

The Raphidioptera of the World: A Review of Present Knowledge

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A monograph of the Raphidioptera of the world, which we (H. ASPÖCK, U. ASPÖCK and H. RAUSCH) intend to publish in the near future, facilitates a summary of the present knowledge of the taxonomy, systematics, ecology, biology and zoogeography of the order. This revision is based upon:

1. 20 years of intensive field work in all biogeographically significant parts of the western Palaearctic, in Europe, Africa and Asia, and the collection of about 30.000 adults and 15.000 larvae.
2. Rearing of most western palaearctic species from larvae collected in the field on one hand, and from eggs on the other.
3. Taxonomic and systematic study and evaluation of all available Raphidioptera from any part of the world, including all important collections and all type specimens.

Results of preceding and precursory studies and of basic research for this monograph have already been published in many other papers, and a complete list of all our papers on Raphidioptera can be found in H. ASPÖCK (1984). The lists of references in these publications also include references to all important papers on Raphidioptera by other authors.

Figure 1 shows the chronological documentation of the Raphidioptera of the world, as indicated by the number of known valid species at certain times. Today, after the revision of all described taxa, these figures can be determined very easily; until recently the validity of many described species was, however, entirely unknown.

The first description of a snake-fly in the scientific literature (under the name "Die kleine langhalsige Landlibelle" = The small longnecked terrestrial dragonfly) was published by RÖSEL von ROSENHOF (1755). Snake-flies were apparently unknown to the zoologists of antiquity, of the Middle Ages, and even of the first part of modern times; at least, as far as we know, no description or even mention of a snake-fly by any of the old authors exists. LINNAEUS (1758) knew one species, SCHNEIDER (1843), in his magnificent "Monographia generis Rhaphidia", described seven species and with ALBARDA's "Révision des Rhaphidides" (1891), a milestone in the history of raphidiopterology, the number of known valid species increased to 29. At those times it was already known that snake-flies occur, not only in Europe and Asia, but also in North America. After the Dutchman H. ALBARDA, it was mainly L. NAVAS, a Spaniard, who dealt with these insects. Within the period 1909 to 1936 he described 41 species of Raphidioptera, many of which proved to be synonyms. Also, his "Monografia de l'ordre dels Rafidiópters" did not contribute to progress, as he based the characterization and systematic interpretation of his species on taxonomically irrelevant criteria (mainly wing venation), whilst he disregarded characters of the genitalia. The difficult and laborious work of revision started in America in 1936 when

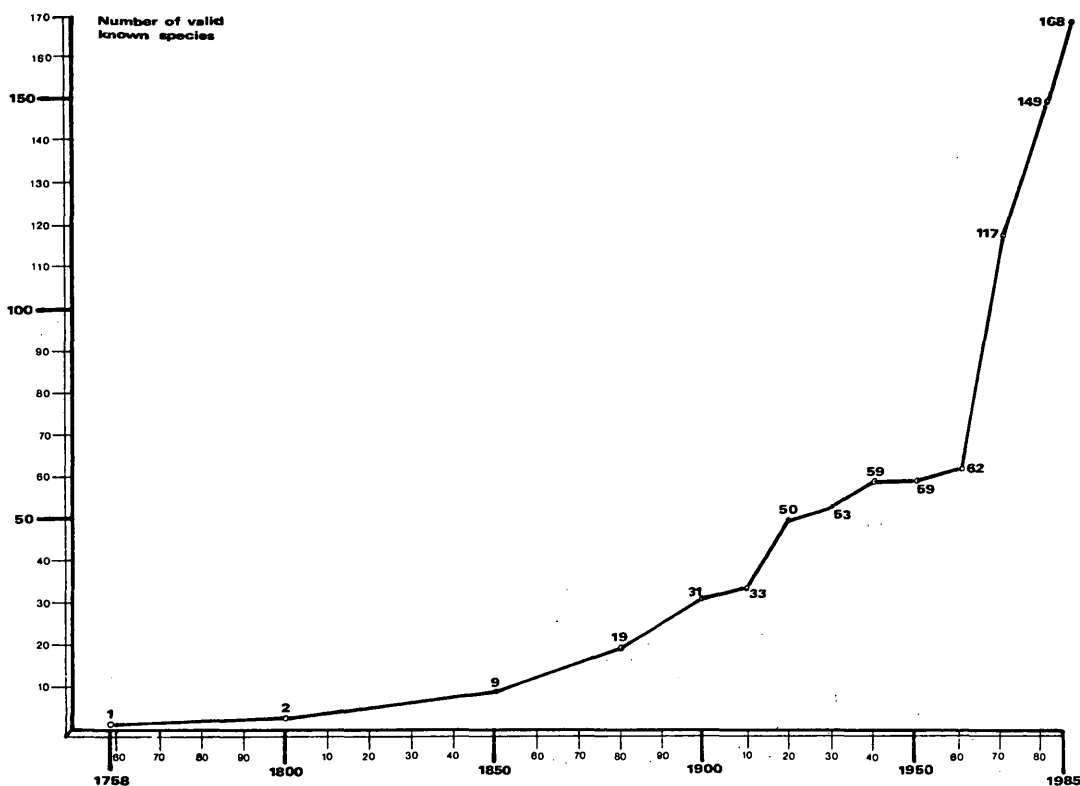


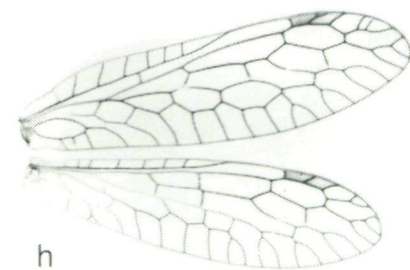
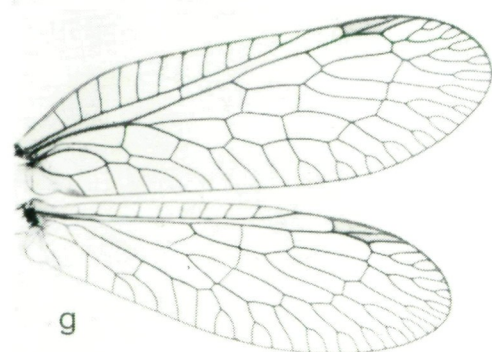
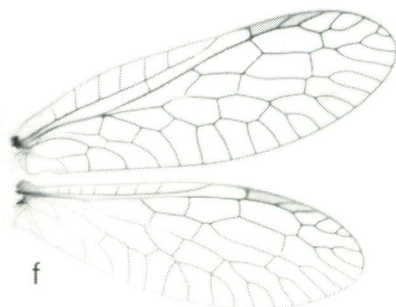
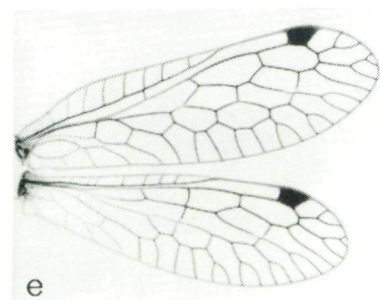
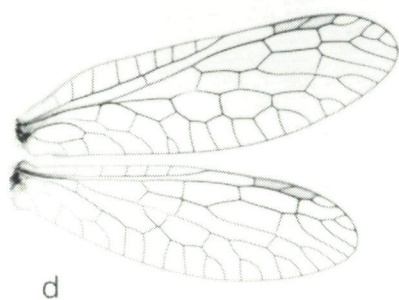
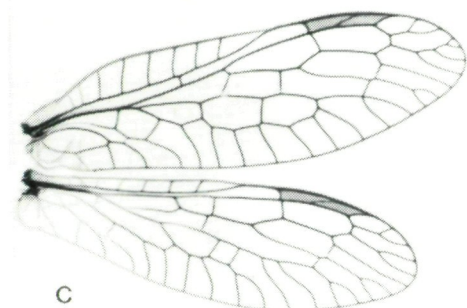
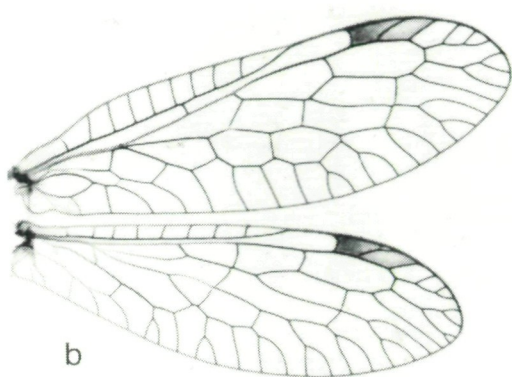
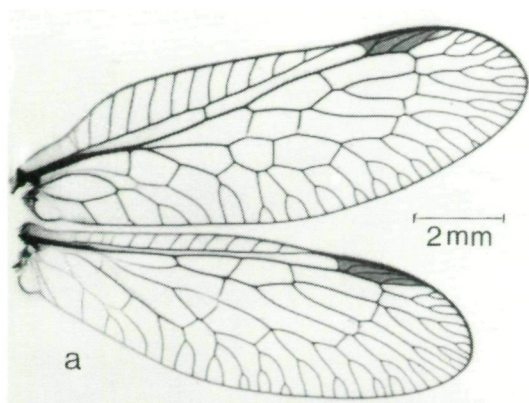
Fig. 1: Progress in documentation of species of Raphidioptera.

CARPENTER published his critical "Revision of the Nearctic Raphidioidea". In Europe a renaissance of raphidiopterology, in accordance with modern requirements, was only initiated at the beginning of the fifties by the Italian scientist Maria M. PRINCIPI. She redescribed and differentiated several European species on the basis of characters of male and female genitalia (PRINCIPI 1952, 1958, 1960), thereby providing an essential basis for further studies. Up to 1940, altogether 59 valid species had been described, and by 1960 this number had increased only slightly to 62 (51 Raphidiidae and 11 Inocelliidae). Most species were discovered and described after 1960.

Today we know 168 species (or more correctly: 168 taxa acknowledged as species) of Raphidioptera, 151 species of Raphidiidae and 17 species of Inocelliidae. These 168 species comprise almost the entire total of the recent snake-fly fauna; the real number of existing species almost certainly does not exceed 200.

With very few exceptions, all described species can be regarded as clarified and differentiated. The characterization of the species (and also of the genera) is based essentially on characters of the male and female genitalia, as characters of head, legs and

Fig. 2: Wings of six species belonging to six different genera of Raphidiidae demonstrating differences in pterostigmas, but also the uniformity of wing venation within the family. - a: *Phaeostigma notata* (FBR.), b: *Dichrostigma flavipes* (STEIN), c: *Subilla confinis* (STEPH.), d: *Atlantoraphidia maculicollis* (STEPH.), e: *Parvoraphidia microstigma* (STEIN), f: *Xanthostigma xanthostigma* (SCHUM.), g: *Agulla* (A.) *astuta* (BANKS), h: *Alena* (*Aztekoraphidia*) *minuta* (BANKS).



wings (including wing venation) are of minor importance. The experienced specialist will, of course, be able to identify most species according to their eidonomic¹⁾ characters in combination with distributional information. The wing venation is, however, so uniform in both families (Fig. 2), that clear differentiations of species on one hand, and an understanding of relationships on the other, would be impossible without a consideration of genital criteria.

The structures of the genitalia are, in most species, very constant; this applies to both ♂♂ and ♀♀. Species with a large and particularly disjunctive distribution, however, often show considerable geographic variation. In some species a subdivision into subspecies has therefore proved to be useful and necessary. In some geographically isolated, morphologically distinct, but closely related phena, it cannot be definitely decided whether or not genetic barriers exist; a problem very well known to every taxonomist.

Particular taxonomic problems exist, however, in several nearctic species. They show a surprisingly high degree of polymorphism, even within small geographical areas, which cannot be adequately explained (U. ASPÖCK 1974, 1975, 1982). Figure 3 gives an example of this phenomenon showing the variability of the ♂ genitalia of *Agulla (Glavia) paramerica* U.A., a species occurring in California.

Distribution maps have been prepared for all 168 species, and the distributional patterns have been chorologically and biogeographically analysed. The distribution of the order can be regarded as resolved, and it comprises the Holarctic except for the northern and eastern parts of North America. The two families have a very similar distribution, both occur over the whole of Europe, in the non-tropical parts of Asia, in North Africa and in the western and southern parts of North America (Fig. 4,5), with the largest number of species occurring between 35° N and 50° N. The northern-most parts of Europe and of Asia are inhabited by very few (two or three) species. In America the northern-most records of snake-flies lie near 55° N. In the southern parts of East Asia the order extends beyond the palaearctic region. The southern-most records of Raphidioptera in Asia are from Israel, the northern parts of Iran, Pakistan, Kashmir, Burma, Vietnam and Taiwan, in Africa from the High Atlas Mountains, and in America from the central parts of Mexico (table 1). In the southern parts of their distribution the occurrence of Raphidioptera is more or less restricted to higher altitudes with low temperatures during winter.

The majority of species show a monocentric and rather static distribution. There are only very few widely distributed species; this applies, however, to nearly all species also occurring in the northern temperate zones. At least two species are distributed from Central and Northern Europe throughout the north of Asia almost as far as Kamtchatka. However, there are certainly no species which occur in the Palaearctic as well as in the Nearctic. All species occurring in Europe, Africa or Asia belong to entirely different genera than the Raphidioptera of America. This supports the assumption that the raphidiopterous fauna of America should be traced back to very early immigrations from Asia during the Tertiary. At least in the recent snake-fly fauna there is no indication of an immigration of Raphidioptera from Asia since the late Tertiary.

Focal points of distribution of the Raphidioptera are the Mediterranean region with about 100 species, Central Asia with about 30 species and the southwest of North America with more than 25 species. By far the most species occur in the eastern Mediterranean region (table 1). Also in this regard, the restricted distribution of most species should be emphasized. We do not know any holomediterranean species, in fact, we do not even know any species which occur in the Iberian Peninsula as well as in the Balkan Peninsula, and we only know very few species which occur in more than one of the southern European peninsulas (Iberian, Apennines, Balkan).

The larvae of most western palaearctic species are known and their taxonomy has been studied in detail. Also the biology and ecology of most of these species are well-known.

¹⁾ eidonomic characters = morphological characters visible without dissection

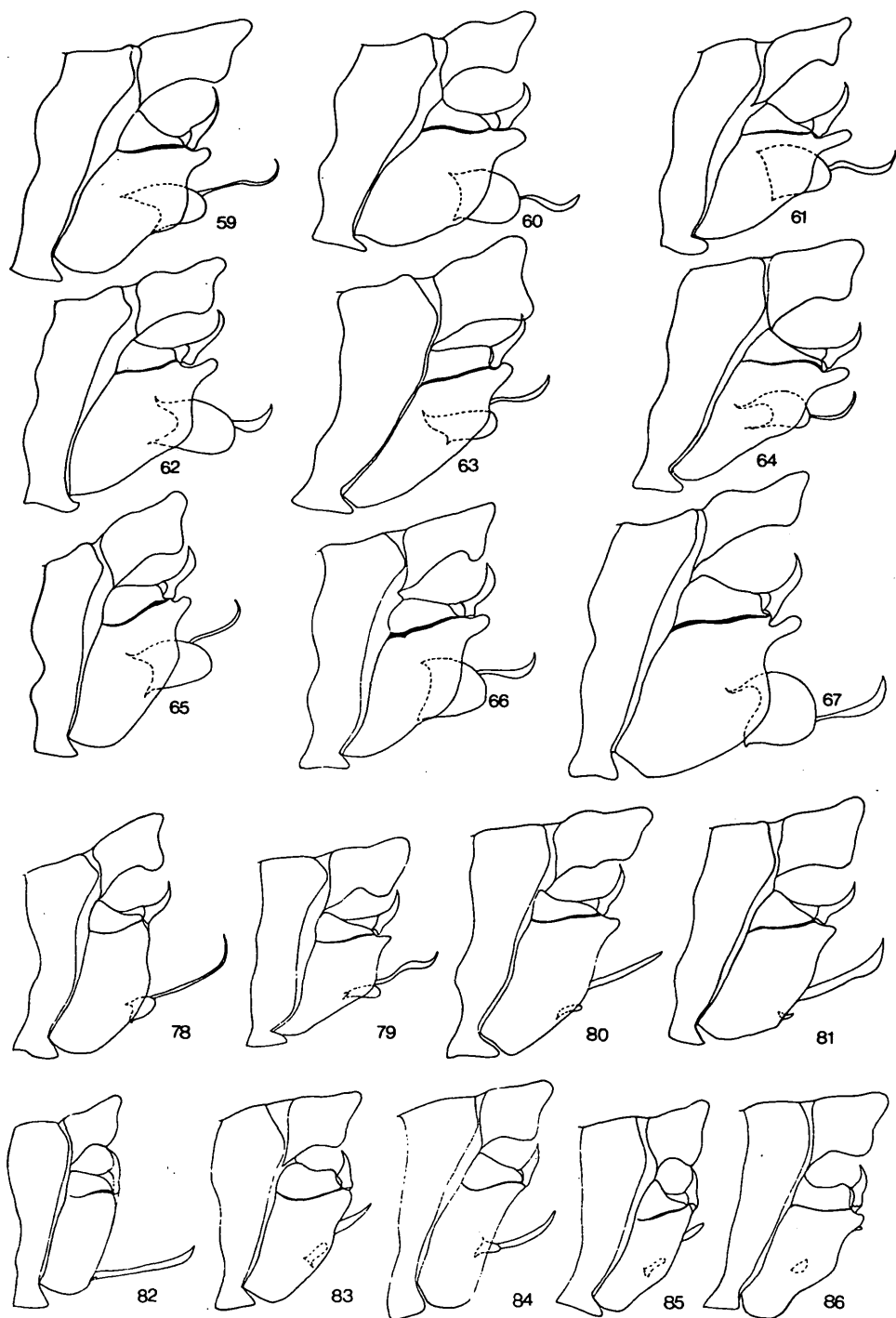


Fig. 3: Variability of ♂ genitalia (lateral) of *Agulla (Glavia) paramerica* U. A. (from U. ASPÖCK 1982). Numbers refer to the original publication.

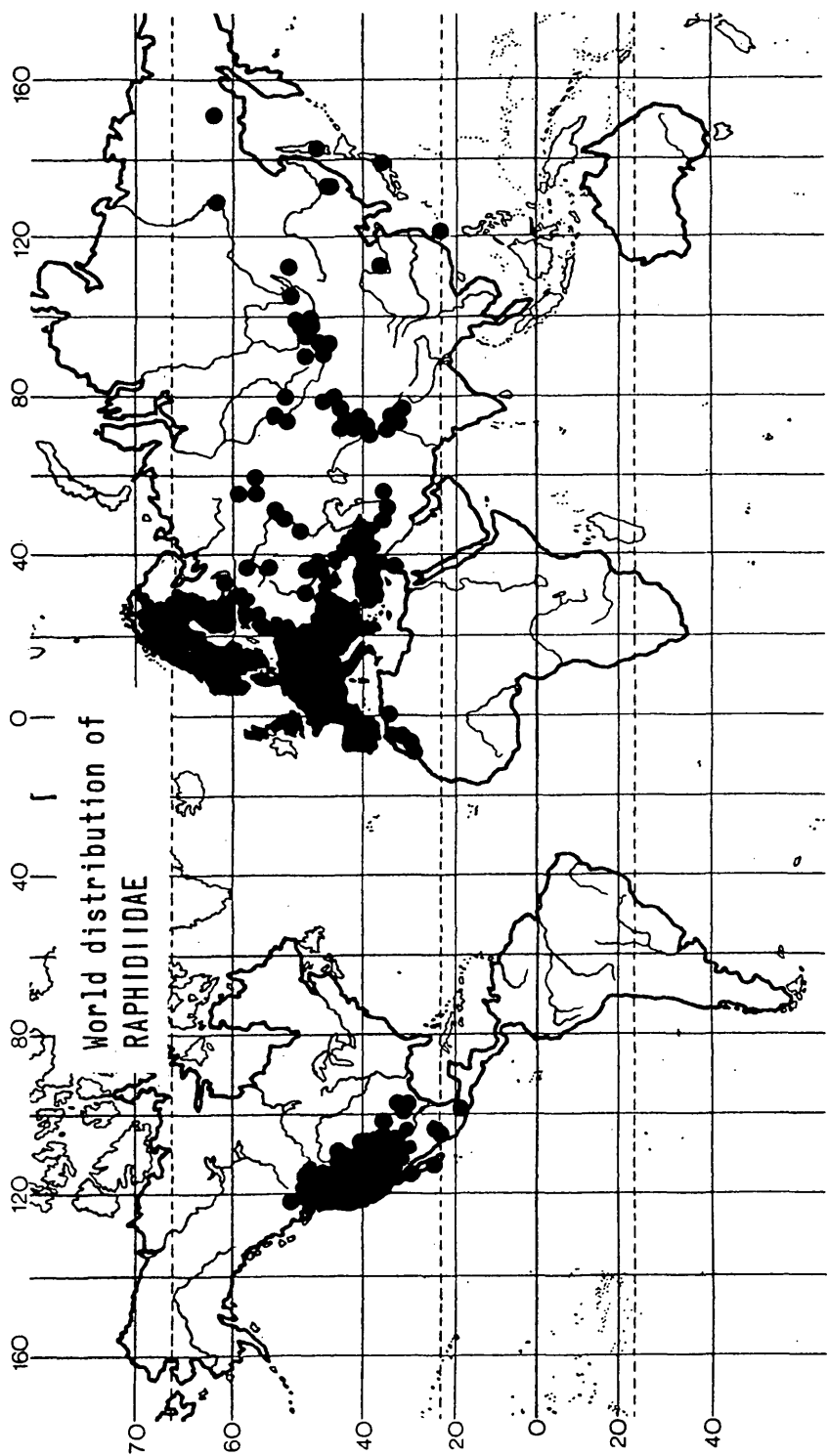


Fig. 4: World distribution of the family Raphidiidae.

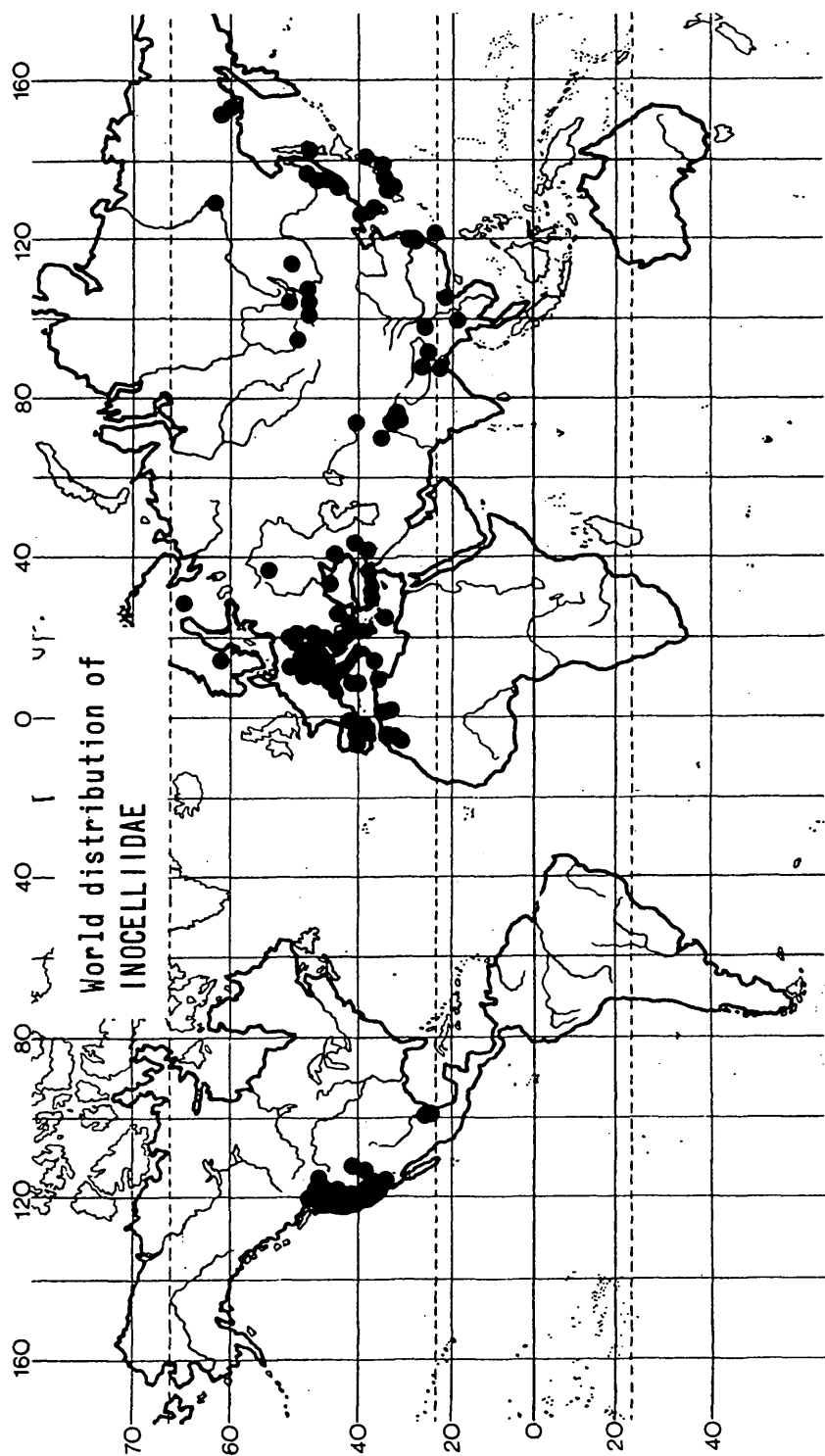


Fig. 5: World distribution of the family Inocelliidae.

The dorsal and lateral, and, to a lesser degree, also the ventral patterns of pigmentation of the abdominal segments of the larvae offer excellent characters for differentiation (Fig. 7). If distributional criteria are also taken into consideration, an identification can be obtained in almost every case, although the variability of these patterns may be high in some species.

The development of all Raphidioptera is confined to arboreal habitats in a broad sense. Larvae live either in crevices in the bark of trees or shrubs or in the superficial strata of the soil around the roots of shrubs. In most species there is a strict association either with bark or with soil, only few species are arboreal as well as terrestrial. Many species are associated with certain genera or higher taxa of trees (e.g. *Quercus* spp., coniferous trees, etc.) and are frequently restricted to certain habitats.

The duration of development is, in most species, not strictly constant. Most Raphidiidae have a two-year development period, but may also need three years or, more rarely, can develop from the egg to the adult within one year. A regular one-year development period only occurs in very few species. Inocelliidae have a longer larval period, they normally need three years. Under laboratory conditions we have occasionally found a development period of five years in Inocelliidae. Apparently all Raphidioptera need the stimulus of low temperature at a certain time during the larval (in some genera in the pupal) stage to initiate the prepupal phase and further development to the adult, or for continuation of development of the pupa. Larvae kept permanently in the laboratory at room temperature may live for many years but will never yield a pupa or an imago; more often they develop prothetely and eventually die. This leads to the assumption that the lack of low temperatures in the south of the northern hemisphere has prevented snake-flies from immigrating into the southern hemisphere where they could find, without doubt, excellent ecological conditions in many regions.

In recent years much information has been obtained on parasites of Raphidioptera. Among more than 10,000 larvae collected in different parts of the western Palearctic, and kept alive for further rearing, about 10 % proved to be parasitized, mainly by Ichneumonidae and, to a much less degree, by Braconidae. By far the most frequent parasites are species of the ichneumonid genus *Nemeritis* HOLMGREN. While some species of the genus *Nemeritis* are parasites of other insects (e.g. beetles), probably all *Nemeritis* obtained from larvae of Raphidioptera (so far 13 species) are exclusively parasites of snake-flies. Most, if not all of them can develop in many species, even of both families, Raphidiidae and Inocelliidae. Two species, *Nemeritis caudatula* THOMSON and *N. specularis* HORSTMANN s.l. have particular significance; they proved to be the causative agent of more than 80 % of all cases of parasitized larvae (H. ASPÖCK, U. ASPÖCK & RAUSCH 1985b).

The generic classification of the two families, Raphidiidae and Inocelliidae, which are characterized by a number of distinct apomorphies, still presents some problems, mainly with respect to the supra-generic classification. At least the definition of the genera can now, after all, be regarded as clarified.

All classifications hitherto proposed do not reflect reality in any way. The systems of NAVAS (1918), LESTAGE (1928) and STEINMANN (1963) need no further discussion, but CARPENTER (1936), who recognized the weaknesses of the old systems, could not find a convincing solution either. Until 1980 we used an elementary classification in order to group the large variety of species; thus, we subdivided the genera *Raphidia* L. (as the only genus of Raphidiidae) as well as *Inocellia* SCHNEIDER (as the only genus of Inocelliidae) into several subgenera (H. ASPÖCK & U. ASPÖCK 1968; H. ASPÖCK, U. ASPÖCK & HÖLZEL 1980). The results of critical studies of all structures of the head and thorax and of wing venation have led to the conclusion that, because of their uniformity, synplesiomorphies and several parallelisms, all these characters are unsuitable for a clarification of relationships. Thus, only the genital structures show a high degree of diversity in both families and offer very valuable criteria. There is no doubt that they indicate several

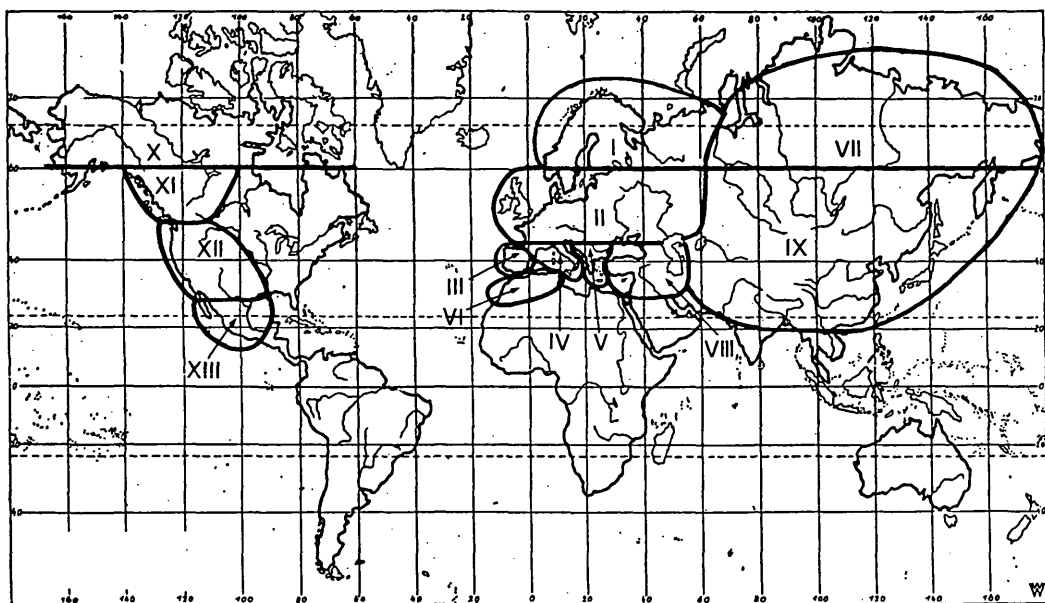


Fig. 6: Zones according to table 1.

divergent phylogenetic lines and that they are very suitable for differentiations of monophyletic groups. The clarification of the systematic position of these groups in the sense of HENNIG (e.g. 1969) was, however, not possible.

We are convinced of the great value of HENNIG's theory without representing an extreme point of view. We agree that a taxon, in this case the genus, should only be based upon synapomorphic characters and that relationships should be found by detection of sister-groups. We have, however, only occasionally succeeded in finding such sister-groups. The main reason is probably due to the fact that the recent Raphidioptera are the meagre remains of a much richer diversity in earlier geological periods, and that many branches (genera, groups of genera) have become extinct. What we are seeing today, are a few mosaic stones with very few adjacent ones, i.e. sister-groups.

We have therefore tried to find and to characterize monophyletic groups which are as large as possible in both families. To each of these groups which could not be united with another monophyletic group by an overlapping group we have given the rank of genus. Most of these genera have already been described as subgenera of *Raphidia* L. and *Inocellia* SCHNEID., respectively. In our preliminary classification (H. ASPÖCK & U. ASPÖCK 1968) and in later papers, some were already treated as genera, anticipating the new classification (H. ASPÖCK, U. ASPÖCK & RAUSCH 1982a, 1982b, 1983a, 1983b, 1984; U. ASPÖCK 1982), and a few were described as genera after 1980 (H. ASPÖCK, U. ASPÖCK & RAUSCH 1982a, 1983a, 1985a). According to this principle we have divided the family Raphidiidae into 26 genera and the family Inocelliidae into five genera, some of them with two or more subgenera (tables 2, 3).

Within the Raphidiidae, 12 genera comprising 81 species might represent a monophyletic group; it includes the large genus *Phaeostigma* with 34 known species and 11 additional genera (*Dichrostigma*, *Tjederiraphidia*, *Turcoraphidia*, *Iranoraphidia*, *Subilla*, *Tauroraphidia*, *Ornatoraphidia*, *Xanthostigma*, *Parvoraphidia*, *Ulrike*, *Raphidia*), the distributions of which are also confined to Europe, the north of Asia and the Near East. Seven genera

Geographic region		Number of species recorded		
		Raphidiidae	Inocelliidae	Total
Europe		60	7	67
Zone I:	Europe north of 60°N	3	1	4
Zone II:	Europe between 45°N and 60°N eastward as far as to the Ural and including the whole of the Krim Peninsula	17	3	20
Zone III:	Iberian Peninsula south of the main crest of the Pyrenees	9	1	10
Zone IV:	Southern France and Apennine Peninsula, Tyrrhenian islands and Sicily	17	2	19
Zone V:	Balkan Peninsula south of 45°N including all Dalmatian, Jonian and Aegean islands	43	3	46
Africa (Zone VI)		3	1	4
Asia		73	8	81
Zone VII:	Asia north of 60°N	2	1	3
Zone VIII:	Anterior Asia between 30°N and 45°N eastward as far as 55°E (Anatolia, Caucasus, Transcaucasia, Iran, Iraq, Syria, Lebanon, Israel, Cyprus)	38	1	39
Zone IX:	Asia south of 60°N and east of 55°E including Japan and Taiwan	36	7	43
America		22	3	25
Zone X:	America north of 60°N	0	0	0
Zone XI:	America north of 50°N	6	1	7
Zone XII:	America between 30°N and 50°N	17	2	19
Zone XIII:	America south of 30°N	5	1	6
Total number of known recent species		151	17	168

Table 1. The distribution of Raphidioptera in the world (see also Fig. 4 - 6).

Genus	Number of Known species	Geographic zones (see Table 1 and Fig. 4 -6)												
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
Phaeostigma NAVAS	34	●	●	●	●	●			●					
Dichrostigma NAVAS	4		●		●	●			●					
Tjederiraphidia H. A. & U. A. & RAUSCH	1				●									
Turcoraphidia H. A. & U. A.	5		●			●			●					
Iranoraphidia H. A. & U. A.	1		●						●					
Subilla NAVAS	9		●	●	●	●			●					
Tauroraphidia H. A. & U. A. & RAUSCH	2								●					
Ornatoraphidia H. A. & U. A.	2		●		●	●								
Xanthostigma NAVAS	4	●	●	●	●	●		●	●	●				
Parvoraphidia H. A. & U. A.	3					●								
Ulrike H. A.	2					●			●					
Raphidia L.	14	●	●		●	●		●	●	●				
Atlantoraphidia H. A. & U. A.	1		●	●	●									
Harraphidia STEINMANN	2			●			●							
Africoraphidia U. A. & H. A.	1						●							
Hispanoraphidia H. A. & U. A.	1			●										
Ohmella H. A. & U. A.	4			●										
Italoraphidia H. A. & U. A.	1				●									
Puncha NAVAS	1		●		●	●								
Venustoraphidia H. A. & U. A.	2		●		●	●								
Mauroraphidia H. A. & U. A. & RAUSCH	1						●							
Tadshikoraphidia H. A. & U. A.	2									●				
Usbekoraphidia H. A. & U. A.	1									●				
Mongoloraphidia H. A. & U. A.	31									●				
Agulla NAVAS	16									●		●	●	
Alena NAVAS	6													●

Table 2. The distribution of the genera of the family Raphidiidae.

Genus	Number of known species	Geographic zones (see Table I and Fig. 4 - 6)												
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
Parainocellia H. A. & U. A.	5		●		●	●			●	●				
Inocellia SCHNEIDER	5	●	●					●		●				
Fibla NAVAS	4			●	●	●	●							
Negha NAVAS	2			●								●	●	
Indianoinocellia U. A. & H. A.	1													●

Table 3. The distribution of the genera of the family Inocelliidae.

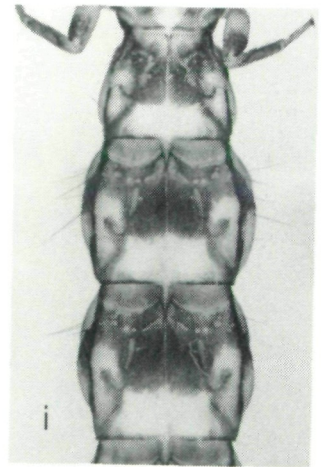
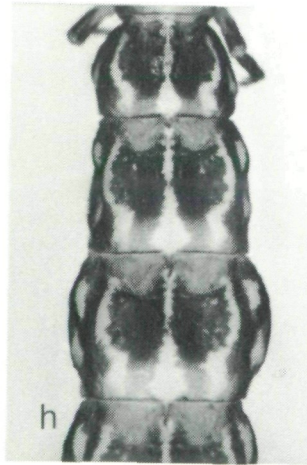
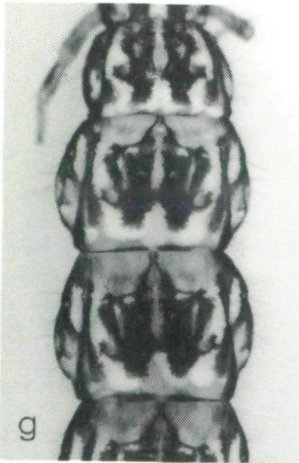
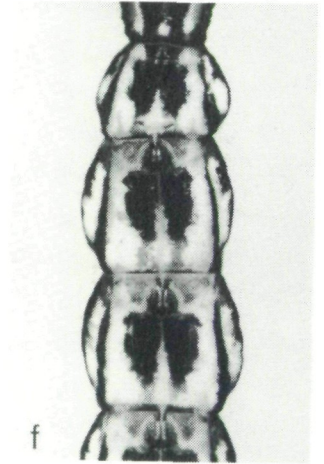
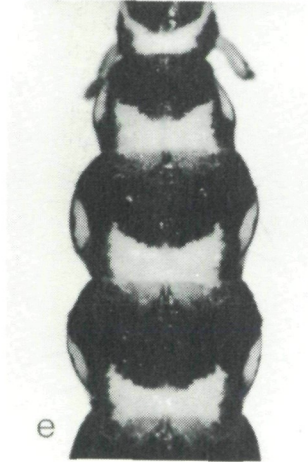
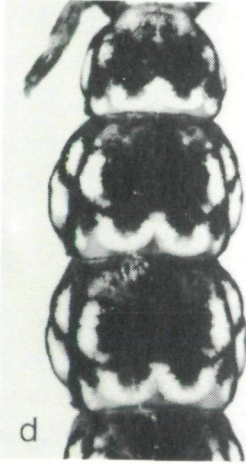
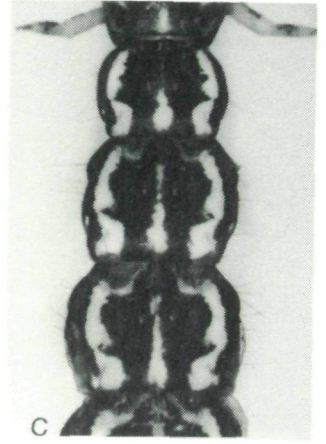
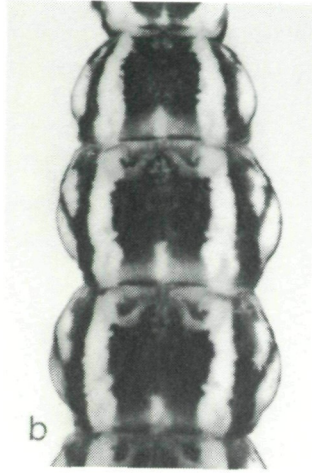
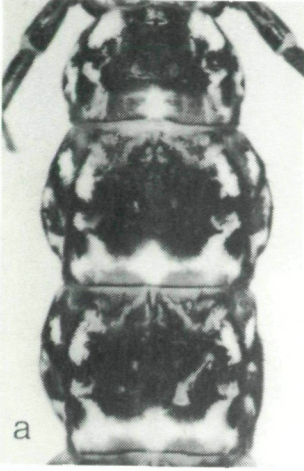
(**Atlantoraphidia**, **Harraphidia**, **Africoraphidia**, **Hispanoraphidia**, **Ohmella**, **Italoraphidia**, **Puncha**) with 11 species, the distributions of which are almost entirely confined to the western Mediterranean region, possibly also represent a monophyletic group. Whether **Venustoraphidia** and **Mauroraphidia** form a monophyletic group, has not yet been clarified. At any rate, none of these three groups, or of the other genera represented in the Palearctic (**Usbekoraphidia**, **Tadshikoraphidia** and the large genus **Mongoloraphidia**, which is distributed in Central Asia and East Asia, and which comprises 31 known species), can be put into a sister-group relationship with any other of these groups (or genera) nor with the nearctic genera. Among the nearctic Raphidiidae, **Alena** shows several striking apomorphies; this genus is possibly the sister-taxon to all other Raphidiidae. The remaining species of the family occurring in North America probably represent a monophyletic group, i.e. the genus **Agulla**.

The small family Inocelliidae has been divided into five genera which differ markedly in several morphological and distributional characters, and which cannot be put into any mutual sister-group relationship.

To summarize: The documentation of the recent species of the order has almost been completed, but the degree of exploration within the area covered by the distribution of snake-flies is still very disproportionate. Europe, the northwest of Africa, and Anatolia, those regions which form the geographic focal point of the order, have been explored very intensely. Larvae, ecology and biology of most species are known, and discoveries of new species can rarely be expected. Also, though with some reservation, the snake-flies of North America can be regarded as documented, although a few new species, particularly in Mexico, still await discovery. Even the Raphidioptera of Central Asia and Northeast Asia (including the north of India, Mongolia and Japan) have been fairly well covered; there is, however, no doubt that these vast areas still harbour some undescribed species. The raphidiopterous fauna of China is, however, almost entirely unknown. Snake-flies certainly do not occur in large parts of China but without doubt many of the mountain ranges with arboreal habitats not affected by monsoon rains do have Raphidioptera, probably not many, and probably mainly or only species of the genus **Mongoloraphidia**. Due to the lack of any information, more accurate estimates are impossible.

The discovery of new species in any part of the world which cannot be put into one of the described genera can, of course, not be excluded, but is rather unlikely.

Fig. 7: Examples for the taxonomic significance of the patterns of dorsal pigmentation in larvae of Raphidiidae. - a: **Phaeostigma major** (BURM.), b: **Phaeostigma rauschi** (H. A. & U. A.), c: **Dichrostigma flavipes** (STEIN), d: **Subilla confinis** (STEPH.). e: **Tauroraphidia netrix** H. A. & U. A. & RAUSCH, f: **Parvoraphidia microstigma** (STEIN), g: **Raphidia ambigua** H. A. & U. A., h: **Puncha ratzeburgi** (BRAU.), i: **Inocellia crassicornis** (SCHUM.).



Knowledge of larvae, ecology and biology is almost entirely restricted to the species of the western Palearctic. There are only three species among the snake-flies of Central and East Asia of which the larvae are known, and among the Raphidioptera of America larvae of only two species are known. All that we know about parasites of Raphidioptera refers exclusively to species of the western Palearctic.

Another still unclarified question concerns the possible economic significance of Raphidioptera. There is no doubt that snake-flies may act as very effective predators of many phytophagous arthropods (particularly aphids, coccids, mites, larvae of Lepidoptera, of Coleoptera, and of Tenthredinidae) living on forest trees on the one hand or on fruit trees on the other. Furthermore, it can be assumed that many species of Raphidioptera could be successfully introduced into areas where these insects do not occur naturally, particularly in the southern hemisphere. There is but one trial so far: 90 years ago American snake-flies were introduced into Australia and New Zealand. These efforts were, however, unsuccessful, as the species could not establish, and the experiment was not repeated. Today we know much more, nearly all, species in the order, and some of them could easily be reared in large numbers. It is not our task to investigate these aspects of applied entomology; the monograph mentioned above should, however, present basic information for a possible integration of Raphidioptera in control measures against pest arthropods of trees. It would indeed be greatly satisfying, if these fascinating insects could contribute to the solution of problems in pest control.

Acknowledgement

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