

Encyclopedia of South American Aquatic Insects
Illustrated Keys to Known Families,
Genera, and Species in South America

Charles W. Heckman



Neuroptera (Including Megaloptera)

 Springer

Encyclopedia of South American Aquatic Insects

Illustrated Keys to Known Families, Genera, and Species in South America

Series editor

Charles W. Heckman, Olympia, Washington, USA

This series is designed to provide books permitting entomologists in all special fields of biology to identify the specimens of aquatic insects they acquire in South America, and, if the species has not yet been described, to determine its family and usually also its genus, and to facilitate its description as a species new to science. Volumes in this series provide keys to families, genera, and species of both aquatic and terrestrial insects. All books contain richly illustrated keys and encompass adults of all genera, larvae and pupae.

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Encyclopedia of South American Aquatic Insects
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Introduction

This work was begun to provide keys to the aquatic insect species known from Brazil. The original goal was to include all genera known from South America and all species from Brazil, but for most groups, the scope was expanded to encompass all species in South America and, in some cases, to include terrestrial species of orders that encompass both terrestrial and aquatic taxa. In no case is a taxonomic revision of any group undertaken, although recommendations for such revisions are included where appropriate, and the probable synonymy of nominal species still treated as valid in the literature is noted.

Two different approaches will be employed according to the taxon being treated. For phylogenetic groups encompassing overwhelmingly or exclusively aquatic species, such as the orders Plecoptera and Ephemeroptera or the families Dytiscidae and Culicidae, keys are provided to distinguish all genera and species known to occur in South America. An effort has been made to include every identifiable species so that the user of the key can determine with reasonable certainty whether or not his specimen belongs to a species that has already been described or whether it is one that is not yet known to science. Where feasible, complete keys will be prepared for groups containing both aquatic and terrestrial species, if they do not encompass an extraordinarily large number of species. This has already been done for the order Collembola.

The second approach will be used for aquatic species belonging to predominantly terrestrial taxa, such as the order Lepidoptera or the families Curculionidae and Muscidae. In such cases, the number of terrestrial species involved is too great to deal with conveniently. For example, a work confined to aquatic insects cannot include a key to all of the approximately 45,000 weevil species (O'Brien and Wibmer 1978) or even the portion of its enormous fauna inhabiting South America because only a small percentage of them live in or on aquatic plants. However, without such a comprehensive key, it becomes difficult for a person not specializing in the taxonomy of this group to be sure in which genus or subfamily his specimen belongs. For aquatic species in such groups, a descriptive approach is used. It is attempted to describe the morphology completely enough for the nonspecialist to recognize his aquatic species. At the same time, descriptions or keys to higher taxa

within these groups are provided as necessary so that the aquatic species can be distinguished from the terrestrial ones and phylogenetic affinities of the specimens can be recognized.

The geographical limitations of this work are not strictly maintained throughout. For some genera, keys are provided that include mention or descriptions of species still known only from Central America or Caribbean islands, while for others, the keys are strictly limited to the South American fauna. The choice of comprehensiveness was dictated mainly by convenience. For genera encompassing few species and those that have been revised by competent taxonomists, keys to most or all Neotropical species could easily be provided. In the cases of other genera encompassing poorly described species, those which have not been reported south of Panama and the Antilles were not included in the keys.

In general, the ranges of the aquatic insect species are very poorly known. The reported occurrences indicate more the locations at which entomologists have worked than the actual distribution of the species. The type specimens of a great many South American species were collected during expeditions to individual regions of the continent, and systematic surveys of the fauna have only been undertaken for a few groups. Among the prominent early collectors was Charles Darwin. Larger expeditions were undertaken during the late nineteenth and early twentieth century. A considerable number of species have been described after examination of the specimens collected in Patagonia and South Chile during the early part of the twentieth century. In Brazil, Rio de Janeiro and Santa Catarina appear very frequently in the distribution reports due to the extensive collection in those states by F. Plaumann, while many other species were described from Amazonas because of the presence of a large research station, the Instituto Nacional de Pesquisas da Amazônia, at Manaus. Naturally, a great many species were described from specimens collected at São Paulo and Rio de Janeiro, where most of the Brazilian institutes of research are located. Reports from other Brazilian states are generally much rarer, so the ranges of Brazilian species can generally be expected to be much more extensive than indicated by the published reports. Notable research efforts in other parts of South America have resulted in large numbers of species being recorded for Surinam and the Amazon region of Peru. Knowledge of the fauna in other regions varies considerably from taxon to taxon, depending upon the efforts of talented individuals specializing in individual orders or families. Generally, the insect taxa with the greatest impact on public health and agriculture are the best known.

For some rarer species in neglected taxa, the ranges are scarcely defined at all. Specimens described during the nineteenth century were sometimes reported from "Brazil" or even "South America" without any more exact collecting data. The fact that the descriptions of such species are generally sketchy, at best, makes it doubtful whether they can be recognized again. There is mention in many of the review papers cited in this work of the confusion caused by falsely labeled specimens, incomplete collecting data, and doubt among the collectors about the names of the places from which their specimens originated. Names such as "Chapada" in Brazil frequently appear without mention of which Chapada is meant. This problem will continue to cause confusion in the future as it has in the past.

The problems encountered in systematic biology worldwide are especially pronounced in the Neotropical region. This is due to the dearth of detailed taxonomic studies on the regional fauna. Theoretically, the scientist who needs to know the correct name of a specimen can accomplish this by a procedure that assures a high probability of success, although a good deal of time and expense may be required. The first step in this procedure is the use of a comprehensive key treating the higher taxon to which the specimen belongs. This process is much easier for a specialist familiar with the group than for a person who needs to know the identity of species being used in physiological experiments or surveyed in synecological studies. In most cases, after the specimens have been identified using the keys, original or revised descriptions listed by the author of the key should be consulted to confirm the identifications. If the available descriptions are so poor that the identity of the species remains uncertain, a comprehensive taxonomic review of the taxon to which it belongs must be consulted. If such a review has not yet been published, the specimen to be identified must be compared with type specimens of each species belonging to the higher taxon to which the specimen belongs. These should be found in museum collections.

According to taxonomic convention, the author of a published original description of a new species should designate one of his specimens as a holotype. This type then becomes the standard on which the identifications of all specimens collected in the future are based. The species to which the holotype belongs is then referred to by the name proposed by the author, at least when the same name has not previously been applied to another species.

In addition to the holotype, other specimens believed to be of the same species by the author are designated as paratypes. If a holotype is not available, a paratype can be examined to confirm identifications. If the holotype has been lost or extensively damaged, a specialist revising the taxonomy of the group may designate a lectotype apparently belonging to the species in question. This then replaces the holotype as a standard for recognizing the species, at least until the lost holotype or paratype is found.

Anyone wishing to take the trouble to identify a specimen beyond the shadow of a reasonable doubt should be able to follow this procedure. If his specimen is not the same species as any of the holotypes preserved in museums, he should prepare a description of his specimen and have it published with his proposed name for the new species or give it to a specialist who is interested in doing this.

Unfortunately, the procedures described above often fail to work, especially when South American insects are involved. First of all, keys to identify the species are seldom available, and when they are, they are generally out of date or incomplete for the region being studied. This leaves the researcher with the chore of collecting a large number of original descriptions to match with his specimens. These descriptions are sometimes very sketchy, leaving the reader with no reliable way of identifying his specimen from the available literature. Comparisons with type specimens may not only be difficult in many cases because the types were deposited in museums on other continents, but they also are often impossible because some authors have failed to mention the name of the museum in which they intended to

place their type specimens or because the specimen cannot be found again due to war damage or sloppiness by the curators of the museum in question. Even when the type can be found, it often proves to be in very poor condition, and relatively few paratypes of South American species have been designated that can be examined in the absence of a usable holotype.

Using established procedures for identifying South American insects is made even more problematic by the practice of some authors of describing new species on the basis of only one life stage. Not only have many species been described by taxonomists who examined only adults, some are known only from larvae. Furthermore, countless species are known only from adults of one sex. While the description of an adult may provide a legitimate basis for establishing a new species, it is difficult to find justification for naming a species based only on larvae. Some authors have designated larvae as the types of species congeneric with others known only as adults. These individuals seemed to be in such a hurry to publish that they deliberately left the arduous task of matching larvae with adults to other researchers.

In practice, convention should dictate which gender and life stage should be chosen as the holotype. For example, adult male chironomids are presently those on which species descriptions should be based. Earlier descriptions of female adults are generally useless for determining a species unless someone has taken the trouble to match the female to a described male. In an ideal system of nomenclature, descriptions of adults of both sexes and of the larval stages should be provided. However, the state of the art still requires specimens to be identified according to partial descriptions of one stage and often one sex. Therefore, before fully workable systems for identifying South American species will be possible, an enormous number of revisions and supplemental descriptions will be necessary. This work is meant as a first step in the process: providing keys as reliable as the available publications permit.

Finally, keys to taxa higher than families are provided only to delimit groups of aquatic species from terrestrial ones. It must be noted that obsolete names of insect taxa are defined or noted in the keys whenever users of these books are likely to encounter the names in old publications. They are neither endorsed nor suppressed but merely defined. Keys to insect orders can be found in any number of textbooks on entomology or invertebrate zoology, and most specimens can be quickly assigned to the correct higher taxon by referring to the illustrations in this series. With a little experience, anyone can learn to recognize the order of most insects almost at a glance.

An Appeal for Quality in Taxonomic Work

This appeal is addressed to two groups, the first consisting of those responsible for deciding who obtains what portion of the available research funds and the second being the taxonomists themselves.

It has long been recognized by experienced ecologists that identification of the species present in a community is an absolute necessity for thorough ecological research. The biota of any water body, for example, is more than a quantity of “biomass” or a “pathway for energy.” Many ecologists, especially those beginning their research careers, have the greatest difficulty in identifying the species present, and the quality of their work is limited by this difficulty. The ecologist may indeed investigate systems using methods very different from those engaged in descriptive biology, but he is nevertheless dependent on a sound basis of taxonomic information for the proper reporting of his results. Briefly stated, ten may be equal to ten, but ten oranges are not equal to ten cows, and ten of one dragonfly species are not equal to ten of another. The “emergency measure” of identifying a species only as far as the genus or family is not satisfactory because two congeneric species may have completely different habitat preferences, feeding habits, and seasonal activity cycles. In short, for one ecologist to properly compare his work with that of another, he must know the name of the species he has encountered and of those that have influenced the biotic communities he has been studying.

In the past, ecologists usually relied on taxonomic specialists to identify their specimens. Since the specimens invariably belonged to a wide variety of taxa, they were distributed among a number of taxonomists, each of whom was an expert only for his own small phylogenetic group. This practice has ceased to function in recent years because of the failure of those in charge of distributing research funds to support scientists who wish to engage themselves in taxonomic work professionally. As the taxonomists reached retirement age, they left active research without being able to pass their knowledge on to a successor. As time went on, more and more personal knowledge and skill that is difficult or impossible to get from books was permanently lost.

The disappearance of the best taxonomists was accompanied by a decline in the quality of ecological work. This may not be considered totally undesirable by persons in government and business who are constantly confronted by the demands of environmentalists. As ecology moves increasingly out of the laboratory and into the courtroom, the ground rules change, and where principles remain unclear, the lawyers have more room to maneuver, using their skills of persuasion rather than being forced to confront research results already proven beyond the shadow of a reasonable doubt. Furthermore, laws passed to protect endangered species can be better circumvented if no people can be found who are capable of identifying such species.

Although there may well be incentives to suppress taxonomic research, the virtual demise of taxonomy as a field of biology has been instigated mainly by the scientific community itself. Ambition and the desire for quick success have motivated the staffs of many institutions to seek persons promising to achieve great breakthroughs, and no place was left for routine systematic work, which is by nature slow and methodical. Often, it was the number of publications rather than their quality or length that determined whether or not a person could succeed in finding gainful employment in science. Recently, science citation indices have become the criterion for judging success, prompting young researchers to investigate whatever

everyone else is investigating in order to assure themselves of a maximum number of other scientists who would have reason to cite their work. Pressure was placed on the young scientist to come up with something clever very quickly, leaving no time to learn in depth about the organisms he was encountering. It is especially unfortunate that the worldwide elimination of taxonomist positions came just prior to the development of computer equipment that makes it very easy to establish data banks. Thus, science was robbed of the personnel competent to systematize and disseminate the great body of information that had accumulated during two centuries of intensive work by systematic biologists in all parts of the world.

A long time went by without any crisis becoming evident because the taxonomists and systematic biologists already working in the museums and universities continued donating their time to help identify specimens collected or used in the laboratory by ecologists, physiologists, geneticists, and biochemists. Even after their retirements, many continued contributing time to help younger colleagues in other fields of biology. Moreover, a number of excellent specialists were employed in other fields of work rather than in the biological sciences and made their contributions to the knowledge of the world's flora and fauna as a hobby.

With the gradual elimination of the competent taxonomists and systematic biologists through death or disability, however, the problems of defining community structure, determining species diversity, and identifying the organisms causing some problem in the field have been intensifying. For many taxa, there are no longer experts who can be consulted, or those experts who are still active are hopelessly overworked.

The result is the loss of a vast body of information about the flora and fauna in all parts of the world. Without knowledge of the species that have been encountered, the ecologist is faced with a dilemma. He must learn to identify a vast array of species belonging to the widest variety of phylogenetic groups, or he must limit his research to superficial phenomena. Hence, there has been an increasing tendency to use numbers instead of names and to try to equate quantities of unlike and undefined substances or objects, although this cannot yield any reliable results, as mentioned above.

The second aspect of the problem must be dealt with by the taxonomists themselves, who have in the past often been guilty of laxity in quality control of their work. The ambition to gain status by naming new species has certainly been a motivating factor for many of these scientists, and for this purpose, it is easier to write short papers with sketchy descriptions of aberrant specimens than to produce comprehensive reviews compiling the available information on genera or families together with thorough, well-illustrated descriptions of new taxa. As mentioned above, it is evident that the examination of type specimens for positive identification of South American insects is often impossible because none were designated, or if they were, they have been lost or greatly damaged. For better or worse, the published literature frequently provides the only criteria for identifying species.

While compiling this key, the enormously broad spectrum of quality in the taxonomic publications became evident. Some papers are of very high quality, such as the works of Belle on the Odonata. These publications provide descriptions of all essential morphological characters, the exact locations of type specimens, and precise collecting data. Any morphological details lacking in the text can be seen in the comprehensive illustrations. They make it clear that the species described are actually distinct from all species previously described.

In general, more recent publications tend to include better descriptions than older ones, but this is not the case with all taxa. Many works more than a century old are still useful for identifying species, and some of the information they provide cannot be found in any more recent publications. On the other hand, many recent publications are extremely poor, providing either very sketchy descriptions or showing a very poor comprehension of the concept of species as a closed phylogenetic grouping of individuals, which may possess a considerable degree of individual variability (Mayr 1963).

Many of the better taxonomic publications are rather long, but length is no guarantee of quality. There are some excellent concise works, which can be used with great reliability for the identification of species. Some very long works, including incredible amounts of detail, on the other hand, are very poorly organized and omit much essential information while including vast amounts of trivia. Authors who are more collectors than biologists have used very keen, practiced observation abilities to find the most minor differences among single populations to produce massive numbers of nominal species that are indistinguishable to less skilled observers. Among the European fauna, long lists of synonyms attest to the vast amount of printer's ink that has been squandered on the description and suppression of spurious taxa. Unfortunately, revisions of many South American taxa are still lacking, and many of the nominal species included in the keys will certainly prove to be junior synonyms when more is known about the variability of natural populations.

In the following sections, minimum criteria will be suggested for describing new taxa. All of the features an author should describe to define a new species or subspecies within a particular taxonomic group will be mentioned. It is further suggested, as a general rule, to base descriptions on a holotype and several paratypes. New species described from only one or two specimens should be regarded as questionable, particularly when the morphological differences between them and specimens of other nominal species are very slight. The practice of choosing type specimens that are missing various structures, such as legs, abdomens, or antennae, should be discouraged. With modern means of mass transportation available, there should be no serious obstacle to collecting more material from the locations at which the specimens of the alleged new species were encountered, and funds should be provided for such collecting for the reasons outlined above.

It would probably be justified to declare many names of species poorly described and without known type specimens as *nomen inquerendae* and omit them from the

key. However, whenever distinctive features were found in the original description that can be used to distinguish a species from all other known species in the genus, the name is included in the keys. Names from the keys must therefore be used with caution because one or more undescribed species may also have the characteristics in question. Where such situations are apparent, it is hoped that specialists for the groups in question, if any are presently active, will designate lectotypes for the species most likely to have been referred to by the earlier authors. Holotypes, paratypes, and original descriptions should be provided for any similar, congeneric species that were hitherto undescribed.

Scope of the Work

The families recognized are mainly those found in the key of Brues et al. (1954), and some of the new families that have been described by various authors after the appearance of that key are omitted because they have not been generally accepted, are too poorly defined, are too similar to other families to recognize any general definitive characteristics for use in the key, or seem for another reason to be of doubtful validity.

Geographically, the work is limited to continental South America and islands very close to the coast, such as Tierra del Fuego (Map 1). Islands far enough offshore to be zoogeographically distinctive, such as the Galapagos Islands, are only included in some of the volumes, even though politically, they are parts of South American countries. Case by case decisions to include them depend upon the availability and reliability of published surveys of the local fauna. Except in the case of Brazil, the distribution reported in the keys usually refers only to the country in which the species have been found. When they have been reported in the literature, the Brazilian states are shown, as depicted in Map 2. However, some inaccuracies may have been inadvertently introduced in the cases of states which have changed their boundaries since the insects were described. For example, Mato Grosso formerly encompassed the present states of Mato Grosso, Mato Grosso do Sul, and Rondônia, so species reported in older literature from Mato Grosso may actually be confined to any one of these three present states.

Acknowledgments The preparation of these keys required the search of a large amount of literature. A great deal of help was provided in obtaining many obscure or archaic papers by the staff of the Library of the Zoologisches Institut und Zoologisches Museum of the University of Hamburg and through the Timberland Public Library System in Washington State, USA.



Map 1 The geographical scope of this work is limited to continental South America and the off-shore islands shown on this map



Map 2 The Brazilian states where the species were found are generally reported as shown on this map. Older reports, however, may not reflect the modern political boundaries, so it often requires knowledge of the travels of entomologists to determine the precise locations of known occurrence. D.F. designates the Federal District of Brasília

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Part I
Order 7: Neuroptera (*sensu lato*)

Chapter 1

General Information

Abstract The general characteristics of the order Neuroptera, tentatively including the species in the nominal order Megaloptera, are described, including the morphology, larval development, ecology, and zoogeography. The methods of collecting, preserving, and examining specimens are discussed, and some needs for future research are mentioned. It is shown that many species names, which are still technically valid, may never be correctly used again unless a type specimen is discovered or unless it is possible to provide an up-to-date description and lectotype.

Keywords Morphology • Preservation • Ecology • Zoogeography • Taxonomy

Until the early part of the twentieth century, the order Neuroptera was understood to encompass a large number of insects with two pairs of similar wings, often supported by many veins and with transparent or tinted membranes. Species belonging to Odonata, Plecoptera, Ephemeroptera, Trichoptera, and smaller orders were included by many taxonomists within Neuroptera. As the fundamental differences between some of the major taxa became evident, many insects formerly considered to be neuropterans were placed in orders now recognized as distinct, leaving behind a rather heterogeneous group of families in the order. The variety of common names for the individual groups reflects their diversity in morphology, ecology, and distribution.

Those species regarded as members of Neuroptera at the present time are holometabolic; that is, they have complete metamorphosis, distinguishing them from many of the taxa with which they were formerly grouped. The adults display many similarities, usually including a moderate to complex network of veins in the wing, from which the name Neuroptera is derived. The wings lack scales and are typically folded posteriad to cover the abdomen while at rest. Exceptions to this are owlflies belonging to the family Ascalaphidae, which typically rest with the abdomen pointed dorsad, almost perpendicular to the longitudinal axis of the head and thorax, and thread-winged lacewings in the family Crocidae, which usually point the forewings obliquely dorsad when at rest.

Neuropteran antennae are typically long and often thread-like, but they are clubbed in some members of the Ascalaphidae and Myrmeleontidae, the owlflies and antlions, respectively.

The mouths of most larval and adult neuropterans are modified for chewing, but the jaws of spongillafly larvae, in the family Sisyridae, appear to have adaptations suitable for piercing and sucking. However, they may actually be used for pipetting microscopic prey. Larvae in the family Osmylidae, usually found at the water's edge or under stones and tree bark, also have long, narrow mouthparts, as do larvae in the family Berothidae, which inhabit termite nests and presumably feed chiefly on the termites. Unlike sisyrid larvae, which inhabit freshwater sponges and possibly also unspecified ectoprocts, those in the families Osmylidae and Berothidae lack external gills (Tauber et al. 2003). Sisyridae and Osmylidae are the families of the most conspicuously aquatic species belonging to Planipennia, the taxon also encompassing all of the terrestrial species in this book.

Sialidae, the family of the alder flies, and Corydalidae, the dobsonflies and fishflies, constitute distinctive taxa of aquatic insects. They were originally classified with the Neuroptera, but for many years, they were believed to constitute a group deserving the status of an independent order, which was named Megaloptera. Thus, in early literature, alder flies were considered to be members of the Neuroptera, but during the middle decades of the twentieth century, almost all publications included Megaloptera as an independent order, even though it had long been known that the differences between the adult megalopterans and neuropterans did not justify assigning them to separate orders. Only differences in the larvae seemed to make them distinctive. For the past several decades, doubt has been expressed about whether alder flies, dobsonflies, and their relatives are really different enough phylogenetically to merit their separation from the other groups still classified as subdivisions of Neuroptera. Because the major differences between alder, dobson, and fishflies and members of the Neuroptera *sensu stricto* are observed only during the larval stages, many authors pointed out that this by no means makes the taxon fundamentally different from other groups of neuropterans. All major taxa of true neuropterans are characterized by distinctive morphological modifications during the larval stage, which are necessary for the specialized ways of life they have adopted. As a result, there has been a trend to reintegrate the Megaloptera into the order Neuroptera. However, to avoid controversy, some authors avoid taking sides in the debate by using the term “neuropteroid insects” for all controversial groups. To make the relationship clearer, an additional stratum of classification was introduced, and Neuroptera and Megaloptera have sometimes been maintained as independent orders in a superorder called Neuropteroidea (Aspöck 1986) or Neuropterida (Aspöck et al. 2001; Aspöck 2002).

Pending additional research, there is still no general agreement on the taxonomy of the Neuroptera, *sensu lato*. Some authors treat the taxon as an order encompassing three suborders: Megaloptera, Raphidioptera, and Planipennia. Presently, this seems to be the predominant classification system and is the one used in this volume. Others have continued to treat these three taxa as orders within the superorder Neuropteroidea (Berland and Grass 1951) or Neuropterida (Tauber et al. 2003). At times, the name Sialoidea has been substituted for Megaloptera as a suborder. Those who continue to use the older classification system utilize the name Neuroptera for the Planipennia alone, treating the other two names as those of independent orders.

Of the three main subdivisions of Neuroptera, treated herein as the suborders Megaloptera, Raphidioptera, and Planipennia, only two are positively known from South America. Species of Raphidioptera are not known south of northern Central America, and Aspöck and Aspöck (1969) reported none south of Mexico. While the suborder Megaloptera encompasses two families characterized by aquatic larvae, Planipennia includes mainly families of typically terrestrial insects, although, as already mentioned, distinct groups of species with aquatic or littoral larvae are also included in this suborder.

Neuropteran larvae display a wide variety of modifications for distinctive modes of life. They are found in terrestrial, aquatic, and wetland habitats. The locations at which adults are encountered can be indicative of the habitats in which the larvae develop, even though a few adults are strong flyers and may be found far from the sites at which they will mate and deposit their eggs. Usually, the best places to seek adults of aquatic species are along streams and rivers, as well as near lakes. When more is known about the larvae of South American species, it is likely that wetlands and floating islands of plants will also prove to be particularly rich in aquatic neuropterans. Most larvae and pupae in temperate zones seem to show seasonal growth cycles related to temperature or the seasonal length of the day. In the tropics, seasonal rainfall patterns or changes in the water level of lakes and rivers are apparently determinants of the seasonal reproductive patterns of the species. Unfortunately, reliable information on the seasonal development of South American species is still fragmentary, so our present state of knowledge does not provide a firm basis for more than speculation about the life cycles of most species.

A genus of apparently flightless species in South America is of controversial phylogenetic origin, and after its discovery by Navás (1927a), it was maintained in its own family, Brucheiseridae, which was included in the Megaloptera. More recently, the family was reduced to the status of a subfamily, Brucheiserinae, within the family Coniopterygidae (Riek 1975), which is now assigned to the suborder Planipennia (New 1989). The larvae remained unknown for more than half a century, after which the first specimens were found in one of the driest regions of the world, the Atacama Desert of Chile, at about 1400 m above sea level. These larvae have been described by Sziráki and Flint (2007). To date, four species in two genera have been discovered.

Most other terrestrial species of Planipennia overpower and chew up small to moderately large insects as both larvae and adults. The larvae of antlions, members of the Myrmeleontidae sometimes called doodlebugs, are often encountered in dry sand. Some species dig cone-shaped ant traps. When an ant stumbles into one, it usually descends gradually to the bottom as the sand shifts under its feet. The larval antlion waits buried in the sand at the lowest point of the inverted cone to devour it. If the ant seems to be succeeding in climbing out of the trap, the larva throws sand at it to make it fall to the bottom. Some genera in this family, however, encompass species which do not construct such traps. Their larvae are encountered under pieces of wood or among leaf litter, where they stalk or ambush their prey.

A small family, Ascalaphidae, encompasses only a few relatively large and conspicuous species called owlflies. The habits of the known species in the Americas

include predatory feeding, mainly on small arthropods, and larval development among leaf litter or on trees. The family is considered to be closely related to Myrmeleontidae.

Crocidae is a small family related to Myrmeleontidae and Ascalaphidae. The larvae of crocid species often inhabit hiding places in caves or buildings, where they ambush or stalk prey. They are remarkable for their elongated collars between the head and thorax. Adults have thread-like hind wings and seem to feed on pollen or nectar from flowers (Tauber et al. 2003).

Another remarkable family is Mantispidae, which includes species resembling the preying mantis in both superficial appearance and feeding habits, although they are not closely related to their orthopteran look-alikes phylogenetically. A few species mimic the shape and coloration of wasps. None of the species are known to colonize aquatic or semi-aquatic habitats. Most fly well and seek out locations where relatively large prey can be found, grasped in fore-legs suitably modified and armed with spines, and then devoured. Mantispid larvae have been observed living in the egg cases of spiders to feed on the eggs (Biraben 1960).

The remaining families encompass fully terrestrial species with common names containing the words lacewing or duskywing. Species in the family Dilaridae, known as pleasing lacewings, have larvae differing from those of other lacewings in developing in rotting wood rather than on plants, as well as by transforming to pupae within cocoons. The larvae have been encountered in burrows bored by other insects through wood (Tauber et al. 2003). The dilarids are believed to be primitive relatives of mantisflies in the family Mantispidae.

Many and perhaps most of the South American species in the remaining families prey on small insects, including aphids, which feed on sap sucked from fruits, stems, or leaves of plants, including many valuable cultivated crops. The stomach contents of a few of the lacewings examined, however, included only pollen or other material from plants. A considerable number of lacewing species have been investigated as possible agents for biologically controlling agricultural pests (Souza et al. 1990; Souza and Ciociola 1995, 1997; New 2001; Albuquerque et al. 2001; Frietas and Penny 2001; Anad et al. 2003). Species of Chrysopidae, the green lacewings, are especially promising for facilitating organic farming in the tropics by feeding during both their larval and adult stages on large numbers of small, harmful, herbivorous insects. Also rich in species are the brown lacewings in the family Hemerobiidae and the duskywings in the family Coniopterygidae. The giant lacewings in the family Polystoechotidae are poorly known, in spite of their large size. There are only two species known from South America, both from Chile. A third species is found in North and Central America, as far south as Panama (Oswald 1998).

Neuroptera is an ancient insect order, dating at least from the Permian. Fossil specimens identified as belonging to the Megaloptera and Planipennia date from this geological period. They seem to belong among the oldest known extant taxa of insects with complete metamorphosis (Carpenter 1930).

1.1 Morphology

The species within the individual subdivisions of Neuroptera possess many common features as adults, even though their larvae are quite distinct in morphology and preferred habitats. The distribution patterns of many species are limited by ecological factors affecting the larvae. In the case of the Megaloptera, the morphology and ecological requirements of the larvae were formerly considered distinctive enough from all other neuropteran larvae to merit giving the group the rank of an independent order. As already explained, the general opinion of neuropterologists has swung slowly toward the consensus that the anatomy of the adults should be given more consideration, and the Neuroptera and Megaloptera should be rejoined at or slightly above the level of order.

Naturally, the larval morphology of the individual families will have to be considered on an individual basis. Adults, on the other hand, have many features shared by the entire order, although extreme individual modifications of some of the body parts make each family distinctive and sometimes bizarre in appearance.

The morphological features most frequently used to distinguish the species include the genitalia, especially those males, as well as the shape and venation of the wings, the color pattern, and morphometric characters of various structures and appendages. Unfortunately, a general overview of a typical neuropteran cannot be conveniently provided because the morphology of most families is so distinctive from most others. Needless to say, such morphological differences make identification of specimens easier.

Although the majority of species within this order are terrestrial, keys to all South American taxa as complete as current knowledge permits will be provided because the order is small and can best be handled as an intact group in one volume. Most of the major taxa can be readily distinguished from each other, usually at a glance, by many morphological features, including general shape and size, the form of the head and antennae, the mouthparts, the wing venation, and even the coloration of the body and wings (Fig. 1.1). General features of adult specimens which should be noted at the beginning of any examination include whether the mouth is directed anteriad or ventrad, whether or not the antenna is clubbed, and modifications of the fore-legs, especially those indicating whether these legs are raptorial. The larvae are even more distinctive than the adults, and many can be recognized immediately from their habitats and habits. For example, the antlions in the family Myrmeleontidae are terrestrial, and most larvae live on dry ground, sometimes at the base conical pits, while spongillafly larvae in the family Sisyridae usually inhabit freshwater sponges and possibly also colonies of ectoprocts.

The general morphology of most adults in the order Neuroptera appears to be relatively unspecialized and conforms to a hypothetical body plan of a primitive insect. The **mesothoracic** and **metathoracic wings**, that is, the fore and hind wings, respectively, appear similar in size and venation. However, the **metathoracic wings** of most species tend to be slightly smaller, lack a few veins that are present in the fore-wing, and often have fewer markings. A few species, however, such as the

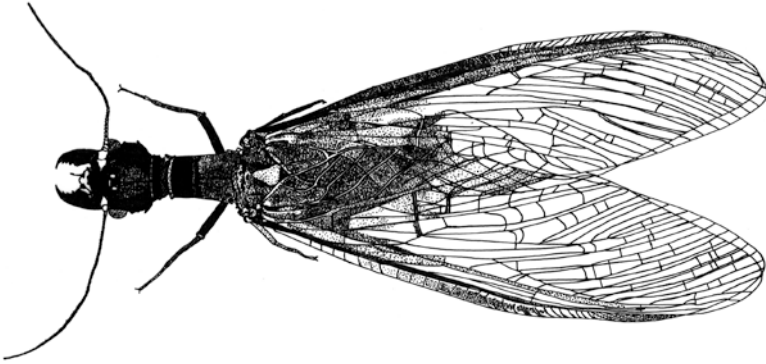


Fig. 1.1 Habitus of a male member of the suborder Megaloptera, *Corydalus wanningeri*, in dorsal view. Based on Contreras-Ramos and von der Dunk (2010).

threadwinged lacewings of the family Crocidae, have highly modified hind wings, as the common name of these insects implies.

The legs of most species are not notably modified. Typically, the **prothoracic legs** are similar to, although smaller than the mesothoracic and metathoracic legs. A notable exception to this is found in members of the mantisflies of the family Mantispidae, which are characterized by greatly enlarged prothoracic legs modified for seizing and holding prey. The **mesothoracic** and **metathoracic legs** are modified for walking rapidly and stabilizing the body of the mantisfly while it holds relatively large, struggling prey in its modified fore-legs. In the keys, the legs will be referred to by the less technical terms: fore, middle, and hind legs. The resemblance of the legs of these insects to those of the preying mantis, belonging to the very distantly related order Orthoptera, accounts for the common name of this family.

As shown in Fig. 1.1, adults of the Megaloptera have no notable modifications of the thorax and abdomen. Only the head displays some eye-catching modifications in some species (Fig. 1.2). Although males and females of many Neuroptera species are generally similar in morphology and coloration, with differences being confined to the genitalia, there are cases of sexual dimorphism or dichromatism affecting other parts of the body. The mouthparts are obviously adapted for grasping and chewing in all species of Megaloptera. However, the **mandibles** of males in some species of the family Corydalidae are greatly enlarged and elongated. The results of investigations of this modification suggest that both males and females of some species always possess short, robust **mandibles** (Fig. 1.3), while the long, forceps-like **mandibles** (Fig. 1.2) are characteristic of all males of other species (Contreras-Ramos 1998). A few species, however, encompass both males with elongated mandibles and those with short ones, like those of females.

Bowles et al. (2007) noted that the males of some South American species, including *Corydalus arpi*, *C. cephalotes*, *C. hecate*, and *C. ignotus*, have only short mandibles similar to those of the females, while *C. colombianus* develops somewhat elongated mandibles of a length the authors designated as “transitional”

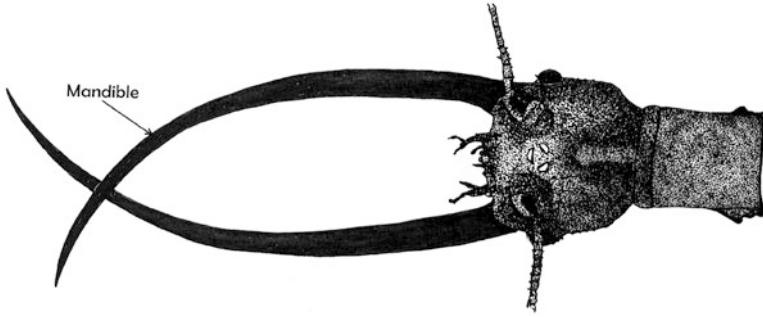


Fig. 1.2 The head and prothorax of a male *Corydalus imperiosus*, showing its elongate mandibles. Based on Contreras-Ramos (1998).

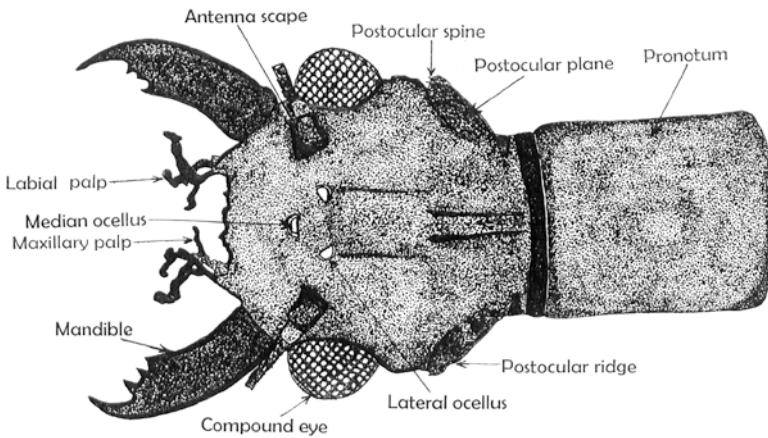


Fig. 1.3 The head and prothorax of a male *Corydalus affinis*, showing its mandibles, which are similar to those of the female. Based on Contreras-Ramos (1998).

between the extremely long “tusks” of *Corydalus longicornis* and *C. imperiosus* and those mandibles without notable elongation. *Corydalus nubilus* exhibits variable development, so males display different degrees of mandibular elongation. Subsequent investigations will be necessary to reveal the genetic and ecological implications of this phenomenon, especially the use to which the long mandibles are put in each species.

The heads of adult planipennians show a much greater spectrum of modification than those of megalopterans. Most have mouthparts modified for grasping and chewing prey. However, those of species in the family Sisyridae are elongated and appear to be suitable for piercing and sucking, although the modification seems more suitable to permit the insects to “pipette” particularly small prey.

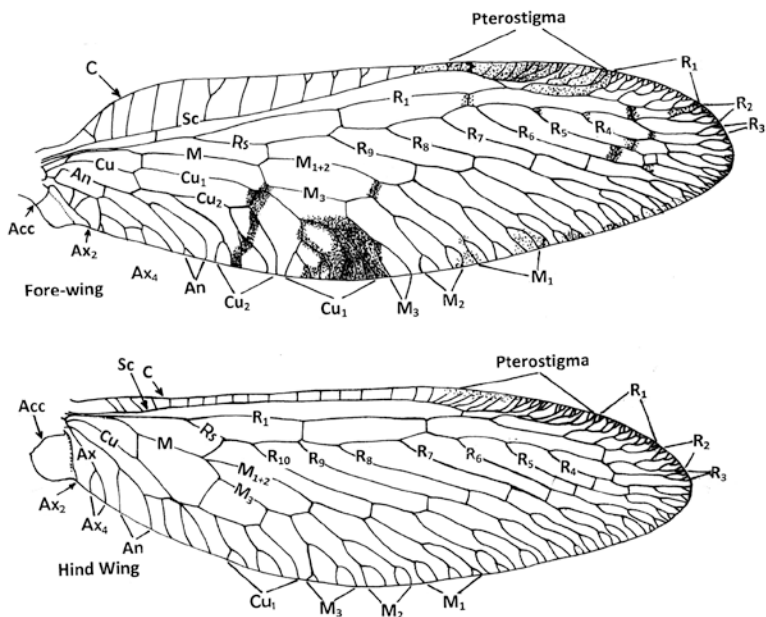


Fig. 1.4 Commonly used abbreviations for the wing veins of *Gerstaeckerella gigantea*, in the family Mantispidae and suborder Planipennia, modified somewhat from those used by Enderlein (1910) to conform to English names. Based on Enderlein (1910).

The morphological characteristics of each family are best presented in the keys. The general review will outline only the nomenclature of the morphological structures commonly used to distinguish the species.

To identify the species of adult neuropterans, it is often necessary to examine the wing venation (Fig. 1.4). Although most families and many genera can be recognized from this feature at a glance, anomalies in the arrangement of the veins can make identifications of some species difficult. More recently, some neuropterologists have begun using the color pattern to distinguish species, although this is sometimes a poor criterion for identification when the intraspecific variability in this feature is not well known. The shape of the male genitalia is usually the most definitive feature, but, as the keys clearly illustrate, either the male or the female of many species remain undescribed, forcing the researcher to seek other distinguishing characters. The disadvantage of relying on almost any other character for identification when specimens of only one sex have been examined is the lack of certainty whether differences may exist due to sexual dimorphism or dichromatism. The size of the adult, measured either as total body length or wing length, is also a poorly defined feature of neuropterans, especially when descriptions are based on only one or a few specimens. Size variability within this insect order seems to be considerable in comparison to that of most other insect orders, but little can be said with certainty until greater numbers of specimens have been examined.

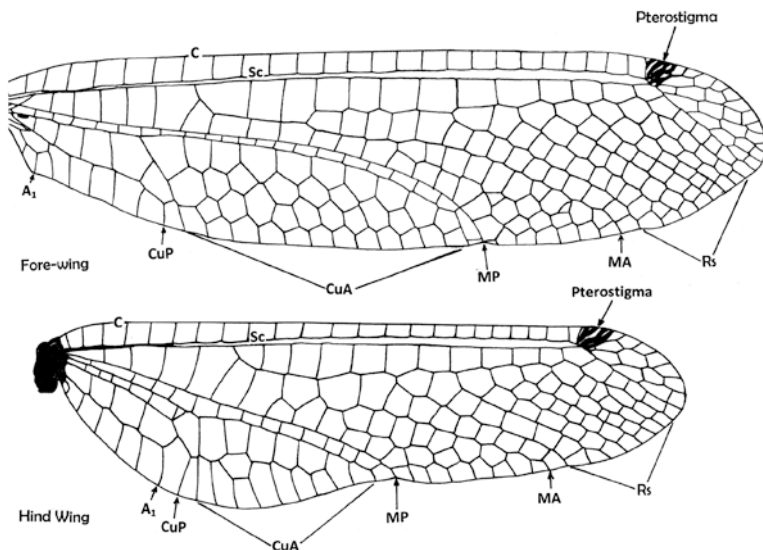


Fig. 1.5 The nomenclature of the wing veins of *Fillis amazonicus*, a species in the family Ascalaphidae using a somewhat different set of abbreviations from that employed in Fig. 1.4. Based on Machado and Rafael (2011).

Fossils of neuropterans are not uncommon, and they show that the order is ancient. Modifications from the primitive body plan of winged insects are remarkable in only a few taxa. However, most families have distinctive characteristics that facilitate their identification almost at a glance. The arrangement of the wing veins is usually one such character.

The nomenclature of the wing veins has not deviated too much in the literature, although fundamental inconsistencies persist. For example, some authors use the abbreviations M_1 , M_2 , Cu_1 , Cu_2 , 1A, 2A, and 3A for the same veins designated by others as MA, MP, CuA, CuP, A_1 , A_2 , and A_3 , respectively. This discrepancy also exists in the literature on the other orders, which had been grouped in the Neuroptera during the nineteenth century. The commonly used alternative abbreviations for the wing veins are shown for a species of Ascalaphidae (Fig. 1.5), which has a network of wing veins that is roughly equal in complexity to that shown in Fig. 1.4.

The names of the wing veins followed by the abbreviations used for them in parentheses are the **costa** (C), **subcosta** (Sc), **radial sector** (Rs), **radial** (R), **median** (M), **cubital** (Cu), and **anal** (A) veins. The abbreviations sometimes also include designations for the positions of the veins, either with A and P, standing for anterior and posterior, respectively, or as a number written as a subscript, noting the first to final branch of the vein, counting clockwise on a dorsal view of the right wing. Thus, R_1 , R_2 , R_3 , R_4 , R_5 , R_6 , R_7 , R_8 , and R_9 , shown on the fore-wing in Fig. 1.4, are the first branch of the **radial vein** to reach the wing margin through the ninth to do so. These are followed by the first through third branches of the **median vein** to reach the margin, abbreviated as M_1 , M_2 , and M_3 , respectively. In species with

multiple anal veins, the numbering may be 1A, 2A, and 3A, presumably allowing the branches of each to be numbered by subscript, as 1A₁, 1A₂, and so forth.

The abbreviations employed for a species of Megaloptera, *Corydalus wanningeri*, are shown in Fig. 1.6. The wings of an aquatic species of Planipennia, the spongillafly, *Sisyra minuta*, are shown in Fig. 1.7.

The differences in the alternate sets of abbreviations for the veins can be seen by comparing those used on Figs. 1.4 and 1.5. Great variations in degrees of complexity can be seen in the key to the families in Chap. 2, p. 47.

In some cases, specific wing cells are important for distinguishing species. Some of the important ones are shown in Fig. 1.8., which illustrates wings of a chrysopid species, *Titanochrysa ferreirai*. The illustration also shows the positions of two series of cross veins connecting branches of the radial vein, which are especially important for identifying the genera and species belonging to Chrysopidae, which are presently being evaluated as biological control agents in subtropical and tropical agriculture. These are known as the **inner** and **outer gradate cross veins**. In the descriptions of chrysopid genera and species, one small cell in the fore-wing, the **intramedian cell**, has become a very important. Its presence or absence and its shape are defining features of certain genera.

Other features commonly used to distinguish species are morphometric, based on the relationships between individual dimensions of the body structures. Some of the more common ones include size relationships between the length and width of the antennal segments, pronotum, thorax, femora, and tarsal segments. They may also include the relationships between the lengths of the femora, tibiae, and tarsi to one another; the lengths of certain setae relative to other structures; and the

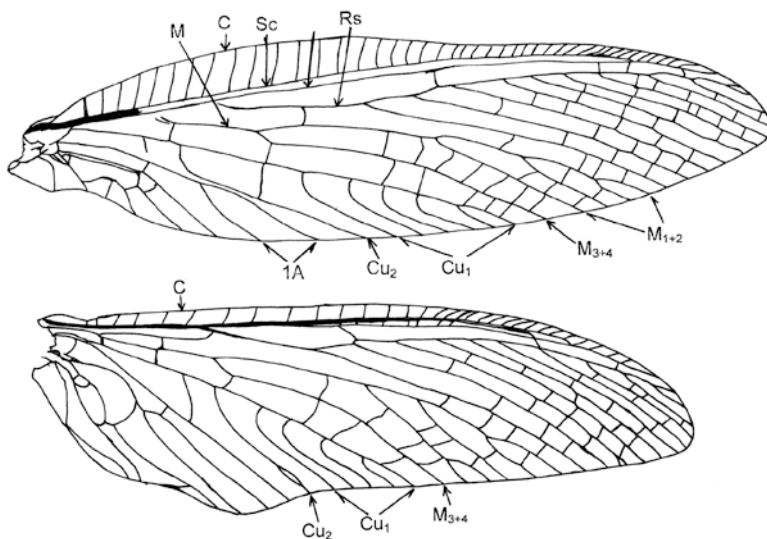


Fig. 1.6 The wing veins of a megalopteran in the family Corydalidae, *Corydalus wanningeri*, showing their nomenclature. Based on Contreras-Ramos and von der Dunk (2010).

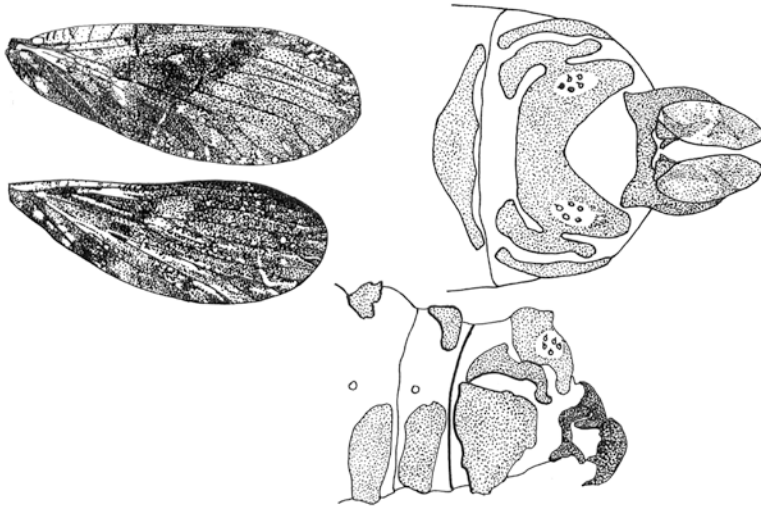


Fig. 1.7 *Sisyra minuta* male: fore and hind wing (left) and apex of the abdomen in dorsal (upper left) and lateral view (lower center). Based on Parfin and Gurney (1956).

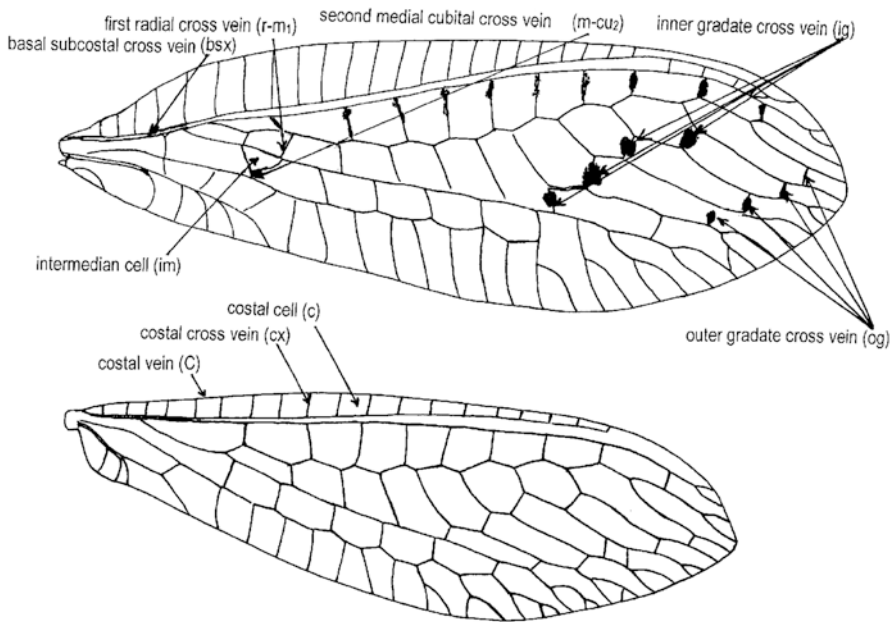


Fig. 1.8 Fore and hind wing of *Titanochrysa ferreirai*, showing the names of veins and wing cells particularly important for the identification of species. The wing membrane adjacent to the gradate cross veins of the fore-wing is darkened. The numbers of inner and outer gradate cross veins on one or both wings are sometimes important characters used to identify species. The intermedian cell, often abbreviated “im,” has become a particularly important character for the identification of chloropids. The presence or absence of this cell and its shape are characteristic of certain genera. Based on Sosa and de Freitas (2012).

dimensions of the wings. However, these characters are used less frequently for species of Neuroptera than they are for most other insect orders. Within certain genera, species are more frequently distinguished on the basis of whether or not the forewing is falcate, that is, concave along the posterior margin proximal to the wing tip.

The color pattern has become important for distinguishing many species which otherwise resemble each other closely. For most insect groups, coloration is a particularly unreliable taxonomic character. This is especially true for poorly known species. Clearly, when only a few specimens are available for study, almost nothing can be determined about the natural intraspecific variability.

As in the case of almost all insects, the structure of the genitalia, especially those of males, is an important, and probably the most important morphological character for distinguishing the species. Taxonomists have developed a nomenclature for the genital structure of neuropteran species, which includes names for structures unique to the order. The names of important structures characteristic for males from several families are shown in Figs. 1.9, 1.10, and 1.11. It is important to keep in mind that some of the structures may be completely absent from species believed to be closely related to others which possess the structure, a situation which will be encountered when using the keys to the species.

Learning the vocabulary used by neuropterologists to distinguish the taxonomically important parts of the genitalia is necessary before the keys can be used effectively. The parts of the male genitalia of Megaloptera species are often easy to see without any special methods of examination (Fig. 1.9). However, the taxonomically important structures of some species of Planipennia, as well as the spermatheca of the female, are not evident unless dissected out of the specimen or observed after clearing, as described in Sect. 1.3, p. 33. The main male structures are usually moderately to extremely modified parts of the ninth and tenth abdominal segments. The seventh and eighth segments are usually also modified structurally in characteristic ways to accommodate the genitalia. The visible parts of the male genitalia of a megalopteran, *Corydalus mayri*, are shown in Fig. 1.9.

In general, the structure of the male genitalia of megalopteran species is simpler and less variable than that of planipennians. The identification of corydalid species

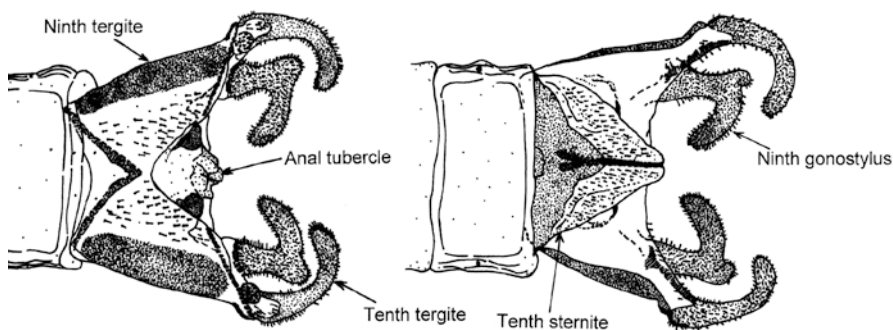


Fig. 1.9 The apex of the male abdomen of a species in the suborder Megaloptera, *Corydalus mayri*, shown in dorsal (left) and ventral view (right). Based on Contreras-Ramos (2002).