisphere. Within this huge area there are large regions with ecologically very favourable conditions for Raphidioptera.

2. This means that an introduction of Raphidioptera into these areas could be promising, particularly in reforestation areas and in fruit plantations.

3. On the other hand, manipulations within the natural distribution area are most probably of no use.

Snakeflies are believed to be rare insects. This is indeed true for many species and many regions, but it is not correct for a number of species that often occur in large numbers.

Here is an overview of arguments for and against effective use of snakeflies in integrated pest control:

ADVANTAGES

– Rearing techniques as a basic prerequisite are well-established.
– Introduction of parasite-free populations would consequently be possible.
– Biology of many potential species is very well-known.
– Larvae (and adults of at least of Raphidiidae) are predacious.
– Long larval period.
– Polyphagy?
– Snakeflies do not have important specific natural enemies.

DISADVANTAGES

– Long developmental period.
– Polyphagy?
– Due to long life-cycles only slow change of population densities, which means slow and delayed adaptation to altered conditions.
– High stenotopy and therefore slow disperse.
– Association with certain plants (trees) weak.

No substatial experimental data available.

As early as 100 years ago there were several attempts to use snakeflies as biological control agents in pest management. One or two unidentified North American species were introduced into Australia and New Zealand, but apparently they could not be established. At that time, however, nobody knew that low temperatures at a certain period in the development are necessary. And at that time it was also impossible to rear snakeflies.

Today we are in a much better position. During the past thirty years we have gathered much experience in general, and a large amount of substantial data in particular which have enabled us to standardise the rearing of snakeflies.

REARING METHODS

Rearing usually commences with a female collected in the field. For oviposition we use plastic vials of about 25 mm diameter and 40 mm in length with a densely packed roll of cellulose. A damaged fly (or any squashed insect) or a few aphids provide adequate food, and the female will readily start laying eggs between the layers of the cellulose. The eggs are usually fertile, as a female taken in the field has usually already copulated. After a few days the larvae hatch and will spread into the various parts of the cellulose. This prevents them from eating each other, particularly if a few immobilised *Drosophila* adults are added. These serve as a source of food as well as providing humidity. The larvae may be kept in this first vial for a few months, then they should be separated as they become an increasing danger to one another. The same vials can be used for the separated larvae. Mealworms cut into pieces are an excellent food, but other (soft-bodied) insects (e.g. *Drosophila*) should occasionally be added. Food should be changed every 4–8 weeks. It is essential that the larvae are transferred to low temperatures in autumn and kept at low temperature for some time. It is not yet known how long and which temperatures are necessary – possibly exposure to low temperature (perhaps in many species only around 0°C) for a few days – will be sufficient for standardisation. As long as we do not know the answer to this question, we keep them at low temperatures for at least four months. In early spring they should be transferred to room temperature again and be kept in the vials as described. For the second hibernation of the larva or for hibernation of pupae the same procedure is necessary. Usually (type I), after two or three hibernations, the larvae will pupate and the pupae will develop to adults within ten to twenty days. Mating is necessary for a continuation of the culture, and this is certainly the most laborious part, mainly due to the long and complicated mating ritual. Nevertheless we have repeatedly successfully induced copulation of snakeflies in captivity. Some species copulate readily even in small vials, other need branches in larger cages for their mating ritual. As soon as copulation has been completed, females may be placed in vials for oviposition and the procedure can be repeated as described above.

These methods of rearing Raphidioptera have been an indispensable prerequisite for clarifying both taxonomy of larvae and biology of many snakeflies. They will, however, also be helpful to clarify a number of unanswered questions. There are several species of which the larvae are still unknown. And there are some important questions concerning the biology of snakeflies that have not yet been resolved. One of the most urgent is the question of factors that induce or which prevent prothetely, *i.e.* which temperatures are essential at particular stages of development, and are there other factors?

OUTLOOK

In summary, there are still many open questions concerning the biology of Raphidioptera. There is, however, an excellent basis with respect to the taxonomy on one hand and established field and laboratory methods on the other, so that essential progress of our knowledge may be expected in the near future.

*

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