

Fossil insects: the Syrphidae (Diptera) revisited - the heritage of the past

Henri G Dirickx (2009)

Bulletin de la Société Royal Belge d'Entomologie 145: 49-86

Abstract

The Syrphidae are a fairly well-known group of Brachyceran flies to which much attention has been given by professional dipterists and amateurs alike. The family has nearly 6000 recent known species and it is anticipated that many more will still be discovered, especially in the Southern Hemisphere. It would seem that general agreement has been reached on the higher level systematics but the generic and species levels are still in a state of flux. As for most Dipteran families, the biology of adult Syrphidae is still relatively poorly known and the early stages of most tropical species remain undiscovered. Geologically, the first Syrphid was reported from the Late Cretaceous. In comparison to any other Brachyceran families, the fossil record for the Tertiary is relatively important, surpassed only by the Empididae and the Dolichopodidae. The present note is intended to give an overview of the present status of our knowledge about the palaeontological record of the Syrphidae. After a brief introductory chapter on the main characteristics of the family, a review will be given of the general issues related to the study of the legacy of the past, including reference to the contributions of palaeoclimatology and palaeobotany. Next, a description of the major Lagerstätten, with comments on the most interesting species, is provided. Finally, a tentative synthesis of the available data is offered as well as some qualitative and quantitative conclusions.

1. Introduction

Among the great order of the Diptera, the family Syrphidae occupies a special place for more than one reason. With nearly 6,000 species described, it ranks fourth in the suborder Brachycera, after Tachinidae (8000), Asilidae (6440) and Dolichopodidae (6200) (ZIEGLER, 2003). The adults of the great majority of syrphids visit flowers assiduously and thus actively contribute to the fertilization of entomophilous plants. They feed mainly on nectar and pollen, but more rarely on aphid honeydew. In contrast to the very uniform feeding habits of adults, larvae show a remarkable diversity in the choice of their food. Some groups are zoophagous, while others have phytophagous larvae, scavengers or feed on decomposing organic material.

For nearly two centuries, syrphids have been favoured by naturalists, whether amateur or professional, as evidenced by a very abundant literature. Their generally brightly coloured livery, highlighted when they forage for flowers, as well as features of flight behaviour, have captured the attention of naturalists since the 18th century. The number of syrphids described by LINNAEUS (1758) testifies to the knowledge already known by the ancient authors of these flies. This interest has been maintained during the two centuries that followed, to the point that the syrphids are reputed to be among the best known Diptera.

The six thousand or so species currently inhabiting the Earth have differentiated during geological times, depending on the tectonic and palaeoclimatic vicissitudes that have resulted in the world as we know it. This evolution has left traces in the form of fossils more or less well preserved and whose study provides useful lessons on the evolutionary course of the family from its presumed origin, at the end of the Mesozoic. This note will be devoted to a brief overview of the main palaeontological archives that have yielded Syrphidae, in parallel with a summary of the evolution of palaeoclimatological and palaeobotanical elements. It will call on some analyses inspired by methods, mainly statistical, used in particular in palaeobiology to test the quality of the fossil record of Syrphidae. The interpretation of the results of these analyses calls for a degree of caution. Although the number of fossil syrphid specimens may seem reasonable in comparison with that of most other Diptera families, it is nevertheless quite insufficient to justify the application of these methods used in palaeobiology.

These approaches include, but are not limited to, cohort analysis or longevity assessment of specific taxa

using the intervals between first occurrence (FAD) and phyletic extinction (LAD). The first requires a much larger database than we have available, while the second is not applicable to syrphids, as no species has been found in more than one fossil site. We have not seen, moreover, attempts to establish an estimate of the rates of speciation and extinction of evolutionary lineages over time. It should also be noted that the taphonomic biases specific to the different types of conservation of the samples (sedimentary deposits, entrapment in resins) lead to reservations about the valid comparison of the deposits and, in particular, for the reconstitution of contemporary fossil biocenoses.

Despite the limitations enumerated above, the study of the Diptera Syrphidae nevertheless seemed to us to be sufficiently advanced to warrant a synthesis. In this note, we propose, in the introduction, to briefly comment on some of the peculiarities of the family. Then, the fossil record will be examined under several lights: (1) the impact of taphonomic processes on the preservation of samples, (2) the identification and dating of fossil taxa, and (3) the recent techniques for studying the fossil record, including cellular ultrastructure, as well as palaeocommunities. These few methodological considerations are followed by a brief overview of palaeoclimatology and palaeobotany during the Tertiary period, designed to situate environmental conditions during the evolution of the Syrphidae family. Finally, the rest of this essay will be devoted entirely to the analysis of the palaeontological archives discovered to date and to the still temporary encumbrances that emerge.

Often, simply summarizing the results of studies in a given field leads to highlighting the gaps in accumulated knowledge and to suggesting future research to fill them. We hope that this contribution, dedicated to the family Diptera Syrphidae, can in turn open new avenues of research.

2. General considerations for Syrphidae

The Syrphidae are one of the most diversified families among the Diptera Brachycera. Their representatives populate in large numbers most of the natural environments where they are noted as much by their habitus as by several peculiarities of their behaviour. The general appearance of syrphids shows a great variety of colours and an ornamentation composed of various patterns. The thorax and abdomen may be covered with yellow or orange bands or spots, contrasting with the brown or black tegument. Other species, on the other hand, show an unequivocally black colour without lustre while a third group is distinguished by generally shimmering coppery or metallic reflections, shaded with green or blue. These already marked disparities are highlighted and reinforced by the general silhouette of the different species, which varies from a very slender profile to a compact or squat form. A third element accentuating even more the diversity of the taxa of the family is their size, which varies from 3 to 35 mm.

In terms of behavioural traits, syrphids are distinguished by their astonishing flying abilities. Aerial movements include stationary flights where the individual is keeps motionless a few metres above the ground for a certain period of time to then make sudden, unpredictable darts. These manoeuvres, which generally correspond to mating flights, often occur in groups, producing a characteristic buzz that is clearly perceptible even from a distance. Not all species practise these aerial acrobatics, but they are the hallmark of most syrphids.

The present clades of the family Syrphidae have a remarkable eclecticism regarding functional adaptations in both adults and pre-imaginal stages. This ecological diversity is reflected in particular by the multiplicity of trophic guilds to which larvae belong and the variety of often very specialized biotopes that harbour different taxa. Extrapolation of these features to fossil species or clades of corresponding higher rank implicitly admits their constancy over time. To establish in the fossil record the close relations observed between syrphids and their abiotic and biotic environment, including in particular the multiplicity of larval diets (predators, endophytophages, scavengers, xylophages) and adults, as well as the spatial distribution of occupied habitats, the principle of uniformity (or "actualism" [realism?]) has often been used. An alternative is to use a probabilistic method of phylogenetic inference proposed by NEL (1997). In particular, the author draws a parallel with the Mutual Climate Range model (MCR), which we allude to in the

discussion of Florissant's fossils (section 4.2.3.), and also specifies possible applications in palaeoclimatology.

As with most Dipteran families, the preimaginal stages of most species of Syrphidae remain unknown. Despite some rare old observations, some of which date back to the end of the nineteenth century, few larvae have been described, and the biology and ecology of the preimaginal stages have only been the subject of occasional studies, limited mainly to the holarctic fauna and to the Indian subcontinent. In Europe, ROTHERAY (1993) estimated the number of known larvae at 14% of the fauna, while a similar estimate for the South American continent led THOMPSON (1972) to suggest a figure of 1%. For nearly two decades, a considerable effort has been made to promote research on larval morphology and biology and to clarify their contribution to the systematics and evolution of Syrphidae (ROTHERAY, 1997, ROTHERAY & GILBERT, 1999, STUKE 2000, MAZANEK et al., 2001). It should be noted, however, that almost all of this research concerns the Palearctic region. The preimaginal stages of pantropical syrphids remain, in practice, totally unknown. The earliest contributions are almost all recent (GRECO, 1995, 1998, ROTHERAY et al., 2000, KITCHING, 2001, ROTHERAY, 2003; PEREZ-BANON et al., 2003).

At the global level, the total number of species recorded is 5330 in 196 genera (KATZOURAKIS et al., 2001) or 5905 in 293 (THOMPSON, 2008). The distribution of the family is cosmopolitan, excluding the Antarctic continent and some isolated oceanic islands. Since the first modern inventory of Diptera in North America (STONE et al., 1965), similar catalogues have been published for the other five major zoogeographic regions. These various documents provide a provisional enumeration of the geographical distribution of the number of genera and species of syrphids recorded in the world. It should be noted that more recent publications provide useful elements for updating several of these catalogues. Table 1 summarizes the distribution of the genera and species of syrphids recorded around the world.

[**Table 1:** An overview of the number of genera and species of Syrphidae recognized in the major biogeographical regions, based on the most recent inventories we have seen.]

It should be noted that the most diverse regions for Syrphidae are the Palearctic region and the Neotropical region. As far as the former is concerned, systematic and faunistic research that has been running for two centuries has certainly contributed to a better knowledge of the fauna, especially that of Europe. The abundant harvest of material by several generations of Dipterists has allowed for detailed comparative studies of external morphological characteristics, as well as the taking into account of the structure of genitalia, mainly in males. Numerous cryptic species have been recognised and described. In South America, the picture is different: there is an abundance of forms with a very varied habitus but limited to a few very homogeneous groups that are particularly rich in species. More than 50% of the syrphid fauna belong to four endemic genera of the New World (*Copestylum*, *Ocyptamus*, *Palpada* and *Toxomerus*). To date, these groups, each comprising several hundred species, often described from a limited number of individuals, have not been the subject of global revisions likely to clarify their taxonomic status according to modern criteria. The boundaries of the genera remain relatively vague and the number of species included varies according to different authors.

3. Overview of the fossil record

3.1. *The palaeontological message*

The fossil record is only an inferior sample of past life. In fact, the biological richness of past geological epochs was infinitely superior to the inventories established by palaeontologists for most groups of animals. The probability for an individual who once lived, to have been preserved and found today, is indeed close to zero. Although the diversity of fossils currently known may nevertheless seem important, it simply reflects the extraordinary profusion of life in all terrestrial and aquatic environments over the ages.

Favourable conditions for the conservation of insect remains must have been achieved during all geological

periods. Some associations between specific biological groups and appropriate habitats favour the preservation of samples. Although endowed with a more or less resistant cuticle, according to Order, insects seem less predisposed to resist taphonomic hazards than the bivalves and the vertebrates with their respective calcitic shells and bone structures. In addition, they are, for the most part, terrestrial and therefore have a lower probability of being incorporated in a sedimentary series. The combination of these limiting conditions and the small number of palaeoentomologists explain why relatively few deposits studied so far have yielded fossil syrphids. Their discovery is also related to the contingencies of palaeontological explorations which inevitably leads to an uneven geographical and stratigraphic distribution of the samples present in the collections.

The representation of the different supraspecific taxa of Syrphidae is heterogeneous in the fossil record. Isolated and often fragmentary specimens seldom present the characters which, taken as a whole, make it possible to assign them to modern tribes or genera. Fossils that have been correctly assigned are likely to belong to clusters of current lineages, thus providing a minimum age of divergence.

From time immemorial, countless insects, winged or not, have been and are still trapped on the surface of water bodies to run aground in muddy deposits, after a more or less long time. Lakes with rapid sedimentation are typical environments for the formation of fossils on bedrock. Before being coated in sediments, however, individual specimens are subject to the attack of many predators, leading to dislocation accompanied by biological and chemical decomposition and alteration processes. The diversity of preserved communities will be seriously reduced. Insects with their articulated structure and reduced resistance of exoskeleton sclerites are vulnerable to these hazards, as are vertebrates on a different scale. It is interesting to note that the finely laminated fossiliferous layers of some sites have nevertheless yielded a particularly well preserved fluvio-lacustrine entomological fauna. In some cases, the interlocking microbial mats composed of filamentous species, mainly cyanobacteria, floating on the surface of ponds and lakes, has been able to protect insects from biological and hydrodynamic disturbances by dragging them to the bottom. Microbial ecosystems thus play an important role in taphonomy (GALL et al., 1994, GALL 1995, SCHIEBER 1999). With regard to Florissant's break-up, HARDING & CHANT (2000) demonstrated the action of biofilms formed by diatom frustules and associated microbial communities on the fidelity of the preservation of fossil insects, especially Diptera. The SEM examination revealed examples of preservation of three-dimensional geometry, such as the implantation of costal macrotrichia and wing microtrichia in Diptera specimens. Similarly, concretions formed by early biomineralization during the early stages of diagenesis in stratified lacustrine environments may contain organisms that have not been deformed by compression, particularly insects. The more generalized use of new techniques in palaeoentomology, of which several examples are mentioned in this note, could undoubtedly make an important contribution by making it possible to specify better the identity and the systematic position of the fossil samples, particularly at species and genus level by taking into account structural characters not accessible before. However, their implementation raises the problem of the non-reversibility of certain types of examination that are sometimes destructive.

In general, the crushing of the impressions, however fine the grain of the fossiliferous bed, leads to the almost systematic obliteration of the structural details of the habitus, in particular by the almost complete absence of relief, making the identification of the fossils problematic. Nevertheless, it is often possible to assign Diptera whose wings are kept flat to the appropriate family and, in practice, it is the use of the venation which is the most-used means for identification in palaeoentomology. The characteristic outline of the veins and the arrangement of the cells they delimit contribute in the majority of cases to the faithful diagnosis of specimens belonging to the family Syrphidae. For Mesozoic and even Cenozoic fossils, the exclusive use of the features of the wing is, in many cases, an expedient that can lead to significant errors. First, purely the use of wing characters is not always sufficient to guarantee an unequivocal identification (WEDMANN, 2000). Then, observation of the course of the veins is dependent on preservation of their impression, which can lead observers to complete an obliterated path at random. Finally, identifications often use figures published in the literature, especially those that accompany descriptions of new species. The vagueness, if not inaccuracy, of many such illustrations, and the insufficiency of the diagnoses they are supposed to clarify, increase the risk of error in assigning a specimen to a given taxon. These

inconsistencies have been repeatedly emphasized in the palaeontological literature (OBENBERGER, 1957, HENNIG, 1981, GRIMALDI, 2001; AMORIM DE SOUZA & SILVA, 2002).

To these difficulties, related mainly to the imponderables of taphonomy, are added elements specific to the study of the material collected during palaeontological excavations. The first appearance of a taxon in the fossil record is indicative of the minimal age of the evolutionary branch of which it is a part. But it does not exclude its presence in an earlier era. In the middle of the last century, the age of the oldest fossilized syrphid did not go back beyond the Lutetian (Middle Eocene). As on this level more than half of the present tribes were already present, as well as many modern kinds, the origin of the family was likely to go back to the Mesozoic. By the discovery of a syrphid in the resins of the Taimyr Peninsula (Russia), the minimum age of the family has indeed been pushed back to more than ~ 83 Ma (Upper Cretaceous) (KOVALEV, 1979, ZHERIKIN & ESKOV, 1999) [*note: rejected as a syrphid by Popov 2015*]. ROSS & JARZEMBOWSKI (1993) situate the appearance of the family in the Cenomanian, without citing any precise reference. A temporal scale, based on Bayesian analysis of Brachyceran molecular sequences using the 28S rDNA gene, attributes a mean age of 87 Ma to the diversification of Syrphidae and Schizophora under the assumption of a variable rate of evolution. The 95% confidence limits of the posterior distribution is approximately 148-72 BP (WIEGMANN et al. 2003). To our knowledge, no estimate of the age of divergence of taxa within the family has so far been made from syrphid DNA sequences using a molecular clock calibrated by fossils. Published research has been limited to the preparation of cladograms based on morphological characters (adults and larvae) and 28S rRNA mitochondrial and COI gene sequences (ROTHERAY & GILBERT, 1999, STAHL et al. , 1999, 2003, MENGUAL et al., 2008, VUJIC et al., 2008).

It should also be noted that many fossils, from one or another specific site of particular interest to an author, have been described by the latter in taxa outside their specialty, resulting sometimes in a problematic appreciation of the diagnostic characters. Finally, few revisions of fossil Dipteran families have been undertaken based on the study of available material including examination of types. Most publications merely present a summary of earlier diagnoses or a textual copy of the original descriptions; these reservations have also been highlighted for other systematic groups as well (ENGEL, 2002).

In the Mesozoic and Tertiary, the mosaic of faunistic and floristic provinces based on the notion of biozones, was not identical to the biogeographical division of the world today. During geological time, tectonic and palaeoclimatic events have led to large-scale intercontinental faunal exchanges, induced by palaeogeographic scenarios. It follows that the distribution of taxa has constantly changed. The identification and classification of Tertiary fossils (and even more so of older ones) requires the consideration of the world fauna. Until the middle of the 20th century, this imperative was not always respected by palaeontologists generally exploring isolated fossil deposits, uninformed by work published or under way elsewhere.

In contrast to lacustrine or fluvial lithofacies of a very diverse nature and origin, whose palaeontological message is dependent on numerous conditions of selective fossilization, resins have undergone a much simpler and more uniform physical and chemical taphonomic process. The insects of amber are, in most cases, perfectly identifiable, especially with the modern techniques used for their study (RODER, 1980; SZADZIEWSKI, 1988; GRIMALDI, 1993; ROSCHMANN & MOHRIG, 1995; PENALVER, 1996; HAENNI & PERRENOUD 1998; NASCIMBENE & SILVERSTEIN 2000; PODENAS 2003). They provide, in particular, elements for comparison with current faunas and indications of evolutionary trends at the supraspecific level. Taking into account such inclusions [resin fossils] in cladistic studies is, however, still very limited despite the precision of the morphological and anatomical details, in particular the genitalia, which they make it possible to highlight.

Some insects have been more likely to be conserved in exudations, either statistically by their greater numerical abundance in contemporary amber forest ecosystems, or as a result of behavioural or biotic factors associated with different phases of the developmental cycle, or through sampling which favours the trapping of small organisms. It is essential to identify the elements that have favoured the preferential trapping of certain insects in the resin in order to explain the relationship between their abundance in the

samples and that in the ecosystems. Traditionally, the assumptions for terrestrial palaeobiotopes and related palaeobiocoenoses are based on reconstructions from stratigraphic, sedimentological and palaeogeographic data in a broad sense. These methods, however, are subject to many direct or indirect uncertainties, and provide at best only qualitative indications which limit their interest in the evaluation of both animal and plant fossil communities. An innovative approach has recently been presented by COIFFARD et al. (2004), supplemented and refined more recently (COIFFARD et al., 2008). It constitutes a palaeobotanical application of an approach initially proposed in synecology by NEL et al. (1998). The palaeosynecological study of fossil flora is addressed by Wagner's method of parsimony applied to the links between palaeobiocoenoses (floristic lists) and the palaeobiotopes corresponding to the Albian and Cenomanian stages (Middle Cretaceous) defined from sedimentological data. The method allows the development of consensus trees reflecting good agreement between the sedimentary layers and the structure of plant communities. Its application in palaeoentomology deserves to be examined.

The set of limiting factors enumerated briefly in the preceding paragraphs explain and justify the mistrust often expressed with respect to conclusions based on the study of fossils, especially their consideration together with modern taxa in the development of cladograms.

3.2. Palaeoclimatology

Palaeoclimatic parameters being inaccessible to any direct measurement, their evaluation is necessarily based on indicators. In the past, the main reference used is the history of the oceans. Microfossils such as planktonic and benthic foraminifera and diatoms have been prominent. Classical marine biostratigraphies, however, reach the limit of their validity approaching the coasts. In addition, the best continental divisions based mainly on fossil vertebrates mainly concern terrestrial regions far from the sea. The link with the marine chronology is often incomplete. In particular, it uses dinoflagellates and pollens, which are often well represented in transition zones. More recently, the isotopes of several simple elements, in particular oxygen and carbon, have proved to be more accurate physical indicators which, supplemented by other radiometric dates (e.g. $^{39}\text{Ar} / ^{40}\text{Ar}$) and by magnetostratigraphic data, have done much to refine the scale for the Cenozoic. The oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotopes provide an assessment of seawater palaeotemperature and ice sheet volume respectively, and indicate the nature of global carbon cycle disturbances and its consequences particularly on the general circulation of deep oceanic waters (SAVIN, 1975, BOCHERENS et al., 1994).

The general picture that emerges from the reconstruction of climates, mainly from the marine environment and their integration into the chronostratigraphic terrestrial canvas, is that of very active climate dynamics at least since the K/T limit. From a global environment warmed by greenhouse effect ("greenhouse"), temperatures have changed from a succession of transient levels and often abrupt punctuated events to the cold period of the Pleistocene/Holocene with a strong freezing of the poles ("icehouse").

Three major palaeoclimatic trends emerge from the timescale that characterizes them. In the first place, a long-term global change effects the transition from a world of "greenhouse" to a climate of "icehouse". It underlies a series of oscillations reflecting warming and cooling episodes of varying duration and intensity superimposed on the general trend. The details of these climate phases have been summarized by ZACHOS et al (2001). Thirdly, the research has revealed low-amplitude climatic anomalies whose duration is between 10^3 and 10^5 years. In the Pleistocene, the alternation of successive glacial and interglacial cycles at this rate has been known for a long time. Events of a similar magnitude have been identified also at much earlier times. Positive fluctuations in the $\text{O}^{18}/\text{O}^{16}$ ratio were recorded during the Tertiary period, leading to widespread cooling of the Earth. At the beginning of the Oligocene, a rapid and brutal positive change of $\delta^{18}\text{O}$ testifies to the significant drop in ocean temperature at depth, and the first Antarctic glaciations appear. This event was followed by a major turnover, mainly in mammals, known since the beginning of the 20th century and designated by the name of the 'Grande Coupure' [note: the Eocene-Oligocene extinction event] (STEHLIN, 1909).

Finally, an abiotic factor that contributes to conditioning the temperature on the earth's surface is the

carbon dioxide content ($p\text{CO}_2$), considered an agent that has played an active role in the mechanisms that shaped past climates.

3.3. *Palaeobotany*

The close correlation between the types of vegetation and the climate of a region has long been the focus of botanists. By the beginning of the 20th century, BAILEY & SINNOTT (1915, 1916) had observed that certain leaf characteristics of angiosperms varied according to the climatic conditions of the environment. For example, entire leaves are typical of tropical climates, while divided leaves dominate in temperate regions. These findings, further elaborated by other botanists were subsequently applied to fossil flora to attempt palaeoclimatic reconstructions (WILF, 1997, REICH et al., 1999, GREENWOOD 2005, ROYER et al., 2005).

The most widely used method of reconstructing the probable nature of palaeoclimates and palaeoenvironments in the Cenozoic from fossil flora is that of the modern analogue known as the "closest living relative". Its principle is based on the comparison of fossil samples with current taxa with similar or identical morphological traits, especially foliar architecture (venation, size, limb shape and type of cut, leaflets, petiole). It is recognized that the ecological patterns of fossil species, reflecting their tolerance of environmental factors, are similar to those of their closest living relatives. Using transfer functions, a response surface can be defined for each plant in relation to climatic parameters. Multivariate analyses, including ordination techniques, are used to evaluate the mean values and magnitude of temperature and presumed precipitation changes in palaeoenvironment.

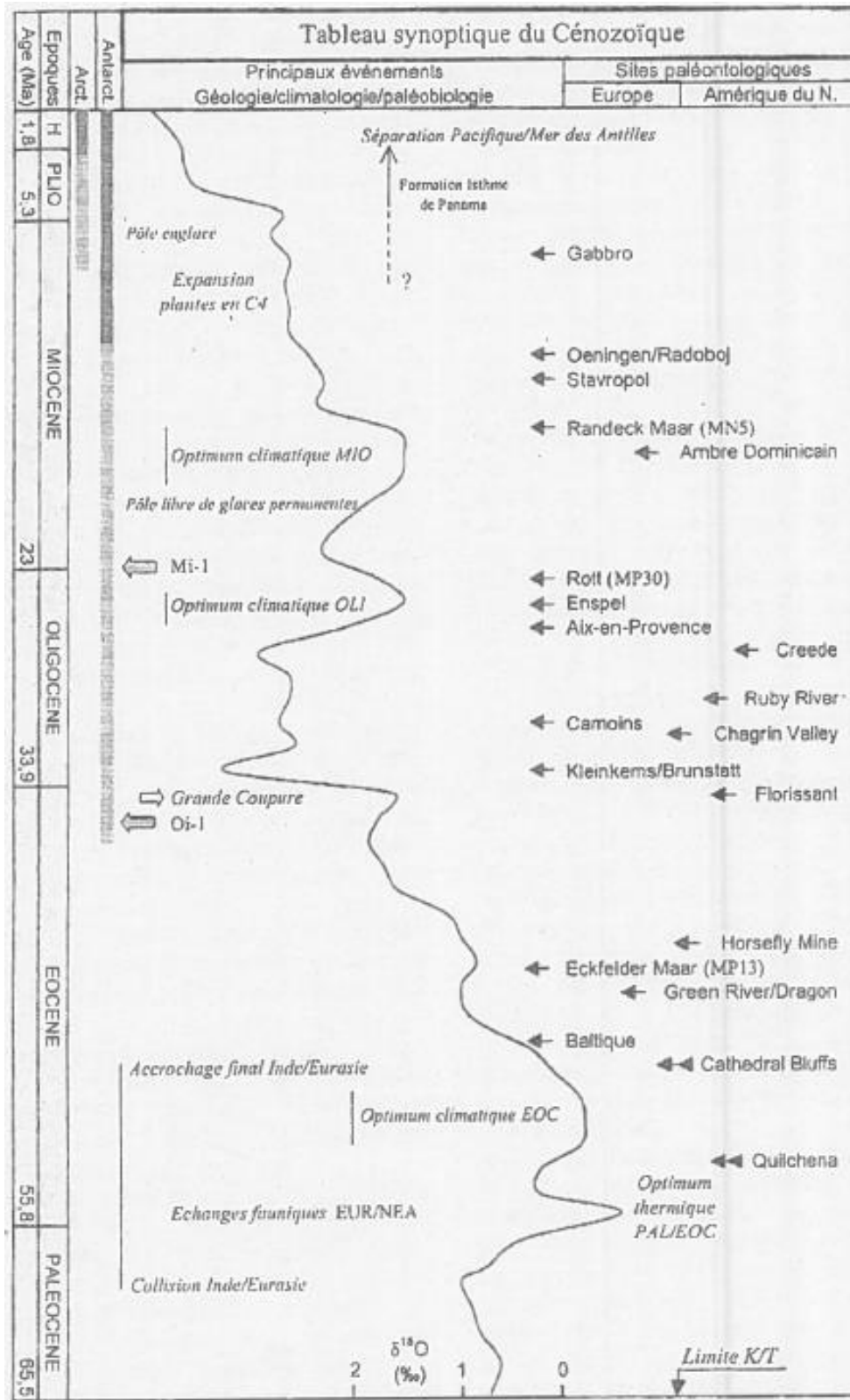
The method of the closest living relative or "floristic method" has been the subject of recent criticism and has been described as unfounded by WOLFE (1994). This author has developed a method of analysis, CLAMP (Climate-Leaf Analysis Multivariate Program) in order to assess tertiary palaeoclimates from fossil assemblages more accurately.

It will be noted that MOSBRUGGER & UTESCHER (1997) revalidated the floristic method under the term "coexistence approach" (CA). It is based on the basic assumption that the environmental requirements of Tertiary plants are identical to the requirements of those considered to be their current closest relatives. On this premise we attribute to each of these a range of tolerances with respect to a number of climatic factors. These intervals, deduced from the distribution of taxa taken into account, will then be transposed to fossil flora. The set of limits on the values of the various parameters will make it possible to determine a coexistence interval for the fossil flora considered.

The few methods mentioned, whose list is not exhaustive, are based on quantitative analysis of leaf physiognomy. A comparative analysis of several techniques applied to Europe's fossil flora can be found in recent contributions by UHL (2006) and UHL et al (2006, 2007).

3.4. *Conclusions*

To conclude this chapter on the fossil record, from various sources we have summarized (Figure 1) the main elements that have punctuated geological and palaeoclimatic history during the Cenozoic. The main thread that conditioned the gradients of biological evolution was first and foremost the variation in temperature, both of the oceans and the earth. Since the advent of oxygen and carbon isotope analyses, the reconstruction of palaeotemperatures curves has dramatically altered the interpretation of the Earth's history (ZACHOS et al., 2001; BILLUPS & SCHRAGE, 2002). We have shown in Figure 1 the curve indicating the fluctuations of $\delta^{18}\text{O}$ which via a scale factor is homothetic [*identical*] to the plot of temperature. Some key events that shaped, directly or indirectly, the current world geologically, climatically and palaeobiologically, have been plotted on the table. Finally, the table also contains an enumeration of all the sites where fossil Syrphidae have been recorded.

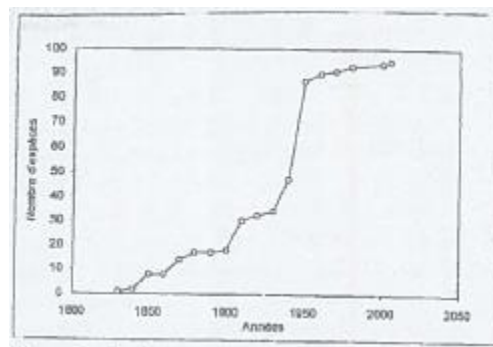


[Figure 1: Synoptic table of the major events that marked the Cenozoic. The changes in $\delta^{18}O$ reflect changes in temperature and the volume of ice. A curve of $\delta^{18}O$ is shown in the figure. The palaeochronological scale is according to GRADSTEIN et al. (2005). Several important climatic, geological and palaeobiological episodes are indicated. The right part of the figure shows all the fossil sites that yielded fossil Syrphidae with their estimated age (see Table 2). The data are adapted from many sources, cited in this article.]

4. The fossil Syrphidae

4.1 History

A total of 3125 fossil Diptera species have been identified (EVENHUIS, 1994) which corresponds to about 3% of the number of current taxa. This proportion varies greatly according to Sub-order: it is 1% for Brachycera, whereas it reaches 5% for Nematocera. Such variations are even more marked at the level of families. Bibionidae is an extreme case with 344 fossil species for about 1000 taxa currently identified (ZIEGLER, 2003). The family Syrphidae is, with Empididae, Dolichopodidae and Phoridae, the best represented Brachycera in palaeontological faunal samples (EVENHUIS, 1994). So far, 106 fossil syrphids have been recognized, of which 86 have been unspecified as species, accounting for nearly 1.5% of the taxa currently inhabiting the world.



[Figure 2: History of the description of fossil Syrphidae. Graph of the number of new species described by decade. Note the very important increase in the period 1940- 1950 following the revision of HULL (1945) as well as the obvious slowdown during the 50 years since that date.]

They are divided into 39 genera, of which 18 are extinct. Of the taxa cited in the literature, 11 are identified only at the level of the family and 9 at that of the genus. The inventory of fossil forms is therefore 95 taxa attributed to the specific level, of which 9 are not yet described. We assigned the status of species to each of the two *Quilchena* specimens reported by ARCHIBALD & MATHEWES (2000) and the 5 *Enspel* impressions (WEDMANN, 2000). The history of descriptions of fossil Syrphids since the beginning of the 19th century is shown in Figure 2.

The first reference to a fossil syrphid is due to DE SERRES (1829) who noted the presence of a species attributed to the genus *Microdon* in the Oligocene marls of Aix-en-Provence. It was neither described nor illustrated by the discoverer. While stating that the type could not be located, HULL (1945) nevertheless considered the attribution of this unique specimen to *Microdon* as plausible, given the well-marked peculiarities of this genus. Eight years later, *Helophilus primarius* GERMAR, 1837 was described from the Upper Oligocene around Bonn. The description does not allow us to characterize the species and since the type could not be found, HULL (1945) considered the species as *incertae sedis*. This view is confirmed by KOTTHOFF & SCHMID (2005) who point out that in the absence of the distal half of the wings, it is not possible to attribute the specimen positively to the Syrphidae.

In the middle of the 19th century, several naturalists became interested in the study of insects discovered during palaeontological surveys in different European countries. During this period, nine species of Syrphidae were described from Oeningen, Radoboj and Rott (HEER, 1849, 1864). A general communication originally planned as preliminary to a work on the Diptera of Baltic amber was published by LOEW (1850). This work was however never completed. Among other genera, Loew mentioned seven Syrphidae, including a *Volucella* which he did not describe, but HULL (1945) hypothesized that this may be the taxon he established himself under the name of *Ptilocephala volucelloides* (= *Praeptilocephala* EVENHUIS, 1994, n.n.). Since the sample containing the sole *Volucella* specimen has not been found among the Loew

material deposited at the British Museum (Natural History) in London, it is not possible to ascertain this alleged identity. LOEW (1861) discussed the general problems posed by the Diptera fauna from amber, from which 101 genera had already been identified at the time. At the end of the century, MEUNIER (1899) reconsidered the fossils studied by Loew, giving in particular some details on their probable generic attribution: two syrphids belong to the genus *Palaeoascia*, a specimen to *Syrphus* and a fourth perhaps to *Xylota*. The author did not, however, publish any formal description.

In 1877, SCUDDER inaugurated his research on fossil insects in North America, which he continued until 1890, when he published a bibliography of the species described until then, followed a year later by a world catalogue of known fossil insects (SCUDDER, 1890, 1891). He himself named three Syrphidae. Subsequently, COCKERELL concentrated on the examination of samples collected from the shale clays of Florissant and Green River, from which he described seven Syrphids between 1909 and 1931.

In the last decade of the nineteenth century, there was renewed interest in the study of inclusions in amber, which was continued for nearly forty years. As far as syrphids were concerned, they were the poor relatives during this period of intense activity, [since] only eight new species were described from amber between 1902 and 1910. By way of comparison, it should be noted that just during 1907 and 1908 Meunier named 49 unpublished taxa of Dolichopodidae. This disparity can be attributed to differences in the biology and behaviour of species that lead to entrapment in resin exudates.

The study of Oligocene lignites from Rott, in the Rhineland, initiated by VON HEYDEN (1859) in the second half of the 19th century, was taken over by STATZ (1940) who, on the basis of a large personal collection, added 49 species of Brachycera including seven species of Syrphidae represented by adults and 30 pupae attributed to "*Eristalis*". Some additional contributions covering the first half of the twentieth century brought the number of syrphids known from the fossiliferous deposits of Europe and North America to 48 in 1944.

An important revision of all available historical material, supplemented by the examination of several collections not yet studied, was published by HULL (1945). This author reported that he had seen the great majority of species from the North American continent deposited in three scientific institutions: the Museum of Comparative Biology in Harvard, the American Museum of Natural History in New York, and the University of Colorado Museum at Boulder. This detailed study allowed him to establish five new genera and to describe 13 unpublished species from Florissant and Dragon. As far as Europe is concerned, however, relatively few types of fossil syrphids preserved as sedimentary impressions were located, and only two of them were studied in London and Oxford. For inclusions in Baltic amber, HULL (1945) had the opportunity to examine the important collections of the Geologisch-Paläontologisches Institut und Bernsteinsammlung der Albertus-Universität zu Königsberg (Kaliningrad), the Geologisch-Paläontologisches Institut und Museum der Universität Berlin and the Preussische Geologische Landesanstalt (Berlin) and the British Museum of Natural History (London); [his studies] revealed the presence of nine new genera and 25 new species. The descriptions, largely based on the specimens examined by the author, are generally fairly detailed and represent a definite advance in the knowledge of the morphology of fossil species and their attribution to supraspecific groups. Examination of the samples having been done by the same author, the evaluation criteria are supposed to be uniform and the value given to the individual characters in principle unambiguous. However, although F.M. HULL (in his publications of 1922-1974) was a specialist in Syrphidae and devoted a great deal of research to the modern fauna, he seems to have accepted quite often and without sufficient critical thought the judgment of older authors. It follows that his attributions to genera and sub-families (currently tribes) use characters whose diagnostic validity is now put in question or contested. In a systematic global review of Syrphidae, encompassing both current and fossil species, HULL (1949) updated his 1945 study by presenting a comparative table of recognized fossil subfamilies and their distribution by geological horizon.

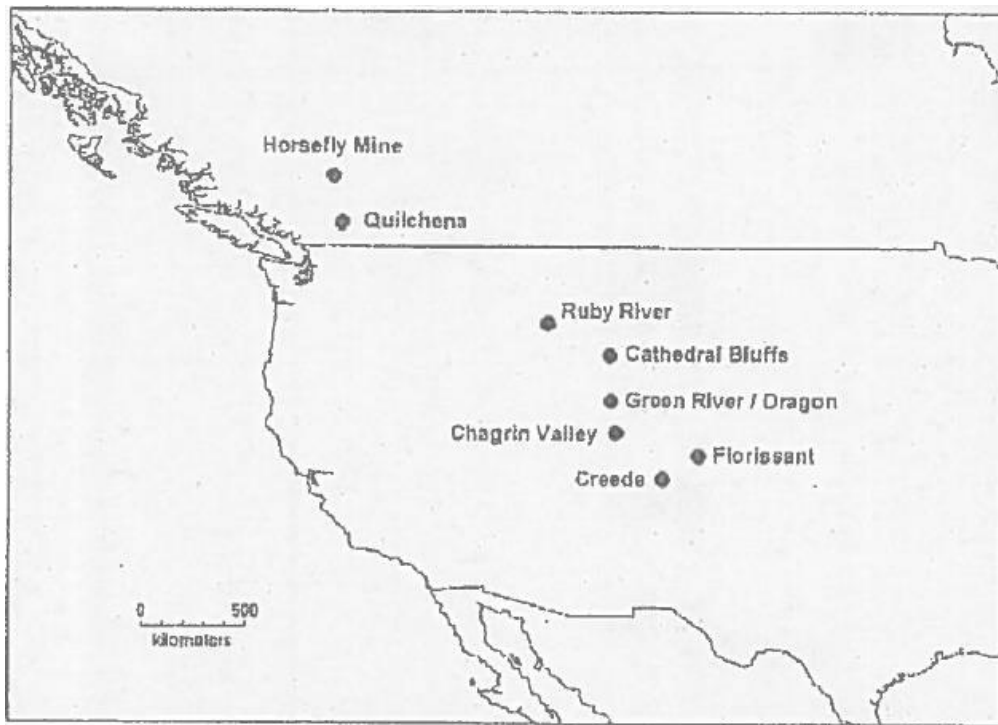
Since the revision of HULL (1945), the fauna of fossil syrphids has been little enriched: between 1949 and 1973, only five new taxa were named. Subsequently, POINAR & POINAR (1999) mentioned the presence of the genus *Copestylum* in Dominican amber and ARCHIBALD & MATHEWES (2000) reported two specimens

of Syrphidae from the lower Eocene at Quilchena, but did not attribute them to one or other tribe of the family. Recently, a new species was described in the genus *Helophilus* by KOTTHOFF & SCHMID (2005). The only female specimen is from the sedimentary deposits of the Randeck Maar, attributed to the late Burdigalian (Early Miocene) dated from the MN5 mammalian zone (HEIZMANN, 1983). In addition, a hoverfly possibly belonging to the subfamily Syrphinae was reported from Eckfelder Maar (WAPPLER, 2003) and five unidentified specimens from Enspel (WEDMANN, 2000), localities in western Germany. Two contributions still deserve special mention: the first concerns the discovery in Russia of a late Cretaceous specimen which represents the oldest known evidence of the family (KOVALEV, 1979) [*now put in doubt as a syrphid by Popov 2015*]. The second publication is the description of a hoverfly included in Baltic amber, whose diagnosis is distinguished by a precision never before reached in the earlier palaeontological literature. The author applied modern methods of analysis for the first time which, given the inevitable loss of some information, led to a description almost identical to those used for current forms (RODER, 1980). Since then, further research on fossil Diptera has been conducted with the same attention to detail. Among these, SZADZTEWSKI (1988) published a revision of the Ceratopogonidae of Baltic amber, while the study of Bitterfeld's Sciaridae and Baltic Limoniidae was approached on the same basis (MOHRIG & ROSCHMANN, 1994; ROSCHMANN & MOHRIG, 1995, PODENAS, 2003). In particular, this work involves the structure of male genitalia to characterize species.

It is worth mentioning some more general publications, including inventories of fossil Diptera. A world catalogue, supplemented by an exhaustive bibliography, of the remains of animals preserved in fossil resins was published by KEILBACH (1982). The Diptera section contains 389 species of Brachycera, including 34 Syrphidae (+5 "varieties"). SPAHR (1985) subsequently made additions and corrections. A few years later Volume 4 of the Treatise on Invertebrate Palaeontology appeared, devoted to Hexapods (CARPENTER, 1992). For Syrphidae, this book lists a total of 31 genera known in the fossil state, of which 16 are extinct. Finally, a complete compilation of all the fossil Diptera was published by EVENHUIS (1994) following the same format as the dedicated catalogues already published of the faunas of current Diptera of the major zoogeographic regions of the world. To facilitate the identification of deposits containing fossil hoverflies, Figures 3 and 4 locate the fossiliferous sites in Europe and North America respectively. We have mapped only those deposits reported in the literature that have recorded hoverflies.



[Figure 3. Map of Western Europe with indication of fossil deposits containing Syrphidae. The shaded area is the Baltic region with Kaliningrad as a landmark. A total of 37 species have been described from all of these deposits]



[Figure 4: NW-North America map showing fossiliferous sites containing Syrphidae in Canada and the United States. These deposits delivered 29 specific taxa]

For more than half a century, palaeontology has made many advances, thanks to increased accuracy in chronostratigraphy and radiometric dating methods. New developments in palaeoclimatology and palaeobotany as well as the emergence of innovative methodologies have led to new approaches in palaeobiology. The study of fossil Syrphidae, however, has benefited little from these alternative orientations and their practical application.

4.2. Fossil deposits

The fossil sites that have revealed the presence of hoverflies, are few. There are only 25 deposits of which 9 are Nearctic, 15 are Palearctic and only one belongs to the Neotropical region. The specimens known to us come from 40% inclusions in fossil resins, mainly Baltic amber. The other Syrphidae listed in palaeontological records belong to lithofacies of origin, usually lacustrine or fluvial. The state of conservation of fossils, especially impression fossils, is very variable. In some cases it is exceptional (Konservat-Lagerstätten) but in general, surface mechanical phenomena and chemical taphonomic processes have led to a more or less profound alteration of the specimens. Despite these limitations, it appears that most known samples have generally been satisfactorily assigned to suprageneric level taxa. However, in the discussion of individual sites, we will discuss several identifications whose accuracy seems to us to be in doubt.

A special effort was made to locate the various deposits on the chronostratigraphic scale. With three exceptions, all the fossiliferous beds that have so far delivered Syrphidae are stratified from Lutetian (Lower Eocene) to Tortonian (Late Miocene). To position the 25 sites in question, we used, as far as possible, the stratigraphy and radiochronology acquired as well as the results obtained by the study of other fossil groups, in particular mammals and, if necessary, the evidence from palaeobotany. The chronostratigraphic scale chosen is that of GRADSTEIN et al. (2005).

Reg.	Localité	Province/Etat	Pays	Genres	Statut	Esp.	Epoque	Etage	Age
NEA	Quilchena	British Columbia	CA	?	?	?	Eoc inf.	Yprésien	53
	Cathedral Bluffs	Colorado/Wyoming	US	1	A	1	Eoc moy	Lutétien	48
	Dragon	Utah	US	2	F	2	Eoc moy	Lutétien	45
	Green River	Wyoming/Colorado/Utah	US	3	A	5	Eoc moy	Lutétien	45
	Horsefly Mine	British Columbia	CA	?	?	?	Eoc moy	Lutétien	43
	Florissant	Colorado	US	11	F/A	16	Eoc sup	Priabonien	35
	Chagrin Valley	Colorado	US	1	A	1	Oli inf.	Rupélien	32
	Ruby River Basin	Montana	US	3	F/A	3	Oli inf.	Rupélien	30
	Creede	Colorado	US	1	A	1	Oli sup.	Chattien	27
PAL	Ugolyak River	Tainyr	RU	?	?	?	Cre sup.	Campanien	83
	Ambre de la Baltique	Région de la Baltique	PL	19	F/A	37	Eoc moy	Lutétien	47
	Ambre de Bitterfeld	Sachsen	DE	?	?	?	Eoc moy	Lutétien	47
	Eckfelder Maar	Rheinland-Pfalz	DE	?	?	?	Eoc moy	Lutétien	44
	Kleinkems	Baden-Württemberg	DE	1	A	1	Eoc sup.	Priabonien	34
	Brunstatt	Haut-Rhin	FR	1	A	1	Eoc sup.	Priabonien	34
	Les Carnoins	Bouches-du-Rhône	FR	1	A	1	Oli inf.	Rupélien	31
	Aix-en-Provence	Bouches-du-Rhône	FR	5	A	5	Oli sup.	Chattien	27
	Enspel	Rheinland-Pfalz	DE	?	?	?	Oli sup.	Chattien	24
	Rott	Nordrhein-Westfalen	DE	10	A	11	Oli sup.	Chattien	24
	Randeck Maar	Baden-Württemberg	DE	1	A	1	Mio inf.	Burdigalien	17
	Stavropol	Stavropol'skiy Kraï	RU	1	A	1	Mio moy.	Serravallien	13
	Oeningen	Baden-Württemberg	DE	2	A	3	Mio moy.	Serravallien	13
	Radoboj	N. de Zagreb	HR	1	A	3	Mio moy.	Serravallien	13
	Gabbro	Toscane	IT	1	A	1	Mio sup.	Tortonien	8
NEO	Ambre Dominicain	Région NE d'Hispaniola	DO	1	A	1	Mio inf.	Burdigalien	18

[Table 2: Listing. 25 sites from which fossil Syrphids have been reported. In 6 of these deposits, the remains found could not be identified below the family level. The table also mentions the status (extinct / current) and the geological age. Abbreviations used: country: two-element ISO code; status: A = current, F = off; eras: Cre = Cretaceous, Eoc = Eocene, Oli = Oligocene, Mio = Miocene.]

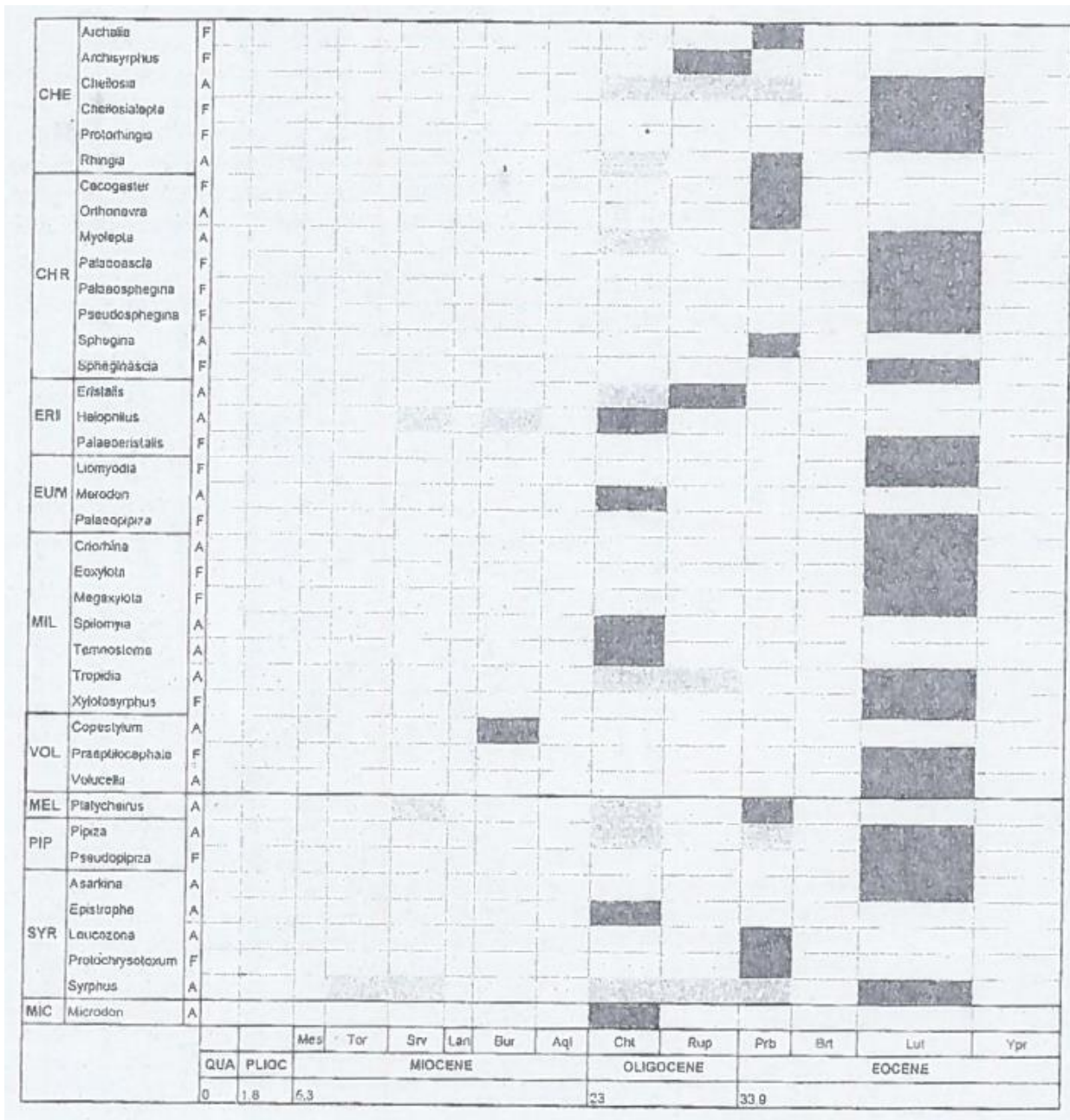
Table 2 illustrates the essential features of each of the deposits quoted in the literature. It summarizes the main geological and geological features of fossil sites where Syrphidae have been identified. We have indicated the number of genera and their status (fossil or current) as well as the corresponding number of species. The age in the last column was assessed primarily by analogy with radiometric and isotopic dating results, or from biostratigraphic elements provided by palaeobotany or Paelearctic and Nearctic mammalian studies. Due to the lack of taphonomic detail and sometimes insufficient stratigraphic resolution, the dates mentioned may be affected by a more or less important margin of uncertainty, variable for the different deposits. In the form of a double entry table, Table 3 enumerates the 39 genera and the stages where fossil taxa have been identified.

The following is a brief overview of the geological features, palaeoclimatology and large landscape units in the formation of some of these sites, in principle those with the richest palaeontological records, as well as some comments on the fossil Syrphidae discovered there. In North America, of the fossiliferous formations so far recorded, nine have delivered hoverflies. We selected three of these sites for detailed comments. In fact, of the 29 species described from the Nearctic region, 24 come from three deposits, all located in the Rocky Mountain Range. In Europe, 11 sites provided specimens identified and described at least at the genus level. Baltic amber accounts for 57% of this fossil fauna, while the remainder is of sedimentary origin. Of these, we selected four deposits totaling 29% of the species. To our knowledge, the only tropical syrphid mentioned in the literature is a *Copestylum* (Volucellini), reported from Dominican amber (POINAR & POINAR, 1999).

4.2.1. Green River Formation

The Eocene rocks of this type were originally deposited in a series of sedimentary basins occupying the bed of several lakes on the edge of the Wyoming, Colorado and Utah states, which probably dried up towards

45 My BP. The lithostratigraphic units are kerogenic schists of variable composition, formed in sedimentary environments whose spatial distribution and nature have constantly changed during the 5-6 Ma period, attributed to the genesis of Green River Formation (BRADLEY, 1931 STOKES, 1978). A schematic map of the approximate extent of the lakes concerned has been published by SCHAEFFER & MANGUS (1965).



[Table 3: Enumeration of the 39 genera plotted with the periods where fossils have been recorded. The first appearance is in dark gray, while the new finds appear in lighter gray on the board. The abbreviations F and A in the third column correspond to the fossil and current genera. The geochronological scale is that of GRADSTEIN et al. (2005). The abbreviations of the stages are those appearing in GRADSTEIN & OOG (1996).]

The age of the sediments containing the fossiliferous layers was the subject of conjectures whose results were not always consistent. Recently, ROEHLER (1992a, b) presented a chronostratigraphic correlation test summarized shortly thereafter in a synoptic table (ROEHLER, 1993), from which it appears that Green River Formation was essentially in the period 48.5-45 BP (Middle Eocene). It should be noted that this duration is less than that proposed by BRADLEY (1931).

The study of the Green River fossil flora (BROWN, 1934, LEOPOLD & MACGINITIE, 1972) made it possible to evaluate the main types of vegetation as well as the thermal and rainfall parameters during this period. In a first contribution, KNOWLTON (1923) pointed out the composite nature of the identified genera, the majority being characteristic of tropical or subtropical regions while a significant number of species were adapted to temperate climates. Recently, GRAHAM (1999) defines vegetation types in the Green River era as a woodland savannah mixed with lowland dry tropical forests (300 m) and deciduous forests on the hills (1300 m). Mean annual temperature and rainfall are estimated at $T_a \sim 20^\circ \text{C}$ and $P_a \sim 1500 \text{ mm}$ (ROEHLER, 1993) while WING & GREENWOOD (1993) proposed $T_a = 15.2^\circ \text{C}$ from analysis of leaf forms. They characterize the environment as a notophyllous evergreen forest, the vegetation also attesting the presence of palms intolerant to frosts.

The number of insects described from Green River by about 1920 amounted to 279 species, of which many Diptera could be assimilated to current genera (COCKERELL, 1920). More recently, WILSON (1978) identified the presence of 83 families among the reported fossil insects of the site, 23 of which belong to the order Diptera. The syrphids described from Green River are five in number, attributed by their respective authors to the genera *Cheilosia* (2), *Syrphus* (2) and *Milesia* (1).

The male type of *Milesia quadrata* SCUDDER 1878 was re-examined by HULL (1945), who transferred the taxon to the genus *Asarkina*: the figure (pl.2, fig.D) is strikingly reminiscent of the abdomen of species currently assigned to *Asarkina*. In our time, this genus has a tropical distribution in the Old World, with a single species, *A. porcina* (COQUILLET, 1898) penetrating marginally into the Palearctic region. The subtropical to tropical climate of the Middle Eocene could probably explain its presence in North America.

The species *Syrphus hendersoni* JAMES 1932 was described from an isolated abdomen of indeterminate sex. Since the macules of the tergites are similar to those of some current *Scaeva* or *Dasysyrphus*, the transfer of the species to another genus would probably be justified. In his review, Hull (1945) emphasized the resemblance to the West American species *Dasysyrphus amalopsis* (OSTEN SACKEN 1875).

From the examination of the holotype (probably a male) of *Cheilosia ampla* SCUDDER 1878, it appears that: (1) the mesonotum is devoid of macrosetae, (2) the posterior tibia is strongly arched, and (3) all legs (femur?) have a double row of obvious spinules (HULL, 1945). These peculiarities do not correspond to the usual profile of the genus *Cheilosia*. The species *Cheilosia scudderi* COCKERELL & LEVEQUE, 1931, known from two females, is distinguished from all its fossil congeners by the presence of light spots on tergites 2 and 3, an exceptional character for the genus, present only in a few rare extant species.

4.2.2. Ruby River Basin

Impression fossils of numerous fossil insects have been found in the shale clays of Ruby River Basin, SW Montana, associated with a diverse and well-studied flora. The lacustrine sediments are finely laminated and consist of volcanic ash and terrigenous clastic particles brought by the erosion of the surrounding reliefs.

The Palaeofloras dating from the upper reaches of Ruby River Basin have long been uncertain. Initially, the origin of floristic successions recorded in lacustrine facies was attributed to the Upper Oligocene. More recent geological and biostratigraphic studies have concluded that fossils are more likely to date from the Rupelian (Early Oligocene, Whitneyan NALMA zone) at 30.8-29.2 BP (WING, 1987).

The vegetation of Ruby River Basin consisted of a mosaic of mixed coniferous and deciduous forests with bushy formations and, at low elevations, a cover of chaparral (maquis). The comparative analysis of the flora of Ruby River Basin and Florissant showed that of the 82 identified species, nearly 40% were common to both deposits (BECKER, 1961). The average annual temperature, estimated by the CLAMP method, was 11-12 °C, the difference between the hottest and the coldest months being 16 °C.

The entomological fauna of Ruby River Basin was probably very rich, judging by the figure of 1000

specimens announced by BECKER (1961). Among the Diptera, he mentions a single individual of a hoverfly "recognized by its head with frontal projections", which evokes certain genera of Cerioidini (*Ceriana*, *Monoceromyia*) or one or other milesiine taxa whose antennae are implanted on a frontal process (*Somula*, *Stilbosoma*). To our knowledge, this specimen has not been the subject of a description. In 1948, a collection of fossil insects was collected in Ruby River Basin (Peterson Creek) by the University of Michigan. According to HULL (1960), much of this material is poorly preserved and lacks the characteristics essential to a satisfactory diagnosis. Among the 38 specimens of Diptera present, however, he described the first two Syrphidae of this formation in the genera *Archisyrphus* (1 male) and *Syrphus* (1 male). Regarding *Syrphus petrographicus* HULL 1960, the description mentions "locality not given; presumably from Ruby Basin". In the introduction, however, the author indicates that the provenance of the specimen was Florissant, Colorado. In the diagnosis of *Archisyrphus opacus*, Hull mentions that the abdomen has only four visible tergites, which classifies the species among the Eristalinae. Subsequently, a third specimen, from Becker's collections around Alder, was also named (LEWIS, 1973). The author attributed this species to the genus *Tropidia*, notably by the presence of a facial keel and a thickened posterior femur.

4.2.3. Florissant

During the Eocene, the site of Florissant, located in central Colorado, consisted of a river bed surrounded by mountain ranges including several volcanic areas. Following a series of eruptions resulting in torrents of mud, the valley was partially filled with pyroclastic rocks and a lake was formed (MCLEROY & ANDERSON, 1966). The lacustrine sediments accumulated in the lake of Florissant contain in addition to diatomite and sapropelic material sequences, layers of siliceous volcanic ash, favorable to the conservation of the insects (MOE, 2005). The thickness of the fossiliferous layers is estimated to be about ten metres (GREGORY & CHASE, 1992) which would correspond to a duration not exceeding 5000 years on the basis of the average rate of accumulation of the various strata (McLEROY & ANDERSON, 1966).

The age attributed to the rich volcanoclastic sediments of Lake Florissant is an example of the adjustments made by the dating methods developed over the past three decades. The authors who studied the insects and plant macrofossils of this Lagerstätte during the first half of the twentieth century had alternately located their formation at the beginning of the Tertiary, in the early Oligocene, or in the Miocene (COCKERELL, 1906; KNOWLTON, 1916; HULL, 1945; MACGINITIE, 1953). These dates, essentially biochronological, were revised later thanks to a better correlation of the biostratigraphic zone units with the results obtained by radiochronology and magnetochronology. Recent research has suggested a $^{40}\text{Ar} / ^{39}\text{Ar}$ age of between 36.7 BP and 34.1 BP (McINTOSH et al., 1992, SCHORN, 1998). Since the base of the Oligocene is currently in the range between 34 BP and 33.4 BP (SWISHER & PROTHERO, 1990), the site of Florissant belongs to the end of the Priabonian.

The Florissant palaeoflora, studied by MACGINITEE (1953), was probably composed of dense riparian vegetation along the river and on the lake's shores. At higher elevations, drier sclerophyllous forests were present mixed with savanna with trees.

The local climate at the end of the Eocene has been the subject of several evaluation attempts, mainly from palaeobotanical data. The palaeoenvironment of Florissant corresponds, as a whole, to the type of mesothermal / microthermal climate characterized by a rainy summer season and a dry winter. The application of the CLAMP technique leads to an evaluation of T_a of 10.7 ± 1.5 °C (GREGORY & CHASE, 1992) or 10.8 °C (WOLFE, 1994), whereas the floristic and physiognomic methods are in the range of 13 °C to 16 °C (MacGINITIE, 1953).

The Mutual Climatic Range (MCR) method (ATKINSON et al., 1987), based on the extrapolation of ecological tolerances from a set of current insects to fossil samples, has recently been applied to Florissant's Diptera to reconstruct the palaeoenvironment (MOE & SMITH, 2005). The basic principle is to recognize that while climate tolerances of a modern species are known, its fossil populations lived under similar palaeoclimatic conditions. If several fossil species are found together, the environmental factors of the site are assumed to be those specific to the intersection of the individual intervals. The method was initially developed to

evaluate summer temperatures in Great Britain since the end of the last Quaternary ice cycle from Coleoptera subfossils. No current species of Diptera are known from the Florissant site, and so MOE & SMITH (2005) used the ecological profiles of the genera. They justify this approach by the assertion that their climatic tolerances are compatible with those of the species that compose them. Examination of Diptera samples from Lake Florissant suggests a temperate to subtropical climate for Syrphidae ($T_a = 12-16$ °C), which corresponds to some results obtained in palaeobotany. The findings of the study also suggest that the riverbed was at a moderate altitude, confirming several previous estimates. In contrast, the work of GREGORY & CHASE (1992) and WOLFE (1994) based on the application of the CLAMP multivariate analysis place Florissant's palaeo-altitude between 2300-2500 m, which corresponds to the current level.

Palaeontological exploration of the Lagerstätte of Florissant has up to now yielded 31 published specimens of hoverflies comprising 16 species in 11 genera, of which 3 are known only from this site, while 5 others appear for the first time, having survived until the present period. Of the total number of recognized individuals, 14 are attributed to *Syrphus willistoni* COCKERELL 1909, a species characterized by widely separated spots in the middle of the abdomen. The three genera known only from Florissant were all established by HULL (1945), who attributed two to the Cheilosiinae (*Archalia*, *Cacogaster*) by estimating their affinity with the Myoleptini. For the third, *Protochrysotoxum sphinx* HULL 1945, the author mentions in the diagnosis of the genus that in the single specimen "the head is wanting", while the text relating to the species nevertheless gives details of the head. Among the wing characters is the mention that R4+5 is unchanged in cell r5, unlike current species of *Chrysotoxum*. There remains a doubt about the identity of this fossil. Of the three *Cheilosia* of Florissant, the only satisfactory description is that of *Cheilosia hecate* HULL 1945: it is sufficiently detailed to justify the generic attribution, inter alia, by mentioning the swollen margins of the face along the eyes. With regard to *Cheilosia miocenica* COCKERELL 1909, the venation seems close to that of *Protorhingia* HULL 1945, described from Baltic amber, from the strong downwards curvature of R4+5 that reaches the costa well beyond the end of the wing. The description of the third species, *Cheilosia sepultula* COCKERELL 1917, is limited to a summary comparison with the previous one.

As for the genus *Cacogaster* attributed to the Cheilosiinae, it was later included in the Rhingini by HULL (1949) in the same way as was *Archalia*. For the latter, it should be noted that the description of the type explicitly mentions the presence of five visible abdominal segments and a highly developed hypopygium. According to current criteria, this character makes it possible to classify the taxon among the Syrphinae (SHATALKIN, 1975, VOCKEROTH & THOMPSON 1987). It should be noted, however, that in the diagnosis of the genus, the author indicates that the apical swelling of the abdomen "is probably a male hypopygium" which leads to doubts about the attribution of sex. Besides, the particular profile of the head of *Archalia femorata* HULL 1945, as well as the strongly bulging posterior femora that are setulose at the base, make all comparison with any kind of Syrphinae difficult. In the description of *Cacogaster novamaculata*, HULL 1945 describes the species as "a very peculiar form", presenting an intermediate habitus between *Syrphus* and *Rhingia*, which does not allow us to locate the taxon.

The other hoverflies described by Florissant fall into the following genera: *Rhingia* (1), *Orthonevra* (1), *Sphegina* (1), *Pipiza* (1), *Leucozona* (1) and *Syrphus* (4).

4.1.4. Rott

In the northwest of the Federal Republic of Germany, the lower basin of the Rhine covers a vast sedimentary territory formed during the transgression of the North Sea during the Oligocene. Large layers of lignite were deposited there, many of which delivered fossil samples. The withdrawal of the sea in the Upper Oligocene and Pliocene gave rise to the establishment of the current tributary system of the Rhine. The slag heaps of the Rott mine have yielded a large amount of macroflora, pollen and many insects and vertebrates. The extraction site is located on the north slope of the Siebengebirge, east of Bonn and close to the Lower Rhine Basin.

The fossiliferous layers consist of pyrobituminous schists. The first sediments are lacustrine, fossil-free, and

correspond to an oligotrophic environment, while the following layers are formed of bituminous laminites and deposited in eutrophic, sapropèle-rich [*sapropèle = dark sediment rich in organic matter*], and mostly fossilized soil. The upper part consists mainly of sands and clays announcing the drying up of Rott Lake.

Rott fossil dating was established using small mammals, mainly rodents, and the entire formation was assigned to MP30 (25-24 BP) (MORS, 1996). By applying the coexistence method to a fossil flora composed of leaves of 28 species, UTESCHER et al. (2000), establish a probable age of 24 Ma.

The physiognomic method and CLAMP were applied to Rott palaeofloras to estimate the mean annual temperature. The results indicate a probable temperature of the order of $T_a = 11.8^\circ\text{C}$ based on leaf characteristics (WILF, 1997). The climate and vegetation of the northwestern part of the Federal Republic of Germany, particularly the Lower Rhine Basin, including the Rott site, have also been the subject of recent research by the authors of the so-called coexistence approach (see section 3.3). The results suggest a value of $T_a = 16.5\text{-}20^\circ\text{C}$ and $T_{\text{max}} = 26\text{-}28^\circ\text{C}$, a relatively warm climate. A recent critical review of the various methods used (physiognomic, CLAMP, co-existence) showed that they were neither comparable nor always reliable. Having made a comparative evaluation of previous results, KOWALSKI & DILCHER (2003) proposed an adjustment to the estimates leading to a value of $T_a = 14.3^\circ\text{C}$.

The Rott palaeoflora marks the beginning of a major reworking in the plant cover of Central Europe, which is changing towards a Neogene-like physiognomy, already including many species playing a more important role since the Middle Miocene. The state of conservation of the fossils is generally very satisfactory and makes it possible to observe the ommatidia, the venation and the microtrichia of the wings as well as details of the pilosity. Like the vast majority of Oligocene insects, Rott's hoverflies have all been attributed to current genera. Of the 12 named taxa, three are assigned to the generic level only. STATZ (1940) also mentions about thirty pupae which he attributes to "*Eristalis*" sp. based on remnants of the mandibular hooks and the larval cephalopharyngeal skeleton. Of the known taxa, three were described in the 19th century by VON HEYDEN (1870), while the others are the result of excavations conducted over more than 20 years by STATZ (1940). As a result of the interruption of contacts between Europe and North America from 1940 to 1945, HULL (1945) was probably not aware of the research conducted at Rott and the work of STATZ (1940), to which he therefore did not refer in his revision.

Reviews of the descriptions suggest some comments. The first named hoverfly of the site is *Helophilus? primarius* GERMAR 1837 (type locality "Bonn"). As this taxon is not identifiable by description or illustrations, and has not been located, it was excluded from the Syrphidae by HULL (1945) and considered *incertae sedis*, a status recently maintained by KOTTHOFF & SCHMID (2005). One species is described by STATZ (1940) as *Chilosia (= Cheilosia) picata*. It is a male with an entirely black integument, the diagnosis of which is largely based on the characters of the venation. The latter does not deviate from the usual pattern of *Cheilosia*, with the exception of the apical and subapical transverse veins, which are bent and arched (STATZ, 1940, pl. XXI, fig. 27). In addition, the author specifies that the abdomen has "fünf Segmente" which, according to current conceptions classifies the species among the Syrphinae.

A specimen is attributed to *Tropidia* on the basis of a single wing: if the comparison of the illustration (PL XXVI, fig. 78) with the current species of the genus does not contradict this identification, it does not allow us formally to conclude to its validity. One of the peculiarities invoked, the presence of bristles along the costal vein, does not constitute an exclusive character of the genus *Tropidia* but is found in many other taxa. Note that STATZ (1940) also described *Epistrophe kastenholzi* from Rott, mentioning in the diagnosis "Augen behaart", which would perhaps justify transfer to a different genus (*Dasysyrphus?*, *Betasyrphus?*). Other taxa described by STATZ (1940) include three specimens attributed to currently recognizable genera. The diagnoses of *Myolepta*, *Spilomyia* and *Temnostoma* present the mainly alar characters of the modern forms.

4.2.5. Radoboj

The Radoboj site in Croatia was part of the Styrian Basin (Central Paratethys) and the main fossiliferous

layers have been worked around Zagreb. These are argillaceous rocks, accompanied by schistose marls, which have revealed a rich flora and fauna composed of insects and numerous organisms of marine origin. The dating is based on the presence of a mammalian fauna of *Hyotherium* whose age in the Croatian part of the basin is attributed to the Serravalien.

The flora was considered tropical to subtropical, in particular by the presence of palm trees, but recent palaeobotany data suggest that it is likely to be composed of deciduous forests mixed with a small laurel forest. The dominant species was *Fagus* sp, but *Liquidambar* sp. and Taxodiaceae were also present, as well as rich marsh vegetation (MAI, 1995). Towards the end of the Badenian (MN 7 + 8), dated in the region of the central Paratethys to ~ 13 Ma (STEINIGER & WESSELY, 2000), a floristic change took shape following the cooling of the climate and temperate elements assumed a dominant role. According to PANTIC (1992) the fossil community would have formed during a wet climate phase on a low-lying Paratethys island.

Three fossil Syrphidae were found in the Radoboj site, all described by HEER (1849) in the genus *Syrphus*. In a contribution to the fauna of fossil insects in Hungary, PONGRACZ (1928) examined two specimens, one deposited at the British Museum of Natural History in London and the other at the Geologischen Bundesanstalt in Vienna, which he attributed to *S. haidingeri* HEER and *S. infumatus* HEER. With respect to the taxon *S. infumatus*, he transferred it to *Platycheirus* on the basis of a strong apparent resemblance to the present-day Nearctic representatives, particularly the wing-like characters. The comparison of fig.53 (PONGRACZ, 1928) with the original drawing by HEER (1849, pl.XVU, fig.14), however, shows considerable divergences. It seems, therefore, that the similarity with *Platycheirus* is, to say the least, doubtful and does not deserve to be taken into consideration. This conclusion applies to the four taxa (Radoboj 3 and Oeningen 1) transferred by PONGRACZ (1928) to *Platycheirus*. We must also point out that the scutellum of *S. freyeri* Heer is called brilliant black in the original diagnosis, which excludes the genus *Syrphus*. The description also makes reference to the species *Melanostoma scalare* and *Platycheirus sexnotatus* (= *scutatus*) that are currently part of the Melanostomatini. As long as the original material is still in existence, a review should clarify the situation.

4.2.6. Baltic Amber

Known since the Neolithic, Baltic amber spread very early throughout Europe, through the commercial channels that have been in place for several millennia. Originally, its use covered the manufacture of decorative objects and jewelry. It was only afterwards that the scientific interest of the inclusions in the resin was recognized and many collections were formed. In the middle Eocene, in a hot and humid climate, northern Europe was covered with mountain forests consisting of very rich vegetation, mostly tropical and subtropical but also including many species characteristic of a climate temperate as we know it now. These forests were to be flooded or covered by a dense network of streams, otherwise the resin falling from the producing trees would have been oxidized and decomposed. Amber is known to degrade in contact with air and is preserved only in an anoxic environment. The drops and blocks of amber were transported by the rivers to an arm of the sea occupying the Baltic furrow from the current North Sea to Ukraine. The floods deposited them in the deltas. The most important layer was Samland (Russia) in former East Prussia (around Kaliningrad). These sediments, referred to as "Blaue Erde" (by reference to their hue) are the richest in resin nuggets.

The precise geographical location of the producing regions as well as the dating of amber pose problems that are not yet solved. With regard to the forests where the species (or species) whose resin has engulfed insects and other fossil organisms grew, it is only possible to locate their palaeogeographic position in a very general way. All modern authors agree in designating the major source as the Baltic Shield. The many changes made to the individual samples and the fact that the identity of the botanical source that produced the resin remains uncertain, renders illusory any attempt to retain a specific region which, moreover, is not necessarily unique. At most, it can be said that in most cases the actual age of inclusions is greater than that of the sediments in which it is found. With regard to dating, several hypotheses have been put forward. The total period of amber deposition was estimated at 55-35 Ma (LARSSON, 1978, SCHLEE & GLOCKNER, 1978). WEITSCHAT & WICHARD (1998) estimate the total duration of the formation at 10 Ma. A

recent radiometric K-Ar dating gives it an age of 44.1 Ma (RITZKOWSKI, 1997).

The flora of the Baltic forests has received the attention of many botanists who have revised ± 150 described species. These studies show that nearly a quarter of the taxa currently have a tropical distribution, while the balance is deciduous forests, of which there are mainly beech forests but also many palm trees. Two hypotheses to explain the presence of temperate elements in a subtropical environment have been put forward: (1) the majority of the fauna and flora suggesting subtropical conditions, the temperate elements may have been confined to territories located at the highest altitudes; (2) during the long period of fossil resin formation, a deterioration of the climate would have resulted in a succession of inclusions, starting from subtropical elements and leading to temperate deposits (LARSSON, 1978, POINAR, 1993).

The nature of the botanical source that produced the enormous amounts of resin that is the source of Baltic amber has been the subject of much controversy. Currently the most probable hypothesis seems to favour a species similar either to *Agathis* (Araucariaceae) or *Pseudolarix* (Pinaceae), but the arguments put forward do not allow us a definitive conclusion (LANGENHEIM, 2003).

The known Syrphidae of amber are 37 species, divided into 19 genera. In the following, we will present some comments, not exhaustive, inspired by the analysis of descriptions of individual taxa. HULL (1945) has described 25 new species of Baltic amber, based for the most part on the examination of the collections of the Geologisch-Paläontologisches Institut und Bernsteinsammlung der Albertus-Universität zu Königsberg (now Kaliningrad). Among these taxa is a species of Vollucellini, attributed to a new genus *Ptilocephala* (= *Praeptilocephala* n.n.). Careful reading of the description reveals the presence of a large number of characters considered to be diagnostic of *Graptomyza*. Among these we will first of all remember the scutellum provided with an oval depression, filled with macrochetae. On the other hand, the profile of the head (HULL, 1945, pl.6, fig.31) evokes *Graptomyza*, and can be compared to that of *G. pallidinota* WHITTINGTON (1992, fig.16). Finally, the presence of notopleural macrochetae as well as the posterior margin of the scutellum also correspond to the peculiarities of *Graptomyza*. As long as the material was not destroyed during the Second World War, a re-examination of the fossil would undoubtedly make it possible to provide details.

Two *Myolepta* were described in the first half of the twentieth century, *M. luhei* COCKERRELL 1910 and *M. elisabethae* STATZ 1940. HULL (1945) added four species as well as two monotypic genera considered very close: *Sericolepta* and *Arctolepta*. These last two were cited by EVENHUIS (1994) as subgenera of *Myolepta*. The diagnoses of the two new genera contain certain characters belonging to the current *Myolepta*: (1) face of the female concave, without facial prominence, (2) femura thickened and serrated on the ventral side, mainly towards the apex, (3) length of the first flagellomere equal to or slightly greater than its width. Despite these concordances, there are also points where *Sericolepta* and *Arctolepta* differentiate themselves from each other and from current genera. Thus, the first has the first orbicular flagellomere with pubescent arista, scutellum and post-alar caluses with many stiff bristles on the posterior margin and wings shorter than the abdomen. As for *Arctolepta* the first flagellomere is longer than broad, the scutellum with only a few bristles and the wings are very long, clearly beyond the abdomen, and finally the apical transverse vein is very sinuous. The figures of Hull (1945) show that in the two genera he describes, the transverse subapical and apical veins have a clearly marked branch, contrary to modern taxa. In the description of the group of *Myolepta*, no allusion is made to the bristles of the radial vein (up to its bifurcation) nor to the possible hairiness of the face. These few remarks suggest considering the genera *Arctolepta* and *Sericolepta* as well-founded. Recourse to the nomenclatural category of subgenus, although provided for by the Code, often poses serious problems in neontology [*comparative study of extant forms*] owing to the inadequacies of taxonomy. As far as their utility is concerned, their extension to the palaeontological domain seems to us, however, to be at least premature for groups such as Syrphidae, where the number of fossils is very small, and the assessment of the degree of morphological variation within species still remains out of reach. It should be noted that *Sericolepta maculata* HULL 1945 was considered as belonging to the Xylotini by HIPPA (1978). This author suggests the same affiliation for *Myolepta andreii* HULL 1945 based on the shape of the head and the venation.

In his review, HULL (1945) describes another six new genera, five of which are included with the Cheilosiniinae, the sixth being attributed to the Eumeriniinae. The diagnoses and illustrations that accompany them, suggest some comments. The genus *Pseudopipiza*, first mentioned as a subgenus but defined in the text as a full-fledged genus, comprises two species: the type, *P. antiqua* HULL, showing the essential characters of the modern genus *Pipiza*, and the species *P. europa* HULL, divergent by several peculiarities. The illustration of the wing given by Hull (1945, pl.13, fig.121) shows that in the latter species the angle between the apical transverse vein and R4+5 is practically a right-angle, which recalls the genus *Pipizella*. The face of *P. antiqua* is densely covered with silver hair, as in the modern species *Pipiza signata* MEIGEN 1822 and *P. noctiluca* (L., 1758), but the profile of the head is very different, especially by the projection of the lower part of the face and epistome. The whole contrasts with *P. europa* where the hairiness of the face is sparse and the epistome is not projecting. It cannot be ruled out, moreover, that the taxon described as *P. antiqua* is close to the current *Trichopsomyia*, but the diagnostic character, ie the hairiness of the proanepisternum, was not taken into consideration, assuming that it is accessible to observation.

The genus *Palaeopipiza* is classified by HULL (1945) among the Eumeriniinae for the following reasons: (1) seen in profile, the antennae are implanted in the middle of the head, (2) the concave face is adorned with a sparse white hairiness (3) the first flagellomere is more or less quadratic, and (4) the venation is considered similar. The illustration of the wing of *Palaeopipiza xenos* HULL 1945, however, shows no resemblance to the modern Eumerini, especially the characteristic course of the apical transverse median vein: the latter joins R4+5 at an acute angle, exactly as in *Pipiza*, and is not bent.

Of the six genera referred to above, four were associated with the group comprising *Neoascia* and *Sphegina* (Chrysogasterini) of the present-day fauna. HULL (1945) described the taxa *Palaeoascia*, *Palaeosphegina*, *Pseudosphegina* and *Spheginascia*, all attributed to the Cheilosiniinae. The first two genera were found to be very close, both with very strong bristles on the margin of the scutellum and a row of spines on the underside of the posterior femur. Males of all genera are holoptic, with the exception of *Pseudosphegina* which is slightly dichoptic but has the other characteristics mentioned above. HULL (1945) was able to study important material of *Palaeoascia* and *Palaeosphegina* including about 100 individuals. As for the second genus, the author insisted particularly on its phenotypic instability, especially for *Palaeosphegina elegantula* MEUNIER 1904 where he had studied many male and female specimens. The variation is perceived mainly in the profile of the scutellum and the venation of the wing. It will be noted that among the four genera belonging to the group, all have the tuberculous face in the male. Despite the similarities with the modern genus *Sphegina* (wing, abdomen, leg), HULL (1945) rejected any connection between the fossil and the current genus purely on the basis of the holoptism character of *Palaeosphegina*. If we stick to the structural characters, the presence of macrochetiae on the scutellum removes the four Baltic forms from the current genus *Neoascia*. The obvious conclusion is that the descriptions are not detailed enough to allow a meaningful comparison of the four proposed genera. From the point of view of biodiversity, it should be noted that Baltic amber has yielded a large number of specimens of some taxa: *Palaeoascia* (2 taxa), *Palaeosphegina* (1) and *Spheginascia* (1) have a total of 116 specimens (male and female). Given the presumed forest palaeoenvironments where insects became stuck in resin, the abundance of these genera is perfectly credible. They were small species, measuring 3.5-8 mm (HULL, 1945), which corresponds to the size of the current *Sphegina* (4-8 mm) and *Neoascia* (3.5-6 mm) (THOMPSON & TORP PEDERSEN, 1986, VERLINDEN, 1994). On the other hand, the larvae of modern species of *Sphegina* develop in sap flows and under wet bark of various forest species (HARTLEY, 1961, ROTHERAY, 1993, SPEIGHT et al., 2001, 2006), micro-habitats that were abundantly represented in the Baltic amber forests. It is therefore not impossible that the descendants of these Eocene clades may have belonged to the crown-group of the current Spheginina.

The genus *Megaxygota* described by HULL (1945) was placed by its author among the Xylotinae. Most of the diagnostic characters assigned to it correspond, or are indeed similar to those of the Xylotini, but HIPPA (1978) noted that according to the original description and the accompanying illustrations, the conformation of the posterior femur and the particular vein pattern R2+3 do not justify the inclusion of *Megaxygota* among this tribe.

5. Results

5.1 Preliminary remarks

The remains of Syrphids in fossilized sedimentary layers in the vast majority of cases allow us to recognize the diagnostic characters of the venation for correct attribution at the level of the family. For the distinction between subfamilies, the observation of the hairiness (or lack thereof) of the postpronotum, as well as the more or less important recovery of the humeral callus by the posterior part of the head is often more uncertain. With regard to the males, the number of visible tergites is a generally reliable character that deserves to be corroborated by other features, such as the pattern of the veins. As for the identification of the currently recognized tribes, this relies for the most part on the venation, on characteristics of the head, in particular the conformation of the antennae and the profile of the face, and on structural modifications of certain parts of the body (legs, abdomen). Observation and appreciation of the corresponding significant features will be conditioned mainly by the integrity and the state of preservation of the sample as well as by its position relative to the substratum. Amber inclusions, of course, allow a much finer analysis of morphological features that are crucial for identification.

It should also be noted that the fossil larvae and pupae of Syrphidae remain virtually unknown. In a note on the microfossils of the Green River pyrobituminous schists, BRADLEY (1931) noted the abundance of larvae of five Dipteran families, including syrphids. He did not, however, give any indication of their probable identity, merely observing that "the larvae of this family live in putrefying vegetable matter" (which is not valid except for phytosaprophagous groups and is therefore an inaccurate generalization). STATZ (1940) mentioned the presence of 30 pupae attributed to "*Eristalis*" sp. in Rott's lignites, stating that the remains of the mandibular hooks and the cephalopharyngeal skeleton remained visible. Later, a larva of *Microdon* was also reported, without details, from Baltic amber (WEIDNER, 1952).

All descriptions of fossil Syrphidae predate the introduction of the modern phylogenetic approach, based on cladistic methodology. In the past, taxa were defined exclusively typologically and the attribution of a fossil specimen was, in most cases, from a general resemblance evaluated by the author from genera and species familiar to them. We have already made reference to inaccuracies that may taint the descriptions made by palaeoentomologists not specialized in the taxonomy of the group studied. It is difficult, if not impossible, to compare satisfactorily the descriptions of many syrphids discovered in fossil deposits with representatives of the present fauna. Generally, it can be seen that, even for well-preserved samples, the old authors have contented themselves with standard descriptions, only rarely highlighting the traits currently considered as diagnostic for the genus or tribe. The majority of fossils, with the exception of the inclusions in amber, allow only a small number of morphological characters to be observed, which varies according to the state of preservation of the sample. Internal structures, like genitalia, remain in principle always inaccessible.

The use of the taxonomic category of the species for the analysis of fossil fauna is, in general, limited by several considerations:

- (1) The samples are randomly distributed in space and time and rarely allow us to get an idea, even approximate, of the biodiversity of the group studied and its change over time. Of the 19 fossiliferous sites known to contain Syrphidae identified at the genus level, 11 contain only one or two specific taxa (Table 2).
- (2) The vast majority of the recorded samples contain only a few individuals attributable to the same species: for Syrphidae, their number varies from 1 to 3 for 90 of the 95 species recorded, the exceptions being *Palaeoascia atrata* (8 specimens), *P. uniappendiculata* (51), *Palaeosphegina elegantula* (37), *Spheginascia biappendiculata* (20) and *Syrphus willistoni* (14). Note that except for this last taxon from Florissant, they are all inclusions in Baltic amber.
- (3) The preserved traits do not always allow us to integrate the fossil chronospecies satisfactorily among extant taxa, especially if the diagnostic characters are cryptic or even more pertinently concern internal structures such as genitalia, which are preserved and visible only in fossil resins only in rare specimens.

Despite the number of described syrphids from Baltic amber, 40% of known species, no study has yet been devoted to genitalia, unlike other families such as Sciaridae and Ceratopogonidae.

(4) None of the species of fossil hoverflies mentioned in the literature have been recorded from a site other than the original deposit. Two main factors can explain this geographical and temporal uniqueness of the samples: (a) the partial and often deformed nature of fossil insect impressions limits recognition of the diagnostic similarities with taxa that are already known, making their comparative identification difficult; (2) the lifespan of a species is reduced to the geological unit; as the time intervals between the main fossiliferous deposits where syrphids have been identified are generally much greater than this longevity, the gradual renewal of the species pool by extinction and by anagenesis will logically prevent the diachronic durability of the taxa.

The dynamics of terrestrial environments have helped to affect the rate of renewal of taxa, with the corollary of an unequal lifespan of species, but [this is] always short geologically. Life expectancy estimates vary according to the authors and taxonomic groups considered. For insects, the specific turnover rates quoted in the literature are estimated at 1 to 2 Ma (STANLEY, 1979), > 2 Ma (STANLEY, 1985) and 5 Ma (MÜLLER-MOTZFELD, 1984), and can even reach 7 Ma (KRZEMINSKA & KRZEMINSKI, 1992). The average lifespan of a species is, in all likelihood, variable according to the systematic group of which they are part.

Note that going up the taxonomic hierarchy we find that in insects the categories of the family level present very low turnover rates throughout the Cenozoic. More than 80% of the living insect families are known as Middle Cretaceous fossils. In addition, around the middle of the Tertiary, nearly 60% of the genera populating the regions of the present world were present, as well as several species morphologically very close to contemporary forms (CARPENTER & BURNAM, 1985).

	Syrphinae	Chrysotoxinae ¹	Cheilosinae	Eumerinae	Eristalinae	Volucellinae	Xylotinae ²	Total
EOC	4		2		2		1	9
OLJ	3		30	2	3	1	1	40
MIO	12	1	9		1			23
Total	19	1	41	2	6	1	2	72
Notes	¹ Actuellement inclus dans la tribu des Syrphini ² Souvent inclus dans les Eristalini (=Milesiini)							

[Table 4. Excerpt from the revision of HULL (1949) showing the breakdown of the 72 species recognized by the author among the subfamilies (currently tribes) at the great Tertiary Periods (Eocene, Oligocene, Miocene). It is not easy to deduce this figure from the HULL monograph (1945) where, besides the description of four "varieties", several taxa were considered *incertae sedis*.]

5.2 Composition and structure of fossil fauna

In his worldwide revision of the family, HULL (1949) presented a table of fossil Syrphidae, an extract of which we reproduce (Table 4). The 72 species mentioned by the author were divided into 7 subfamilies

(currently considered as tribes) among which the Cheilosiinae and the Syrphinae held 85% of the taxa. Curiously, the subfamily Microdontinae is not included in the table since [even though] HULL (1945) recognized the validity of the only fossil specimen mentioned from Aix-en-Provence. Note the low proportion of Eocene-dated species and the predominance of those from the Oligocene. The changes to the chronostratigraphic scale since the publication of HULL's work (1949) and the increased precision of current dating methods lead to a new interpretation of the fossil evidence described so far. Table 5 summarizes the distribution, by geological time, of the number of species in each of the three subfamilies to which fossil Syrphids have been attributed, after updating the fossil record data. A first quick comparison with the HULL (1949) survey reveals a fundamental difference in the distribution of fossil taxa over time. This important reshuffle is motivated mainly by a historical element. The progress made over the last fifty years has profoundly changed our approach to the past and the evidence it has left us. New analytical techniques, as well as the results of the Deep Sea Drilling Project (DSDP) (1968-1974) and ODP (Ocean Drilling Project, 1985-2003), have contributed greatly to integrating the chronostratigraphic scale and palaeobiochronology, mainly through the use of stable isotopes of oxygen and carbon (SHACKLETON, 1986, WEST et al., 2006).

	SYR	PIP	MEL	CHE	CHR	EUM	ERI	MIL	VOL	MIC	Total
EOC	12	3	1	15	22	2	1	5	2		63
OLI	1		1	4			3	1		1	11
MIO	6	1	4	1	1	1	3	3	1		21
Total	19	4	6	20	23	3	7	9	3	1	95

[**Table 5.** Breakdown of 95 taxa named by subfamily and time based on data from this study. The table includes all the species described, except the taxa explicitly excluded from the family by HULL (1945). The distribution of taxa among the different tribes will probably be subject to adjustments in the wake of subsequent revisions of the material.]

These remarks relate to the fossil syrphid species recognized in the palaeontological archives studied to date. On the geological scale, this level of the taxonomic hierarchy has a very ephemeral duration, and we have already pointed out that no species has been found outside its original deposit. The study of fossil organisms in the Phanerozoic Era conducted from sometimes large databases has shown a globally significant correlation between specific and higher diversity (SEPKOSKI et al., 1981, FOOTE, 1996, LEE, 1997). This relationship seems to apply equally to the neontological fauna and flora (WILLIAMS & GASTON, 1994, ANDERSEN, 1995, HALMFORD et al., 1996, LA FERLA et al., 2002). These results justify the use of inclusive taxonomic units when the numbers of basic components are insufficient, both qualitatively and quantitatively. Most of the research to date in palaeobiology and palaeoecology has thus focused on genus and family levels (RAUP 1979, SEPKOSKI et al., 1981, RAUP & SEPKOSKI 1986, FARA 2000). They shed new light on the measurement of biodiversity over the ages, the evolutionary perspectives of fossils and the understanding of the mechanisms of diagenesis. The use of higher-ranking taxa to study the rates of diversification of palaeontological archives does not, however, necessarily give them an ontological status. They will only be used as substitutes, partially addressing the shortcomings in the sampling of fossil species.

Table 6 shows, for each of the three syrphid subfamilies, the number of genera counted in the fossil sites at the Eocene, Oligocene and Miocene periods. As an indication, we have included the corresponding figures for the current period, as we have established in the context of this study. For all perennial taxa with descendants in modern fauna, we have admitted the principle of continuity: they are therefore included in the count of each period after their first appearance.

Epoques	SYR	ERI	MIC	Total
EOC	7	23	-	30
OLI	5	11	1	17
MIO	6	14	1	21
Actuelle	55	135	18	208

[Table 6. Distribution of listed fossil genera in the three subfamilies, from the Epochs. The last line corresponds to the approximate number of current genera obtained by integrating recent inventories.]

Examination of the composition and characteristics of fauna, updated in the palaeontological archives, makes it possible to formulate some thoughts:

- (1) The first stage of the Eocene having delivered named fossil Syrphols, it is the Lutetian which counts representatives of 8 tribes, where Cheilosini and Chrysogasterini dominate with 28 species in 8 genera. The concentration of the Lutetian fossil record, a total of 42 species in 22 genera, is due mainly to inclusions in amber from the Baltic. This circumstance, favourable to the integrity and the quality of the conservation of the samples, makes it possible to grant an increased reliability to the identifications especially the ca.10 older descriptions that go back to the beginning of the 20th century. The fauna of the Eocene has left traces until the present day, thirteen genera having survived (see Table 3). The status of the genera still present today presumably will require some taxonomic adjustments when existing historical collections and the dormant never-studied material is revised.
- (2) the presence of 80% of all ten tribes enumerated as fossils at 20 Ma after the K/T boundary assumes that the origin of the Syrphidae family dates back to at least the late Cretaceous, which is confirmed by the single reported fossil of Ugolyak (Taimyr) (ZHERIKIN & ESKOV, 1999) [but see Popov 2015]. It also corroborates the presumption that the extinctions that followed the K/T event probably did not have a major impact on syrphids, which like other insects resisted the biotic upheavals better, particularly the presumed major reduction in primary production and disturbance of plant communities (Bliffetaut, 1984, Johnson & Hickey, 1990, Sheehan et al., 1996, Nichols & Johnson, 2008). Of the 19 genera described from the Lutetian, 13 were attributed to tribes whose larvae belong to scavenger guilds or live in decomposing organic matter and therefore less sensitive to the decline of the megaflora (SHEEHAN & HANSEN, 1986, WOLFE & UPCHURCH, 1987, LABANDEIRA et al., 2002).
- (3) inclusions in Baltic Amber include 37 species described in 19 genera, of which 12 are extinct. Among these, several taxa have an association of generic and/or specific characters not found in the current representatives of the closest groups. Thus the fossil genus *Palaeosphegina* is very close to *Sphegina*, with which it shares all the essential features with two exceptions: the male is holoptic and the face is tuberculate in both sexes. Other examples could be cited. A review of these seemingly atypical groups, supplemented by an examination of the many collections accumulated over the last century and never studied, would be essential to analyze the taxonomic and phylogenetic implications of the modifications found. The status of pseudo-aberrant characters compared to those of current forms is also a critical element for the identification of crown groups and the inclusion of fossils in cladograms.
- (4) out of a total of 63 described species of the Eocene, 36 were attributed by their authors to current genera. This high proportion is no doubt indicative of the propensity of palaeoentomologists of the 19th

and early 20th centuries to integrate newly discovered fossil taxa among those familiar to them, and to supra-specific groups considered to be well characterized and easily identifiable. Although, for some genera, long-term temporal stability can not be ruled out a priori, it seems plausible that a re-examination of the samples still available would lead to different generic assignments. From 1854 to 1960, fourteen species of the genus *Syrphus* were described. After the revision of HULL (1945), three of these taxa (including the single sample of Baltic amber) were considered *incertae sedis* by this author. Of the 11 species of *Syrphus* fossils currently recognized, several groups can be distinguished from the drawing of the habitus. In the abdomen, some descriptions indicate isolated lateral spots on the tergites (*willistoni*, *lithaphidis*, *freyeri*), while others mention yellow bands, interrupted or not in the middle (*aphidopsidis*, *platychiralis*, *eocenicus*). The abdomen profile of the various taxa varies from slender to stocky according to the authors, but these can be the result of deformations during the taphonomic process. For other multispecific taxa, similar remarks can be made: thus the characters mentioned in the original descriptions do not allow us to place unequivocally the 10 taxa attributed to *Cheilosia* nor the seven *Myolepta*. According to modern criteria, some of these taxa would therefore probably be assigned to different genera. By the middle of the twentieth century, Hull (1945) had clearly perceived the difficulties of identifying and classifying the fossils he had revised.

(5) In dealing with this synthesis, we planned to complete a review of the legacy of fossil Syrphidae with a brief quantitative analysis of trends in family development over time. Critical reading of the palaeontological records, however, showed that the conditions for completing such an exercise were not yet met. Although syrphids are among the three families of Brachycera with the largest number of fossil taxa, sampling is still largely incomplete. On the other hand, out of a total of 86 named species, 82 were described prior to 1950, prior to the work that resulted in the family's current taxonomic reference framework. Finally, since the monograph of HULL (1945), no revision even partial is known to us. An examination of the original descriptions, however, shows that the great majority of taxa were correctly attributed to the family and their classification among the three currently recognized subfamilies offers, with few exceptions, no major difficulties. It is also apparent from this review that of a total of 39 genera, 25 are monospecific while 8 others do not include more than 3 species. The rectifications proposed by HIPPA (1978) and in this note relate for the most part to limited potential transfers at the level of tribes and genera. Reading Table 6 shows that the distribution of the number of genera among the two main sub-families has changed very little since the Eocene. It is only noted that the proportion of known Syrphinae was lower in the Lutetian. This disparity is mainly due to the presence of the Baltic amber fauna, where predators were apparently less well represented. A comparison with the current distribution of subfamilies confirms the rates obtained for the past, except for Microdontinae, whose share has increased considerably. It should be noted, however, that these few comments are based on fossil sampling that is unquestionably insufficient to justify definitive conclusions.

(6) Like all families of current insects, the Syrphidae have dispersed from their origin, an evolutionary trajectory conditioned notably by the vicariant and palaeoclimatic scenarios during the Cenozoic. These events had an impact on the structure and distribution of the continental surface biomes that led to a continual remodelling of the nature, distribution and frequency of taxa. Biodiversity can be measured in many ways, none of them having absolute prominence. It is taxonomic (rich in species) or ecological, measured in particular by the number of trophic guilds or by their numbers. In order to test the possibility of measuring ecological diversity, we made a comparison between palaeocommunities of Baltic amber and all sedimentary deposits. For this purpose, each of the genera has been endowed with a trophic status for its larvae. This attribution is based on the assumed analogy with the current taxa for the 21 genera that have survived to date. For the extinct genera, we evaluated their tribe membership to judge the appropriate trophic guild. Only a few taxa whose affinities were considered too uncertain were not taken into account (*Archisyrphus*, *Archalia*, *Cacogaster*, *Liomyodia*, *Megaxylota*, *Praeptilocephala* and *Protochrysotoxum*). For species, their numbers have been adjusted to account for

taxa considered uncertain by HULL (1945) and taxonomic changes suggested by Hippa (1978) and in this study. These changes led to a total of 76 species of which 28 are from Baltic amber and 48 from sedimentary deposits. For imputation to trophic guilds we selected the following categories: phytophagous, predators, scavengers and (sapro) xylophagous (ROTHERAY, 1993, SPEIGHT, 2006). The number of species in each genus was then split between inclusions in Baltic amber and sedimentary footprints. The resulting table was subjected to a chi-squared test which led to an overall $p < 0.05$, showing that Baltic forest populations differed statistically from those in probably more open environments, accumulated in sediments from lacustrine or fluvial origins. To specify the contribution of each guild, a partition of the crossed table was made. The results are as follows:

phytophages / scavengers ($p=0.707$)

phytophages / scavengers / sapro-xylophages ($p=0.548$)

herbivorous / scavenger / sapro-xylophages / predators ($p=0.002$)

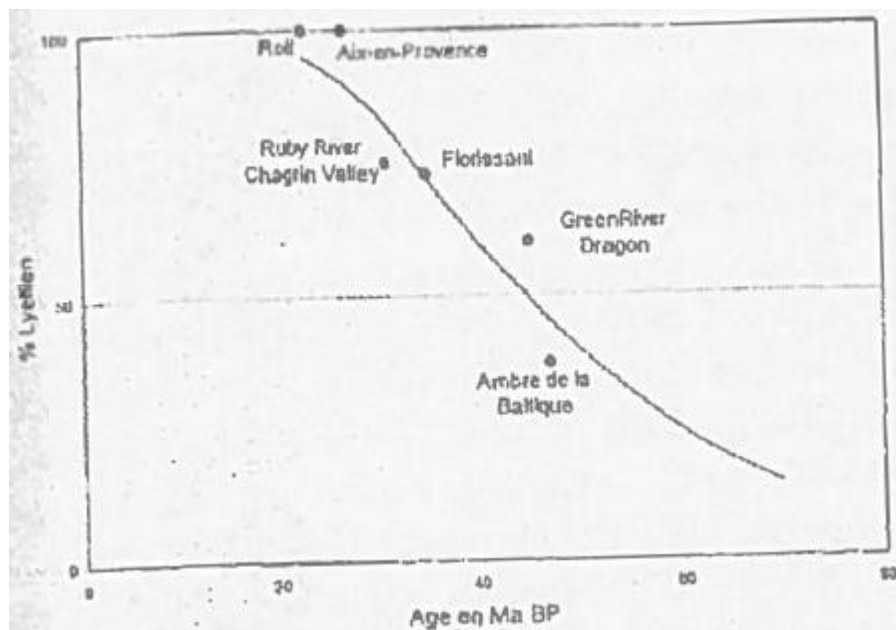
It can be seen that only the third partition is significant at the <0.01 threshold. On the other hand, the addition of detritivores to the phytophages, and of the sapro-xylophages suggest that, for syrphids, there is no association between these trophic guilds and the biocenoses concerned. These results therefore seem to confirm that the palaeoenvironments of the fluvio-lacustrine deposits were undoubtedly considerably distinguishable from the Baltic amber forests. Despite the fact that the numbers at the base of the analysis are relatively modest, and trapping conditions and taphonomic processes were different in sedimentary rocks and resins (MARTINEZ-DELCLOS et al., 2004), the lessons of the comparison appear to us nevertheless to be valid.

5.3. Lyellian curves

The Lyellian percentage of a fossil assemblage corresponds to the proportion of the taxa that compose it that has survived until the present time. This rate can be represented graphically according to the geological age of the faunas considered: the plot of the curves illustrates the decrease of the number of modern taxa when one goes back in time. The method is based on the assumption that the samples taken into account are each statistically representative of the faunal composition at the time the deposit was formed. The curves obtained from several palaeontological samples dated as precisely as possible by independent methods provide an approximate estimate of the taxonomic longevity of the groups studied and make it possible to evaluate variation of extinction rates, either between taxa of different groups, or regionally. The half-life of the taxonomic groups studied corresponds to the age at which exactly half has survived to recent times. The relationship between this value and taxonomic longevity has been the subject of much speculation, summarized in particular by GILLESPIE & RICKLEFS (1979), PEASE (1987) and LEVINTON & FARRIS (1987). Compared to the technique of determining the lifespan from the dates of first and last appearance of a taxon in a stratified series, the Lyellian method is often more reliable and easier to apply (LABANDEIRA & SEPKOSKI, 1993). For Syrphidae this is the only possible approach, no data being available relating to the intervals separating the appearance and extinction of any fossil taxon.

Lyellian curves have been used to study the life span of bivalves and gastropods in Japan and California (STANLEY et al., 1980, STANLEY, 1985) and Plio-Pleistocene mammals in Europe (STANLEY, 1979). As the age of these faunas does not rise beyond 15 Ma and some of them include marine organisms whose longevity is much greater than that of insects, the taxa retained were of the species level. The fidelity of the results obtained by means of the Lyellian curves will obviously depend on the number of faunas and their numbers [of spp]. With regard to Syrphidae, the data available to us are rather modest in this respect. We have nonetheless established a provisional graph of Lyellian percentages for 8 faunas each comprising 4 to 19 genera. The importance of the time intervals separating the studied samples with respect to the specific rapid renewal (~ 2 Ma), encourages us to use the genera. Despite the sparse information that is used as support, the Lyellian percentage reflects a regular variation according to the age of the deposits. From 37%

in the Lutetian, the proportion of genera that have survived so far reaches 100% between the Chattian and Aquitanian. The rare known fossil Syrphidae from later eras (Lower Eocene, Upper Cretaceous) have not yet been described and their scarcity would not allow us anyway to take them into consideration to clarify the plot of the graph. While a relationship between the Lyellian percentage and the age of the faunas is evident, the small number of samples and their numbers do not, however, allow for precise conclusions about the dynamics over time. The assumption of a linear relationship ($r = -0.95$, ie a <0.01) does not allow extrapolation to older age groups. We have therefore substituted a logistic approach to take account of the probable decrease of the slope in more distant times. The fit was obtained by the maximum likelihood, calculated by Marquardt's algorithm (Figure 5).



[Figure 5. Lyellian genus curve for the 8 most important sites, Logistic approximation by Marquardt algorithm. The half-life is ± 45 Ma.]

Lyellian percentages can further contribute to assessing the average longevity of taxa. We have already recalled the notion of half-life that can be conventionally represented by T_{50} . The corresponding lifetime will be denoted $D = k \cdot T_{50}$ where k is a factor that depends on the model chosen (PEASE, 1987). If we accept that the extinction rate is constant and follows a Poisson distribution, $k = 1.44$ which corresponds to an average life of about ± 60 Ma for the genera of the Syrphidae.

5.4. Seriation

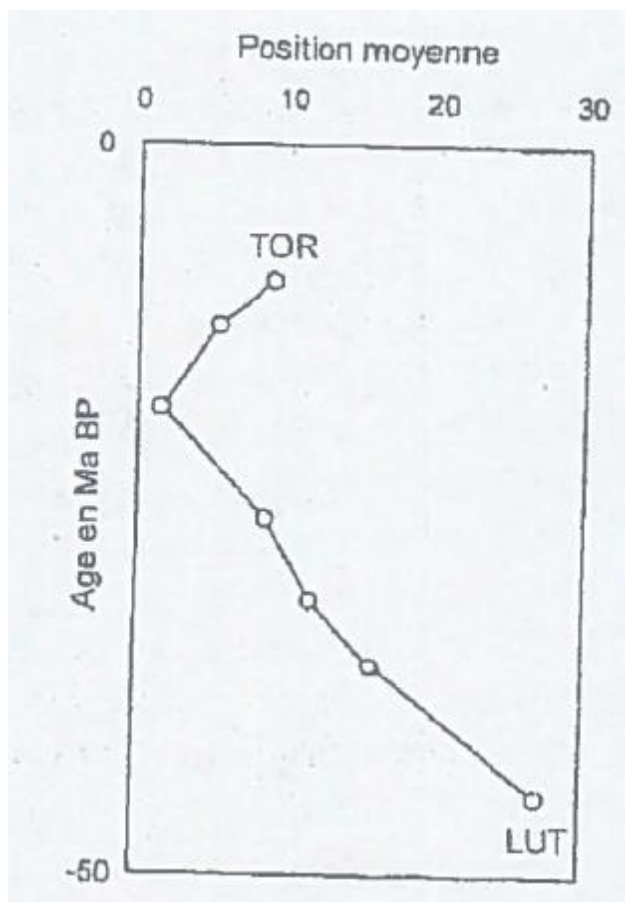
Seriation techniques, long known in archeology, are used in palaeontology to order the fossiliferous layers in a temporal sequence based on the witnesses of the past that are present there. The implementation involves numerical methods that interpret any fossil sample of a given site as a collection of taxa that lived in a certain biome at the same time. Each of these three elements is, in essence, subject to variation introducing a more or less important error term. Thus, the number of preserved taxa corresponds to only a variable part of the actual biodiversity and the spatial and temporal coverage of the samples is often random. Seriation is based on the analysis of a presence/absence matrix where rows and columns correspond to taxa and sites. A simple algorithm makes it possible to group presences along the diagonal of the matrix. This concentration is measured by an index whose value is 1.0 when the seriation is perfect. The technique was applied to the data matrix including the presence/absence of the 39 fossil genera in each of

the 7 geological stages where syrphids were recognized. We have used stratigraphic constraint, which amounts to taking into account the geochronological scale, thus imposing on each site a temporal sequence in the final matrix (BROWER & KILE, 1988, HAMMER et al., 2001).

Genres	TOR	SRV	BUR	CHT	RUP	PRB	LUT
Copestylum							
Helophilus							
Microdon							
Spilonyia							
Platycheirus							
Epistrophe							
Temnostoma							
Merodon							
Syrphus							
Eristalis							
Archisyrphus							
Rhingia							
Tropidia							
Myolepta							
Cheilosia							
Pipiza							
Archalia							
Cacogaster							
Sphegina							
Leucozona							
Protochrysotoxum							
Orthonevra							
Asarkina							
Pseudosphegina							
Pseudopipiza							
Cheilosialepta							
Praeptilocephala							
Liomyodia							
Protorhingia							
Palaeosphegina							
Megaxylota							
Spheginascia							
Eoxylota							
Volucella							
Xylotosyrphus							
Palaeoascia							
Palaeoeristalis							
Criorhina							
Palaeopipiza							

[Figure 6. Seriation of the 39 genera of fossil Syrphidae. The application of a stratigraphic constraint forced the columns to respect the chronological order of the stages. The association criterion obtained by Monte Carlo simulation is $C \sim 0.879$.]

The result of the seriation of the matrix is shown in Figure 6. The criterion measuring the concentration of presences along the diagonal is 0.879. The average position of the presences in the different stages has been plotted on a graph according to the average age of each one (Figure 7). Despite the relatively small number of syrphids in resins and sedimentary deposits, a correlation seems obvious. However, too many hiatuses in the fossil record, already noted by many palaeontologists, often hinder an accurate overall analysis of biochronological gradients.



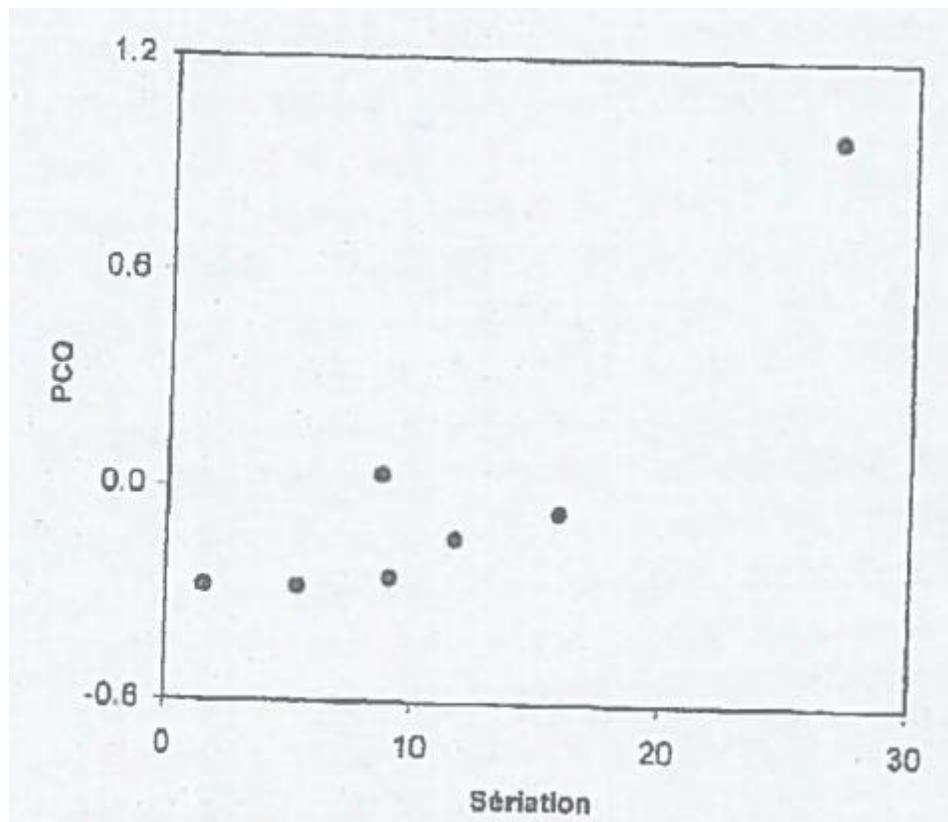
[Figure 7. Average position of the stages selected for seriation in relation to the average age of each of them.]

We also compared the result of seriation with the conventional methods of multivariate analysis of the presence / absence table, in particular principal coordinate analysis (PCO). The calculation was done on a distance matrix using the Gower metric. The percentage of inertia of the first main axis is 38.13% representing the share of the total variance taken into account. Figure 8 shows the comparison of the seriation with the first axis of the principal coordinate analysis. This graph shows a close relationship between the average positions of the stages extracted from the seriation and the first main axis: the correlation coefficient of Kendall is $T = 0.62$ ($p = 0.05$). Although based on a small number of data, this correspondence indicates that the same type of pattern of underlying palaeobiological phenomena is evidenced by the two techniques used.

6. Conclusions

Despite the relatively high number of known fossil Syrphids, compared to other Brachyceran families, their study is still in its infancy and the integration of our knowledge of present and past fauna has not begun.

Given the doubts surrounding the identification of many taxa at the genus and species levels, it is not currently possible to recognize with certainty the monophyletic groups and to identify evolutionary trends. Similarly, inferences about the composition of fossil insect communities and their trajectory over time can only be conjectural, as can the role of syrphids in past ecosystems.



[Figure 8. Comparison of the result of the serialization with the value of the first axis of a principal coordinate analysis (PCO) of the matrix genera / stages. Note that the correlation between the two approaches is very good ($T = 0.62$, $p = 0.05$).]

Although the ancestral biology of Syrphidae and the ecophysiological pathways of tribes and genera since their first appearance remain unknown, the family ranks fourth among the Brachycera for species richness, and showed remarkable rates of diversification as well as evolutionary plasticity. The wide variety of reproductive and behavioural strategies, however, makes it difficult to identify the biotic and abiotic factors that have played a catalytic role in the genesis of the modern fauna. The construction of phylogenetic trees incorporating fossil taxa would help to clarify and explore testable hypotheses. In this view, however, it can not be ruled out that certain monophyletic groups, while retaining globally the characteristic attributes of the lineage, have acquired a different ecological silhouette.

The taking into account of fossils to establish or specify the stages of evolution traditionally involves the direct comparison of morphological and anatomical structures with those of their current counterparts. In most sediment samples, however, these characters are often altered or obliterated and therefore difficult to use in practice. Reading the descriptions of fossil syrphids shows that their generic attribution often proceeds from a generally implicit comparison with a current taxon. Several new techniques open up interesting perspectives in this field. They should contribute to highlighting the detail and fine structure of the essential elements of the cuticle, thereby broadening the range of usable phenotypic traits and thus further specifying generic characters. The inclusions in resins, for their part, faithfully preserve the details, including those of the internal tissues, and thus constitute privileged witnesses of the past, likely to contribute to phylogenetic studies. Two promising techniques have recently been applied to the study of insects and spiders of amber. Firstly, confocal laser-scanning microscopy allows us to observe morphological structures with very high magnification and considerable depth of field. The results are

comparable to those obtained by SEM for current organisms (RUST, 2004). The second method is X-ray microtomography. This is the application to palaeontology of a technique similar to medical imaging. It provides a three-dimensional representation of a fossil sample, highlighting minute details. The method also has the advantage of being non-destructive (TAFFOREAU et al., 2006, PENNEY et al., 2007). LAK et al. (2008) have also suggested a protocol for the study of opaque amber by microradiographic examination using a synchrotron.

The analyses that we have carried out, however imprecise and provisional, nevertheless suggest some general conclusions. It appears that at the supra-generic level, the relative share of taxa belonging to the subfamilies of Syrphinae and Eristalinae has not changed significantly since the Middle Eocene. On the other hand, out of a total of 39 genera listed in palaeontological records, 21 are still part of the present fauna, provided, of course, that they have been correctly assigned. The available data are nevertheless biased in their temporal dimension: examination of Table 3 shows that 90% of the fossil samples belonging to the genera enumerated so far come from the Eocene and the Oligocene. Evidence from Miocene and Pliocene fauna are therefore almost absent. From the biological point of view, we have shown that, as early as the Lutetian, the communities living in the Baltic amber forests were probably different from those in more open areas.

In this context, the acquisition of new information on the available samples is as important as the discovery of new fossil taxa obtained during excavation campaigns. The latter should concern, wherever possible, territories and epochs that have not yet been the subject of palaeontological research. With the exception of a single citation of Dominican amber, all fossil syrphid samples come from 60% sedimentary facies in the Rocky Mountains in North America and Europe and 40% from amber of the Baltic. Over the past decade, large deposits of Cretaceous amber (Turonian) from New Jersey have been studied, notably by GRIMALDI et al. (2000). In France, several recent excavation campaigns have led to the harvest of an abundant and varied entomological fauna, still under study. The main sites explored are Céreste and Asson wood (Middle Oligocene), Alès (Upper Eocene) and Oise amber (Lower Eocene) (NEL, pers. comm 2008). In Charente Maritime, an amber deposit (Albian terminal) has already collected 44 specimens of Brachycera (NÉRAUDEAU et al., 2002). NEL et al. (2004) published a summary of the amber deposits in France. At the present time, all known material is therefore practically limited to the Holarctic region. In the tropical zone, Myanmar amber, which probably dates from the Turonian-Cenomanian, has a rich insect fauna, of which the Diptera represent 40% (GRIMALDI et al., 2002). In addition, a Miocene-age deposit located in the Amazon basin (Tamshiyacu, Peru) identified, among other things, 13 families of hexapods embedded in fossilized resin blocks (ANTOINE et al. 2006). So far, however, no Syrphidae has been reported collected in all the sites mentioned, all of which have not yet been studied.

In the discussion of individual sites, we pointed out a number of issues that would merit further consideration. The points that should be clarified in priority relate in particular to the real identity of the palaeontological genera as well as their position within tribes. This approach should be based on a re-examination of the types, as long as they are still extant and localisable, in the light of current conceptions of syrphid systematics. Many of the family's fossil specimens are probably held in palaeontological collections around the world without any scrutiny. Two recent publications list, for the main European museums, the number of arthropods included in amber (BAKER et al., 2003, HAENNI, 2003). As far as Baltic amber is concerned, the large Königsberg collections were largely scattered during the Second World War. Subsequently, specimens may have been transferred to other institutions, including the Institute und Museum of Geology and Palaeontology in Göttingen and the Museum für Naturkunde, Humboldt Universität in Berlin. More than forty years ago, HENNIG (1965) already underlined the lack of interest of the dipterists of his time in the study of fossil fauna. This remark is still relevant. We therefore invite taxonomists interested in advances in evolutionary biology to resume the analysis of available fossil samples in a broader perspective, including aspects related to phylogeny and biogeography.

8. Acknowledgments

The author wishes warmly to thank Danielle Decrouez for her wise counsel on many points concerning the palaeontological aspects of this note. His gratitude also goes to his colleague Jean-Paul Haenni (Neuchâtel) who kindly made available samples of hoverflies in amber. The remarks of several colleagues have significantly improved the presentation of the manuscript. I would especially like to thank André Nel (Paris) for his many constructive comments and suggestions as well as Lionel Cavin (Geneva) and Bernhard Merz (Geneva) for discussions.

9. References

Popov GV (2015) Syrphidae from the Cretaceous - refuted ? p.47 in Humphrey-Patton H & Mengual X (eds), Abstracts of the 8th Int Symp on the Syrphidae, Monschau, Germany.

9. Références
- AMORIM DE SOUZA D. & SILVA V. C., 2002.- How far advanced was Diptera evolution in the Pangea ? *Annales de la Société Entomologique de France*, 38: 177-200.
- ANDERSEN A. N., 1995.- Measuring more of biodiversity: genus richness as a surrogate for species richness in Australian ant faunas. *Biological Conservation*, 73: 39-43.
- ANTOINE P.-O. *et al.*, 2006.- Amber from western Amazonia reveals Neotropical diversity during the middle Miocene. *Proceedings of the National Academy of Sciences of the USA*, 103: 13555-13600.
- ARCHIBALD S. B. & MATHEWS R. W., 2000.- Early Eocene insects from Quilchena, British Columbia, and their paleoclimatic implications. *Canadian Journal of Zoology*, 78: 1441-1462.
- ARNETT R. H., Jr., 2000.- American insects. A handbook of the insects of America North of Mexico. CRC Press, Boca Raton. XVII+1003 pp.
- ATKINSON T. C., BRIFFA K. R. & COOPE G. R., 1987.- Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature*, 325: 587-592.
- BAILEY I. W. & SNOODT E. W., 1915.- Botanical index of Cretaceous and Tertiary climates. *Science*, 41: 831-834.
- BAILEY I. W. & SNOODT E. W., 1916.- The climatic distribution of certain types of angiosperm leaves. *American Journal of Botany*, 3: 24-29.
- BAKER R. A., CHMIELEWSKI W. & EYENNETT P. J., 2003.- Amber inclusions of arthropods (particularly insects and mites) in European museums - documentation and photography. *Acta zoologica cracoviensis*, 46: 399-405.
- BALMFORD A., JAYASURIYA A. H. M. & GREEN M. J. B., 1996.- Using higher-taxon richness as a surrogate for species richness: II. Local applications. *Proceedings of the Royal Society of London*, B 263: 1571-1575.
- BECKER H. F., 1961.- Oligocene plants from the upper Ruby River Basin, southwestern Montana. *Geological Society of America Memoir*, 82: 1-127.
- BILLIPS K. & SCHMIDT D. P., 2002.- Paleotemperatures and ice volume of the past 27 Myr revisited with paired Mg/Ca and ¹⁸O/¹⁶O measurements on benthic foraminifera. *Paleoclimatology*, 17: 1-11.
- BOCHERENS H., FRIS E. M., MARIOTTI A. & PEDERSEN K. R., 1994.- Carbon isotopic abundances in Mesozoic and Cenozoic fossil plants: paleoecological implications. *Lethaia*, 26: 347-358.
- BRADLEY W. H., 1931.- Origin and microfossils of the oil shale of the Green River formation of Colorado and Utah. *United States Geological Survey, Professional Paper*, 168: 1-58.
- BROWER J. C. & KILE K. M., 1988.- Senation of an original data matrix as applied to paleoecology. *Lethaia*, 21: 79-93.
- BROWN R. W., 1934.- The recognizable species of the Green River flora. *United States Geological Survey, Professional Paper*, 185-C: 45-77.
- BUFFETAUT E., 1984.- Selective extinctions and terminal Cretaceous events. *Nature*, 310: 276.
- CARPENTER F. M., 1992.- Superclass Hexapoda. In: Kessler, R. L. (ed.). *Treatise on invertebrate paleontology* (R), Arthropoda 4. Geological Society of America, Boulder. XXII+655 pp.
- CARPENTER F. M. & BURNHAM L., 1985.- The geological record of insects. *Annual review of Earth and Planetary Science*, 13: 297-314.
- COCKERELL T. D. A., 1906.- Fossil Hymenoptera from Florissant, Colorado. *Bulletin of the Museum of Comparative Zoology, Harvard College*, 50: 33-58.
- COCKERELL T. D. A., 1920.- Eocene insects from the Rocky Mountains. *Proceedings of the United States National Museum*, 57: 233-260.
- COFFIARD C., GOMZ B., NEL A. & THÉVENARD F., 2004.- Application de la méthode de parsimonie de Wagner à l'étude systématique de flores de l'Étarien et du Cénomannien de l'Europe. *Annales de Paléontologie*, 90: 175-186.
- COFFIARD C. *et al.*, 2008.- Application of the Wagner parsimony method in fossil plant assemblages from the Cretaceous of Europe. *Review of Palaeobotany & Phytology*, 148: 1-12.
- FRANK M. S., 2002.- Holarctic bees from the Eocene-Oligocene boundary of Florissant, Colorado (Hymenoptera: Halictidae). *Neuer Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 225: 251-273.
- EVENHUIS N. L., 1994.- Catalogue of the fossil flies of the world (Insecta: Diptera). Backhuys Publishers, Leiden. 600 pp.
- FARA E., 2000.- Diversity of Cretaceous-Eocene (Middle Jurassic-Eocene) tetrapod families and selectivity of extinctions at the K/T boundary. *Geobios*, 33: 387-396.
- FOOTE M., 1996.- Perspective evolutionary patterns in the fossil record. *Evolution*, 50: 1-11.
- GALL J.-C., 1995.- Biofilms et matras microbiens: leur contribution à la sédimentogénèse. *Comptes rendus de l'Académie des Sciences de Paris*, (II)321: 823-835.
- GALL J.-C., DURINGER P., KRIMBEN W. & PAICHLER J.-C., 1994.- Impact des écosystèmes microbiens sur la sédimentation. *Paleo-geography, Paleoclimatology, Paleoecology*, 111: 17-28.
- GILLESPIE J. H. & REICHERT R. E., 1979.- A note on the estimation of species duration distributions. *Paleobiology*, 5: 60-62.
- GRADSTEIN F. M. & OGG J., 1996.- A Phanerozoic time scale. *Eos*, 19: 3-5.
- GRADSTEIN F. M., OGG J. & SMITH A. G., (eds), 2005.- A geologic time scale 2004. Cambridge University Press, Cambridge. 589 pp.
- GRAHAM A., 1999.- Late Cretaceous and Cenozoic history of North American vegetation, north of Mexico. Oxford University Press, New York. XVIII+350 pp.
- GRECO C. F., 1995.- Fenología y selección de hábitat de las especies de sírfidos afidófagos (Dipt.: Syrphidae) más frecuentes en cultivos cereales y forrajeros en la Provincia de Buenos Aires. *Entomophaga*, 40: 317-320.
- GRECO C. F., 1998.- Sírfidos afidófagos (Diptera, Syrphidae): identificación rápida a campo de estados preiniciales y lista de enemigos naturales de las especies más frecuentes en cereales y forrajeros en la provincia de Buenos Aires (Argentina). *Acta entomológica Chilena*, 22: 7-11.
- GREENWOOD D. R., 2005.- Leaf form and the reconstruction of past climates. *New Phytologist*, 166: 355-357.
- GREGORY K. M. & CHASE C. G., 1991.- Tectonic significance of paleobotanically estimated climate and altitude of the late Eocene erosion surface, Colorado. *Geology*, 20: 583-585.
- GRIMALDI D., 1993.- The care and study of fossiliferous amber. *Curator*, 36: 31-49.
- GRIMALDI D., 2001.- Insect evolutionary history from Handlirsch to Hennig, and beyond. *Journal of Paleontology*, 75: 1152-1160.
- GRIMALDI D., (ed.) 2000.- Studies of fossils in amber, with particular reference to the Cretaceous of New Jersey. Backhuys, Leiden. 504 pp.
- GRIMALDI D. A., ENGEL M. S. & NASCIMBENE P. C., 2002.- Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Neotomas*, 3361: 1-71.
- HAENNI J.-P., 2003.- Fossil Diptera in Baltic amber: the collection of the Muséum d'histoire naturelle de Neuchâtel. *Acta Zoologica cracoviensis*, 46 (suppl.-Fossil Insects): 407-410.
- HAENNI J.-P. & PERRENOD J.-B., 1998.- Ambrax: la collection d'inclusions fossiles dans l'ambre du Muséum d'histoire naturelle de Neuchâtel. I. Techniques de préparation des inclusions (pp. 135-141). Ville de Neuchâtel, Bibliothèques et Musées. Neuchâtel.
- HAMMER Ø., HARPER D. A. T. & RYAN P. D., 2001.- PAST: Paleontological statistics software package for education and data analysis. *Paleontologia electrónica*, 4: 1-9.

- HARDINGI, C. & CHANG, L. S., 2000.- Self-sedimented diatom mats as agents of exceptional fossil preservation in the Oligocene Florissant beds, Colorado, United States. *Geology*, 28: 195-198.
- HANTLEY, J. C., 1963.- A taxonomic account of the larvae of some British Syrphidae. *Proceedings of the Zoological Society of London*, 136: 505-573.
- HEER O., 1849.- Die Insektenfauna der Tertiärgebilde von Geringen und von Radoboj in Croatien. Zweite Teil: Heuschrecken, Florfliegen, Aderflügler, Schmetterlinge und Fliegen. W. Engelmann, Leipzig. IV+264 pp.
- HEER O., 1864.- Die Urwelt der Schweiz. F. Schulthess, Zürich. XXIX+623 pp.
- HEIZMANN E. P. J., 1983.- Die Gattung *Caenotherium* (Caenotheridae) in *Orkneyium* und *Astracium* Süddeutschlands. *Eclogae Geologicae Helveticae*, 36: 781-825.
- HENNIG W., 1965.- Die Acalyptrotaxae des Baltischen Bernstein und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Dipteren-Gruppe. *Stuttgarter Beiträge zur Naturkunde*, 145: 1-215.
- HENNIG W., 1981.- *Insect phylogeny*. John Wiley & Sons, Chichester. XXII+514 pp.
- HEYDEN C. H. O., von, 1859.- Fossile Insekten aus der Rheinischen Braunkohle. *Palaeontographica*, 8: 1-15.
- HEYDEN L. F. G. D., von, 1870.- Fossile Dipteren aus der Braunkohle vom Rott im Siebengebirge. *Palaeontographica*, 17: 237-266.
- HIPP H., 1978.- Classification of Xylotini (Diptera, Syrphidae). *Acta Zoologica Fennica*, n° 156: 1-153.
- HULL F. M., 1945.- A revisional study of the fossil Syrphidae. *Bulletin of the Museum of Comparative Zoology*, 45: 251-355.
- HULL F. M., 1949.- The morphology and inter-relationship of the genera of syrphid flies, recent and fossil. *Transactions of the Zoological Society of London*, 26: 257-408.
- HULL F. M., 1960.- A new genus and four new species of fossil Diptera from Montana and Colorado. *Contributions from the Museum of Paleontology*, 15: 269-279.
- JOHNSON K. R. & HICKY L. J., 1990.- Megafossil change across the Cretaceous/Tertiary boundary in the northern Great Plains and Rocky Mountains, U.S.A. *Geological Society of America, Special Paper*, 247: 433-444.
- KATZOLAKIS A., PURVIS A., AZMIZ S., ROTHERAY G. & GILBERT F., 2001.- Macroevolution of hoverflies (Diptera: Syrphidae): the effect of using higher-level taxa in studies of biodiversity, and correlates of species richness. *Journal of Evolutionary Biology*, 14: 219-227.
- KHILBACH R., 1982.- Bibliographie und Liste des Arten tiercher Einschlüsse in fossilen Harzen sowie ihren Aufbewahrungsorte. Teil 2. *Deutsche Entomologische Zeitschrift, N.F.*, 29: 301-491.
- KITCHING R. L., 2001.- Food webs in phytoselmatas: "bottom-up" and "bottom-down" explanations for community structure. *Annual Review of Entomology*, 46: 729-760.
- KNOWLTON F. H., 1916.- Review of the fossil plants in the United States National Museum from the Florissant lake beds at Florissant, Colorado, with descriptions of new species and list of type specimens. *Proceedings of the United States National Museum*, 51: 241-297.
- KNOWLTON F. H., 1923.- Revision of the flora of the Gros River formation with descriptions of new species. *United States Geological Survey, Professional Paper*, 131-F: 133-182.
- KNUTSON L. V., THOMPSON F. C. & VOCKEROTH J. R., 1975.- Family Syrphidae (pp. 307-374). In: Delfinado, M. D. & Hardy, D. E. (eds) *A Catalog of the Diptera of the Oriental Region*. The University Press of Hawaii, Honolulu. IX+459 pp.
- KOTTICOFF U. & SCHMID U., 2005.- A new hoverfly (Insecta, Diptera: Syrphidae) from the Randeck Maar (Early Miocene, South-West Germany). *Palaeontology*, 48: 1091-1096.
- KOYALEV V. G., 1979.- Main aspects of evolution of Diptera Brachycera in the Mesozoic era (pp. 56-59). In: Skarlato, O. A. (ed.) *Systematics of Diptera (Insecta). Ecological and morphological principles*. Amerind Publishing Co., New Delhi. VIII+185 pp.
- KOWALSKI E. A. & DILCHER D. L., 2003.- Warmer paleotemperatures for terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the USA*, 100: 167-170.
- KRZEMINSKA E. & KRZEMINSKI W., 1992.- Les fantômes de l'ambre. Musée d'Histoire naturelle de Neuchâtel, Neuchâtel. 142 pp.
- LA PERLA B., TAPLIN J., OCKWELL D. & LOVETT J. C., 2002.- Continental scale patterns of biodiversity: can higher taxa accurately predict African plant distributions? *Botanical Journal of the Linnean Society*, 138: 225-235.
- LABANDEIRA C. C. & SEPKOski J. J. JR., 1993.- Insect diversity in the fossil record. *Science*, 261: 310-315.
- LABANDEIRA C. C., JOHNSON K. R. & WILF P., 2002.- Impact of the terminal Cretaceous event on plant-insect associations. *Proceedings of the National Academy of Sciences of the USA*, 99: 2061-2066.
- LAK M. et al., 2008.- Phase contrast X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber. *Microscopy and Microanalysis*, 14: 251-259.
- LANDISHEIM J. H., 2003.- *Plant resins. Chemistry, evolution, ecology, and ethnobotany*. Timber Press, Portland. 586 pp.
- LAUSSON S. G., 1978.- Baltic amber - a palaeobiological study. *Entomograph*, 1: 1-192.
- LEE M. S. Y., 1997.- Documenting present and past

- biodiversity: conservation biology meets palaeontology. *Trends in Ecology and Evolution*, 12: 132-133.
- LEOPOLD E. B. & MACGINNIE H. D., 1972.- Development and affinities of Tertiary forests in the Rocky Mountains (pp. 147-200). In: Graham, A. (ed.) Floristics and paleofloristics of Asia and eastern North America. Elsevier Publishing Co, Amsterdam. XII+278 pp.
- LEVINTON J. S. & FAIRBIE J. S., 1987.- On the estimation of taxonomic longevity from Lyellian curves. *Paleobiology*, 13: 479-483.
- LEWIS S. E., 1972. A new species of fossil *Tropidix* (Diptera: Syrphidae) from the Ruby River basin (Oligocene) of southwestern Montana. *Annals of the Entomological Society of America*, 66: 487-488.
- LINNAEUS C., 1758.- *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus 1 (ed. X). L. Salvii, Holmiae. 824 pp.
- LOEW H., 1850.- Ueber den Bernstein und die Bernsteinfauna. *Programme der Königl. Realchule zu Merseburg*: 1-44.
- LOEW H., 1861.- Ueber die Dipterenfauna des Bernsteins. *Amlicher Berichte über die Versammlung Deutscher Naturforscher*, 35: 88-98.
- MACGINNIE H. D., 1953.- Fossil plants of the Florissant beds, Colorado. *Carnegie Institution of Washington, Publication 599*: 1-198.
- MAI D. H., 1995.- Tertiary Vegetationsgeschichte Europas - Methoden und Ergebnisse. Gustav Fischer, Jena. 691 pp.
- MARTÍNEZ-DELCLÓS X., BRUGS D. E. G. & PERALVER E., 2004.- Taphonomy of insects in carbonates and amber. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 103: 19-64.
- MAZÁNEK L., LÁSKA P., BÍČEK V. & NOVOTNÝ R., 2001.- Descriptions with key to the third larval stage and puparia of the genus *Epirhyne* s.str. (Diptera: Syrphidae). *Acta Universitatis Carolinae, Biologica*, 45: 115-128.
- MCINTOSH W. C., GRISMAN I. W., CHAPIN C. E., KUNK M. J. & HENRY C. D., 1992.- Calibration of the latest Eocene-Oligocene geomagnetic polarity time scale using $^{40}\text{Ar}/^{39}\text{Ar}$ dated ignimbrites. *Geology*, 20: 459-463.
- MCLERUY C. A. & ANDERSON B. Y., 1966.- Laminations of the Oligocene Florissant lake deposits, Colorado. *Geological Society of America Bulletin*, 77: 605-618.
- MENGUAL X., STÄHLI G. & EGJO S., 2008.- First phylogeny of predatory flower flies (Diptera, Syrphidae, Syrphinae) using mitochondrial COI and nuclear 28S rRNA genes: conflict and congruence with the current tribal classification. *Chadronia*, 23: 1-20.
- MEUNIER F., 1899.- Révision des Diptères fossiles types de Loew conservés au Musée Provincial de Königsberg. *Miscellanea entomologica*, 7: 169-182.
- MOE A., 2005.- The fascinating world of fossil insects: a brief look at the Florissant formation. *American Paleontologist*.
- MOR A. P. & SMITH D. M., 2005.- Using pre-Quaternary Diptera as indicators of paleoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 221: 203-214.
- MÖHRIG W. & RÖSCHMANN H., 1994.- Revision der Trauemückenarten von Loew und Meunier aus dem Baltischen Bernstein (Diptera, Sciandae). *Deutsche Entomologische Zeitschrift, N.F.*, 41: 79-136.
- MÖHS T., 1996.- Die Skulpturen der oberoligozänen Fossilagerstätte Rott bei Bonn (Rheinland). *Decheniana*, 149: 205-232.
- MÖHRIG W. & UTECHER T., 1997.- The coexistence approach - a method for quantitative reconstruction of Tertiary terrestrial palaeoclimate data using plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 134: 61-86.
- MÜLLER-MÜTZFELD G., 1984.- Indikation und Zeitmass von Feuchtenveränderungen am Beispiel der Laufkäfer (Insecta, Coleoptera, Carabidae). *Biologische Rundschau*, 77: 163-178.
- NASCIMBENE P. C. & SILVERSTEIN H., 2000.- The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions (pp. 92-102). In: Grimaldi, D. (ed.) *Studies of fossils in amber, with particular reference to the Cretaceous of New Jersey*. Backhuys, Leiden. 504 pp.
- NEL A., 1997.- The probabilistic inference of unknown data in phylogenetic analysis (pp. 305-327). In: Grandcolas, P. (ed.) *The origin of biodiversity in insects: phylogenetic tests of evolutionary scenarios*. Muséum national d'histoire naturelle, Paris. 354 pp.
- NEL A., DE FLOËI G., MILLET J., MEUNIER J.J. & WALLER A., 2004.- The French amber: a general conspectus and the Lowermost Eocene amber deposit of Le Quesnoy in the Paris Basin. *Geologica Acta*, 2: 1-94.
- NEL A., NEL J., MASSELOT G. & THOMAS A., 1998.- An investigation into the application of the Wagner parsimony method in synecology. *Biological Journal of the Linnean Society*, 65: 165-189.
- NÉRALDEAU D. et al., 2002.- Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archampsay (Charente-Maritime, France). *Geobios*, 35: 233-240.
- NICHOLS D. J. & JOHNSON K. K., 2006.- *Plants and the K-T boundary*. Cambridge University Press, Cambridge. X+280 pp.
- OBENBERGER J., 1957.- Eine neue Buprestidenart aus dem baltischen Bernstein nebst Bemerkungen über einige fossile Buprestiden. *Beiträge zur Entomologie*, 7: 308-315.

- PANTIC N. K., 1992.- Ober die vergessenen samnatischen Floren Radoboj und Sused, ihre paläophytogeographische und biostratigraphische Bedeutung (pp. 205-210). In: Kovar-Eder, J. (ed.). Palaeovegetational development in Europe. Naturhistorisches Museum, Wien. 430 pp.
- PLASE C. M., 1987.- Lyellian curves and mean taxonomic durations. *Paleobiology*, 13: 484-487.
- PEÑALVER E., 1996.- Técnicas y métodos de obtención, preparación, conservación y estudio de insectos fósiles. *Boletín de la Sociedad Entomológica Aragonesa*, 16: 157-174.
- PENNEY D. et al., 2007.- First fossil Microphallidommatidae (Arisea), imaged in Eocene Paris amber using X-Ray computed tomography. *Zootaxa*, 1623: 47-51.
- PÉREZ-BARÓN C., ROTHIRAY G., HANCOCK E. G., MARTÍN-GARCÍA M. A. & ZUMBADO M., 2003.- Immature stages and breeding sites of some Neotropical saprophagous syrphids (Diptera: Syrphidae). *Annals of the Entomological Society of America*, 96: 458-471.
- PODINAS S., 2003.- *Dactylosia* crane flies (Diptera: Limoniidae) in Baltic amber (Eocene). *Proceedings of the Academy of Natural Sciences of Philadelphia*, 153: 49-65.
- POINAR G. O. JR., 1993.- Insects in amber. *Annual review of Entomology*, 46: 145-159.
- POINAR G. O. JR. & POINAR R., 1999.- The amber forest. A reconstruction of a vanished world. Princeton University Press, Princeton. XVIII+239 pp.
- PONGRÁCZ A., 1928.- Die fossilen Insekten von Ungarn, mit besonderer Berücksichtigung der Entwicklung der Europäischen Insekten-Fauna. *Annales Historico-Naturales Musei Nationalis Hungarici*, 25: 91-194.
- RALP D. M., 1979.- Bites in the fossil record of species and genera. *Bulletin of the Carnegie Museum of Natural History*, 13: 85-91.
- RAUP D. M. & SEPKOSKI J. J. JR., 1986.- Periodic extinction of families and genera. *Science*, 231: 833-836.
- REICH P. B., ELLSWORTH D. S. & WALTERS M. B., 1999.- Generality of leaf trait relationships: a test across six binomes. *Ecology*, 80: 1955-1969.
- RIECKOWSKI S., 1997.- K-Ar Altersbestimmungen der Bernsteinführenden Sedimente des Saarländes (Paläogen, Bezirke Kalmningrad). *Mitteilungen der Naturwissenschaften*, B 64: 1-18.
- RÖDER G., 1980.- Ein neue *Chelonic*-Art aus Baltischem Bernstein mit REM-Untersuchungen rezenter Arten. *Stuttgarter Beiträge zur Naturkunde*, B 64: 1-18.
- ROHLER H. W., 1992a.- Correlation, composition, areal distribution, and thickness of Eocene stratigraphic units, greater Green River basin, Wyoming, Utah, and Colorado. *United States Geological Survey, Professional Paper*, 1506-E: 1-49.
- ROHLER H. W., 1992b.- Description and correlation of Eocene rocks in stratigraphic reference sections of the Green River and Washakie basins, southwest Wyoming. *United States Geological Survey, Professional Paper*, 1506-D: 1-83.
- ROHLER H. W., 1993.- Eocene climates, depositional environments, and geography, greater Green River basin, Wyoming, Utah, and Colorado. *United States Geological Survey, Professional Paper*, 1506-F.
- RÖSCHMANN F. & MOHRIG W., 1995.- Die Trauermücken des Sächsischen Buntsandsteins aus dem Untermiozän von Butterfeld/Deutschland. *Deutsche Entomologische Zeitschrift, N.F.*, 42: 17-54.
- ROSS A. J. & JARZEMBOWSKI E. A., 1993.- Arthropoda (Hexapoda, Insecta) (pp. 363-426). In: Benton, M. J. (ed.). The fossil record 2. Chapman & Hall, London XVII+845 pp.
- ROTHERAY G. E., 1993.- Colour guide to the hoverfly larvae (Diptera, Syrphidae) in Britain and Europe. *Dipterists Digest*, n°9: 1-156.
- ROTHERAY G. E., 1997.- Larval stages of the predatory hoverflies *Trichopsomyia flavitarsis* (Meigen), *Platychetius melanops* Loew and *Parasyrphus uigrarianus* (Zetterstedt) (Diptera: Syrphidae). *Entomologist's Gazette*, 48: 127-134.
- ROTHERAY G. E., 2003.- The predatory larvae of the *Nepenthoxyphor* species living in pitcher plants (Diptera, Syrphidae). *Studia Dipterologica*, 10: 219-226.
- ROTHERAY G. E. & GILBERT F., 1999.- Phylogeny of Palearctic Syrphidae (Diptera): evidence from larval stages. *Zoological Journal of the Linnean Society*, 127: 1-112.
- ROTHERAY G. E., ZUMBADO M., HANCOCK E. G. & THOMPSON F. C., 2000.- Remarkable aquatic predators in the genus *Oxyptamus* (Diptera, Syrphidae). *Studia Dipterologica*, 7: 383-398.
- ROYER D. L., WILF P., JAMESCO D. A., KOWALSKI E. A. & DILCHUR D. L., 2005.- Correlations of climate and plant ecology to leaf size and shape: potential proxies for the fossil record. *American Journal of Botany*, 92: 1141-1151.
- RUST J., 2004.- Paläobiologie fossiler Insekten. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie*, 14: 443-446.
- SAVIN S. M., 1975.- The history of the earth's surface temperature during the last 100 million years. *Annual review of Earth and Planetary Science*, 5: 319-355.
- SCHAEFFER B. & MANGIN M., 1965.- Fossil lakes from the Eocene. *Natural History*, 74: 10-21.
- SCHNEIDER J., 1999.- Microbial mats in terrigenous clastics: the challenge of identification in the rock record. *Palaeos*, 14: 3-12.
- SCHLEE D. & GLOCKNER W., 1978.- Bernstein. Bernsteine und Bernstein-Fossilien. *Stuttgarter*

- Beiträge zur Naturkunde, C 8: 1-72.
- SCUDER H. E., 1995.- *Holoditesa flvi* (Rotaceae): a new species of ocean spray from the late Eocene Florissant Formation. *PaleoBios*, 18: 21-24.
- SCUDER S. H., 1890.- A classed and annotated bibliography of fossil insects. *United States Geological Survey*, 69: 1-101.
- SCUDER S. H., 1891.- Index to the known fossil insects of the world, including myriapods and arachnids. *United States Geological Survey, Bulletin*, 71: 1-744.
- SEPKOSKI J. J., JR., BAMBACH R. K., RAUF D. M. & VALENTINE J. W., 1981.- Phanerozoic marine diversity and the fossil record. *Nature*, 291: 435-437.
- SERRES P. M. T., DE. 1829.- Géognosie des terrains tertiaires du Midi de la France, ou tableau des principaux animaux invertébrés des terrains marins, Tertiaires de la France. Pomplon-Durville, Montpellier. XCII+276 pp.
- SHACKLETON N. J., 1985.- Paleogene stable isotope events. *Paleogeography, Palaeoclimatology, Palaeoecology*, 57: 91-102.
- SHATALKIN A. I., 1975.- A taxonomic analysis of the hoverflies (Diptera, Syrphidae) I. *Entomologicheskoe Obozrenie*, 54: 164-175.
- SHEEHAN P. M. & HANSEN T. A., 1986.- Detritus feeding as a buffer to extinction at the end of the Cretaceous. *Geology*, 14: 868-870.
- SHEEHAN P. M., COOROUGH P. J. & FASTOVSKY D. E., 1996.- Biotic selectivity during the K/T and late Ordovician extinction events. *Geological Society of America, Special Paper*, 307: 477-489.
- SPAIR U., 1985.- Ergänzungen und Berichtigungen zu R. Keilbach's Bibliographie und Liste der Bernsteinfossilien - Ordnung Diptera. *Saugarter Beiträge zur Naturkunde*, B 111: 1-146.
- SPEIGHT M. C. D., 2006.- Species accounts of European Syrphidae (Diptera), Ferrara 2006. In: Speight, M. C. D. et al. (eds). *Syrph the Net, the database of European Syrphidae*, vol.34. *Syrph the Net publications*, Dublin. 252 pp.
- SPEIGHT M. C. D., CASTELLA E., OBRDLER P. & BALL S. G. 2001. *Syrph the Net on CD - The database of European Syrphidae*, Issue 1. *Syrph the Net Publications*, Dublin.
- STÄHLIS G., HIPPA H., ROTHIERAY G., MUONA J. & GILBERT F., 2003.- Phylogeny of Syrphidae (Diptera) inferred from combined analysis of molecular and morphological characters. *Systematic Entomology*, 28: 433-450.
- STÄHLIS G., ROTHIERAY G., HIPPA H., MUONA J. & GILBERT F. 1999. On the phylogeny of hoverflies (Diptera, Syrphidae) using molecular and morphological characters, p. 1-68. In Stähli, G. (ed.), *Systematics of Syrphidae and taxonomy of Chelidonia* (Diptera): morphological and molecular evidence. Academic Dissertation-University of Helsinki.
- STANLEY S. M., 1979.- *Macroevolution. Pattern and process*. Freeman & Company, San Francisco. XI+332 pp.
- STANLEY S. M., 1985.- Rates of evolution. *Paleobiology*, 11: 13-26.
- STANLEY S. M., ADDICOTT W. O. & CHINGU K., 1980.- Lyellian curves in paleontology: possibilities and limitations. *Geology*, 8: 422-426.
- STATZ G., 1940.- Neue Dipteren (Brachycera et Cyclorhapha) aus dem Obenligesien von Rott. *Palaentographica*, A 91: 120-174.
- STEHLIN H. G., 1909.- Remarques sur les faunes de mammifères des couches Eocènes et Oligocènes du Bassin de Paris. *Bulletin de la Société géologique de France*, (4)9: 488-520.
- STANICIER F. F. & WESSLEY G., 2000.- From the Tethyan ocean to the Paratethys sea: Oligocene to Neogene stratigraphy, paleogeography and paleobiogeography of the circum-Mediterranean region and the Oligocene to neogene basin evolution in Austria. *Mitteilungen der Österreichischen Geologischen Gesellschaft*, 92: 95-116.
- STOKES W. L., 1978.- Transported fossil biota of the Green River formation, Utah. *Paleogeography, Palaeoclimatology, Palaeoecology*, 25: 353-364.
- STONE A., SABROSKY C. W., WIRTH W. W., FOOTER R. & COULSON J. R., 1965.- A catalogue of the Diptera of America North of Mexico. *United States Department of Agriculture, Washington D.C.* IV+1696 pp.
- STUKE J.-H., 2000.- Phylogenetische Rekonstruktion der Verwandtschaftsbeziehungen innerhalb der Gattung *Chelidonia* Meigen, 1822 anhand der Larvenstudien (Diptera: Syrphidae). *Studia Dipterologica*, Supplement 8: 1-118.
- SWIHEN C. C., III & PROTHERO D. R., 1990.- Single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Eocene-Oligocene transition in North America. *Science*, 249: 760-762.
- SZANIEWSKI R., 1988.- Biting midges (Diptera, Ceratopogonidae) from Baltic amber. *Polskie Piśmie Entomologiczne*, 57: 3-283.
- TAFFOREAU P. et al., 2006.- Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. *Applied Physics A*, 83: 195-202.
- THOMPSON F. C., 1972.- A contribution to a generic revision of the Neotropical Milesinae (Diptera: Syrphidae). *Archivos de Zoología*, 23: 73-215.
- THOMPSON F. C., 1999.- A key to the genera of the flower flies (Diptera: Syrphidae) of the Neotropical region including descriptions of new genera and species and a glossary of taxonomic terms. *Contributions on Entomology, International*, 3: 321-378.
- THOMPSON F. C. 2008.- *Syrphidae. The BioSystematic Database of World Diptera. Nomenclator status statistica*, version 10.5.

- <http://www.diptera.org/biosys.htm> (consulté le 12 août 2008).
- THOMPSON F. C. & RUTHERFORD G., 1998.- Family Syrphidae (pp. 81-139). In: Papp, L. & Darvas, B. (eds). *Contributions to a manual of Palearctic Diptera*, vol.3. Science Herald, Budapest. 880 pp.
- THOMPSON F. C. & TORP PEDERSEN E., 1986.- Synopsis of the European species of *Sphingia* Meigen (Diptera: Syrphidae). *Entomologica Scandinavica*, 17: 235-269.
- THOMPSON F. C. & VOCKEROTH J. R., 1989.- Family Syrphidae (pp. 437-458). In: Evenhuis, N. L. (ed.). *Catalog of the Diptera of the Australasian and Oceanian region*. Bishop Museum, Honolulu. 1155 pp.
- UHL D., 2006.- Fossil plants as palaeoenvironmental proxies - some remarks on selected approaches. *Acta Palaeobotanica*, 46: 87-100.
- UHL D., BRUCH A., TRASSER C. & KLOTZ S., 2006.- Palaeoclimate estimates for the Middle Miocene Schönbürg flora (S. Germany) - multi-method approach. *International Journal of Earth Science*, 95: 1071-1085.
- UHL D. et al., 2007.- Cenozoic paleotemperatures and leaf physiognomy - a European perspective. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 248: 24-31.
- UTSCHER T., MOSBRUCKER V. & ASHRAF A. R., 2000.- Terrestrial climate evolution in Northwest Germany over the last 25 million years. *Palaeo*, 15: 430-449.
- VERLINDEN L., 1994.- Faune de Belgique - Syrphides (Syrphidae). Institut Royal des Sciences Naturelles de Belgique, Bruxelles. 289 pp.
- VOCKEROTH J. R. & THOMPSON F. C., 1987.- Syrphidae (pp. 713-743). In: McAlpine, J. F. et al. (eds) *Manual of Nearctic Diptera*, vol.2. Agriculture Canada, Ottawa. VI+675-1332 pp.
- VUČIĆ A., STANIĆ G., ROJO S., RADENKOVIĆ S. & ĐMIĆ S., 2008.- Systematics and phylogeny of the tribe Paragini (Diptera: Syrphidae) based on molecular and morphological characters. *Zoological Journal of the Linnean Society*, 152: 507-536.
- WAPPLER T., 2003.- Die Insekten aus dem Mittel-Eozän des Eckfelder Maars, Vulkaneifel. *Münster Naturwissenschaftliches Archiv*, Beiheft 27: VII+234.
- WERMANN S., 2000.- Die Insekten der oberoligozänen Fossilagerstätte Enspel (Westerwald, Deutschland). *Münster Naturwissenschaftliches Archiv*, Beiheft 23: 1-154.
- WIEDNER H., 1952.- Insektenleben im Bernsteinwald. *Entomologische Zeitschrift*, 62: 62-64; 65-72; 88.
- WIRTSCHAT W. & WICHARD W., 1998.- Atlas der Pflanzen und Tiere im Baltischen Bernstein. Verlag Dr. Friedrich Pfeil, München. 256 pp.
- WEST J. B., BOWEN G. J. & CERLING T. E., 2006.- Stable isotopes as one of nature's ecological recorders. *Trends in Ecology and Evolution*, 21: 408-414.
- WHITTINGTON A. E., 1992.- Revision of the Afrotropical species of *Graptomyza* Wiedemann (Diptera: Syrphidae: Volucellini). *Annals of the Natal Museum*, 33: 209-269.
- WHITTINGTON A. E., 2003.- The Afrotropical Syrphidae fauna: an assessment. *Studia Dipterologica*, 10: 579-607.
- WIEGMANN B. M., YILATES D. K. & THORNTON J. L., 2003.- Time flies, a new molecular time-scale for Brachyteran fly evolution without a clock. *Systematic Biology*, 52: 745-756.
- WELF P., 1997.- When are leaves good thermometers? A new case for leaf margin analysis. *Palaeontology*, 23: 373-390.
- WILLIAMS P. H. & GASTON K. J., 1994.- Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biological Conservation*, 67: 211-217.
- WILSON M. V. H., 1978.- Evolutionary significance of North American Paleogene insect faunas. *Quaestiones Entomologicae*, 14: 35-47.
- WING S. L., 1987.- Eocene and Oligocene floras and vegetation of the Rocky Mountains. *Annals of the Missouri Botanical Garden*, 74: 748-784.
- WING S. L. & GREENWOOD D. R., 1993.- Fossils and fossil climate: the case for equable continental interiors in the Eocene. *Philosophical Transactions of the Royal Society of London*, B 341: 243-252.
- WOLFE J. A., 1994.- Tertiary climatic changes at middle latitudes of western North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 108: 195-205.
- WOLFE J. A. & UPCHURCH G. R., JR., 1987.- Leaf assemblages across the Cretaceous-Tertiary boundary in the Raton Basin, New Mexico and Colorado. *Proceedings of the National Academy of Sciences of the USA*, 84: 5095-5100.
- ZACHOS J. C., PAGANI M. & SLOAN L., 2001.- Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292: 686-693.
- ZHERIKIN V. V. & BSKOV K. Y., 1999.- Mesozoic and lower Tertiary resins in former USSR. *Estudios del Museo de Ciencias Naturales de Alava*, 14: 119-131.
- ZIEGLER J., 2003.- Ordnung Diptera, Zweiflügler (Fliegen und Mücken) (pp. 756-860). In: Dethle, H. H. (ed.). *Lehrbuch der Speziellen Zoologie - Wirbellose Tiere*. Spektrum Akademischer Verlag, Heidelberg. XII+961 pp.