SYSTEMATICS OF THE DOBSONFLY
SUBFAMILY CORYDALINAE
(MEGALOPTERA: CORYDALIDAE)

A Thesis

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by

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Approved by

A handwritten signature in black ink, appearing to read "R. E. Snodgrass", is written over a horizontal line.

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INTRODUCTION

The Megaloptera, long considered among the most primitive of holometabolous insects (Weele, 1910), contains two families, Sialidae and Corydalidae. The Corydalidae, easily separated from the Sialidae by presence of ocelli, non-bilobed fourth tarsomeres, and large size, contains two subfamilies - Chauliodinae, distributed in North and South America, South Africa, Asia, New Zealand and Australia, and Corydalinae, restricted to North and South America, South Africa, and Asia.

Adult Corydalinae are among some of the largest and most bizarre appearing of living insects, males of Acanthacorydalis and Corydalis being noted for disproportionately large mandibles. The formidable appearance of Acanthacorydalis has led at least one collector to regard this insect as extremely dangerous (MacLachlan, 1899).

While not as spectacular looking, the larvae may be of specialized economic importance, those of the North American Corydalis cornutus being considered excellent angling bait. Dried larvae of Protohermes grandis, referred to as "magotaro mushi," were considered a remedy for infant emotional irritation in Japan (Kuwayama, 1962).

Relationships within the Corydalinae are poorly understood, and generic limits have never been firmly established. In this study I redefine the genera and postulate intergeneric relationships based on shared-derived character states, or synapotypies. In searching for sufficient characters to more confidently establish relationships I also hope to generate enough characters and knowledge of character states to eventually resolve intrageneric relationships.

Taxonomic history

Davis (1903) divided the Sialidae into the Sialidinae and Corydalinae, and Weele (1909) divided the Corydalinae into two tribes, Neuromini and Chauliodini. Some authors (Esben-Petersen, 1924; Barnard, 1931; Kimmins, 1948; Kuwayama, 1962) recognized Weele's Neuromini, while Tilyard (1918) and many subsequent authors called this group Corydalinae. Lestage (1927) noted that the name should be based on Corydalis, reducing Neuromini to a junior synonym.

Some early authors (Tilyard, 1918; Lestage, 1927; Barnard, 1931) considered the Sialidae and Corydalidae to be distinct families and elevated Weele's tribes to subfamilial status, while others used Weele's categorical rankings (Banks, 1940, 1943; Kimmins, 1954). More recently (e. g. Chandler, 1956; Flint, 1973; Evans, 1978) the Sialidae and Corydalidae have been considered separate families.

Weele (1910) was the first to revise Corydalinae, recognizing eight genera and 34 species and discussing possible relationships based on general appearance. Navas (1915) proposed the name Neurhermes to replace Gray's Hermes, a homonym with a genus of gastropods, and Esben-Petersen (1924), Navas (1925), and Lestage (1927) proposed additional genera. Lestage (1927) included a list of world genera of Corydalinae and postulated generic affinities based on wing venation in his catalogue of Indo-chinese Corydalinae. Since 1927 work on Corydalinae has been mainly species description, though Banks (1940) included a key to Chinese genera, Kimmins (1948) reviewed the Protohermes in the British Museum, and Penny (1977) listed the New World species.

Natural history

With the exception of Corydalis cornutus, natural history of the Corydalinae is poorly known, though all larvae presumably inhabit flowing water. Larval lifespan may vary from one to five years (Evans, 1978) this being correlated with latitude in C. cornutus (Brown and Fitzpatrick, 1978). Some species have been observed to occupy specific microhabitats within a stream (Geijskes, personal communication), while label data indicate a positive correlation between species and stream type or altitude.

Adults are crepuscular or nocturnal and readily attracted to lights. Though there is some evidence for liquid feeding (Parfin, 1952), adult life is generally short, ranging from three to thirteen days for C. cornutus (Davis, 1903; Parfin, 1952). Adult emergence of some species is seasonal in certain regions, while little or no seasonality is observed in other localities. Seasonality may be expected in temperate regions, but reasons for seasonality in tropical areas remain unclear.

MATERIAL

This study is based on examination of about 2200 specimens of Corydalinae and Chauliodinae borrowed from museum and private collections. Individuals and institutions providing material for study were: P. C. Barnard, British Museum of Natural History, London, England (BMNH); D. H. Kavanaugh, California Academy of Sciences, San Francisco, California (CASC); J. E. H. Martin, Canadian National Collection of Insects, Biosystematics Research Institute, Ottawa, Ontario (CNCC); L. L. Pechuman, Cornell University, Ithaca, New York (CUNY); J. Kethly, Field Museum of Natural History, Chicago, Illinois (FMNH); L. A. Stange, Florida State Collection of Arthropods, Gainesville, Florida (FSCA); G. Ekis, Columbus, Ohio (GEKI); N. D. Penny, Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil (INPA); L. Dieckman, Institut für Pflanzenschutzforschung Kleinmachnow, Eberswalde, DDR (IFPK); C. L. Hogue, Los Angeles County Museum of Natural History, Los Angeles, California (LACM); M. M. Pearce, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZC); M. J. Glorioso, Columbus, Ohio (MJGC); J. Legrand, Museum National d'Histoire Naturelle, Paris, France (MNHN); C. A. Triplehorn, Ohio State University, Entomology, Columbus, Ohio (OSUC); N. W. Britt, Columbus, Ohio (NWBR); P. A. Adams, Fullerton, California (PAAC); G. W. Byers, Snow Entomological Museum, University of Kansas, Lawrence, Kansas (SEMK); S. J. Merritt, Texas A&M University, College Station, Texas (TAMU); W. F. Barr, University of Idaho, Entomology, Moscow, Idaho (UIDC); H. P. Brown, University of Oklahoma, Zoology, Norman, Oklahoma (UOKL); O. S. Flint, Jr., P. J.

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METHODS

Criteria for genera delimitation

Mayr (1969) considers a genus to be a monophyletic category containing a single species or group of species separated from other genera by a decided gap. I likewise believe genera should be monophyletic and recognizable by discontinuities in character states. As the degree of difference between genera or other supraspecific taxa is subjective, criteria for recognition of supraspecific categories should be explicitly stated to allow subsequent workers to judge the validity of such taxonomic decisions (Ekis, 1977b).

Before supraspecific classifications are developed, worldwide knowledge of the investigated taxon should be available (Erwin, 1975). This requires investigation of interspecific, but not intraspecific variation (Herman, 1970), and an attempt should be made to examine all species of the larger taxon before inferring generic limits. While knowledge of all interspecific relationships isn't essential, major monophyletic lineages based on synapotypies must be defined, as well as the relationships of each lineage to the others. After these relationships have been hypothesized discontinuities between lineages can be evaluated, and distinct lineages (defined by autapotypies) can be given categorical status, e. g. generic rank.

Stability and predictability of classifications should be considered when establishing generic limits. Where monophyletic lineages coincide with preexisting genera classification should be conservative, i. e. the preexisting classification should be retained. If the preexisting classification is incongruous with monophyletic lineages,

paraphyletic and polyphyletic genera should be converted into monophyletic ones, as polyphyletic classifications are of limited predictive value, and paraphyletic taxa are less predictive than monophyletic ones (Platnick, 1978). These discrepancies may be rectified by incorporation of excluded lineages in paraphyletic taxa or fragmentation into component monophyletic units.

A consideration of some authors, e. g. Heyer (1974), is that genera should contain a convenient number of species. If I were to consider this premise, then consolidation of small genera would seem logical, with the corollary that splitting would be appropriate where consolidation creates unwieldy genera. However, the splitting of genera only on the basis of number of species should be conservative to avoid proliferation of genera.

In this study several autapotypies involving male genitalia define distinct lineages, with no intergradation between lineages. As these monophyletic units are also recognizable on the basis of other characters, I propose that each be given generic status.

Phylogenetic and classificatory methods

My phylogenetic hypotheses and classifications are based on the results of a cladistic analysis, the principles of which were outlined by Hennig (1965, 1966). Phylogenetic classifications, including phyletic sequencing, a means of deriving a classification from an asymmetrical branch of a cladogram without superfluous supraspecific categories, have been discussed by Wiley (1979b). Proponents of phyletic sequencing include Nelson (1972, 1974), Cracraft (1974), Schuh (1976), and Wheeler (1979a, 1979b).

Dissecting methods

The tip of the abdomen was removed, cleared overnight in KOH or lactic acid, rinsed with water, and stored in a microvial with glycerin. Female internal structures were removed through a slit below the genital opening or were observed after inversion of the abdominal tip. Mouthparts were relaxed with Barber's fluid (53 parts 95% ethanol, 49 parts water, 19 parts ethyl acetate, 7 parts benzene). One maxilla and labial palp were removed, cleared in lactic acid or KOH, rinsed in water, and stored in microvials with glycerin. Examination of genitalia and mouthparts was in glycerin or lactic acid.

General methods

Size ranges were estimated by measuring the largest and smallest available individuals of each genus, selected by eye. Length was measured from tip of clypeus to tip of abdomen; wingspan was determined by summing width of the mesothorax and twice the length of the forewing. Genitalic and mouthpart dissections were made for at least one male and female of each available species. Generic descriptions should be understood to include characters denoted in the subfamilial description, and are based on specimens listed in Appendix A. As species concepts in most genera are poorly understood, necessitating revision before accurate names can be placed on many specimens, many specimens listed in the appendix are denoted as spp.; species I have confidently identified are listed separately. Lists of material only include localities and repositories, other data being summarized under natural history. Due to extreme numbers, Corydalis cornutus localities are given by state only, Mexican C. lutea records are listed as states, and C. lutea records from the United States are listed as counties. Geographic ranges of genera were determined from label data and reliable literature records. Drawings were made with a drawing tube on a Wild M5A stereoscopic microscope. Scale bars accompanying figures represent one millimeter unless otherwise indicated.

COMPARATIVE MORPHOLOGY

Justifications for thorough morphological analyses in revisionary studies were given by Ekis (1977a). As knowledge of internal structure of Corydalinae is limited to Corydalis cornutus, this discussion is restricted to integumental characteristics. Further, due to lack of immatures, I treat only imago features.

Although fluid preserved material of most Corydalinae is scarce, C. cornutus specimens have always been readily available. Consequently both internal and external structures have been described in considerable detail. Leidy (1848) discussed the digestive, reproductive, and nervous systems, Hilton (1909) treated the tracheal system, and Kelsey (1954, 1957) detailed the external morphology and musculature of the head and thorax. The larval nervous system was treated by Krauss (1884), Hammar (1908), and Hilton (1911).

Head

Typical features of the Corydalinae head are embodied in Corydalis cornutus as described by Kelsey (1954). Major variations involve the degree of flattening of the head and development of the lateral postocular margins of the cranium. In Protohermes and Neurhermes the head is robust, about as high as wide, while in other genera it is noticeably flattened.

The postocular ridge (fig. 1) extends laterally behind the eyes to the occiput. Its dorsal extension curves anteriorly at the posterior angle of the head, delimiting the postocular plane. This plane is generally less rugosely sculptured than adjacent regions of the head. In Platyneuromus (fig. 61) the postocular plane occupies the postocular flange, the explanate postocular cranial margin. The postocular spine arises from the posterior angle of the head, forming a lateral acumination of the postocular ridge. This spine, as well as the ridge itself, is barely noticeable in Protohermes and Neurhermes (figs. 56, 57), moderately developed in Chloronia and Neuromus (figs. 58, 62), and very conspicuous in other Corydalinae. In some Platyneuromus the spine is fused with the postocular flange.

The cranial disk, though rugose, is devoid of processes in most genera. However, the disk of Acanthacorydalis (fig. 60) is provided with a pair of lateral spines.

The ocelli occur on nearly contiguous prominences in most genera. The posterior margins of the lateral ocelli are nearly in line with the posterior margins of the compound eyes, occasionally being slightly anterior. The median ocellus is generally transverse, its posterior

margin about at the anterior margin of the lateral ocelli. In most Neurhermes and some Protohermes the median ocellus is distinctly anterior to the lateral ocelli.

The antennae consist of 35 - 75 articles, and are generally about as long as the forebody, though in male Corydalis they may be longer than the body. The antennifer is a ridged area at the postero-median margin of the transverse anterior tentorial pit. The scape is cylindrical, slightly longer than wide, and, together with the shorter, thinner pedicel, parallels the epistomal sulcus when extended laterally. The pedicel and scape are rugosely sculptured, while the antennal articles are covered with small tubercles or short setae. Tubercles are more common on proximal articles, distal articles are moderately setose. All articles are moderately setose in Protohermes and Neurhermes, with all setae very short. The antenna is filiform to sub serrate, anterior serrations being most apparent in Protohermes and Neurhermes.

The clypeal margin may be entire, as in Protohermes and Neurhermes (figs. 4, 5), or medially incised to varying degrees, ranging from the shallow notch in Chloronia (fig. 10) to the deep incision of Acanthacorydalis (fig. 6). The clypeal margin of many Corydalis displays a pair of antero-lateral and median projections, with the incision between the median projections. In some Corydalis the incision is obliterated by fusion of the median projections (fig. 7).

The triangular to broadly truncate or ovoid labrum (figs. 4 - 11) partly covers the mandibles, though in Corydalis and Acanthacorydalis it is slightly deflexed between the mandibles. It is glabrous dorsally,

moderately setose ventrally, and bears two median pairs of long setae and several short, fine setae. In Neuromus and Neoneuromus (figs. 8, 9) the short setae are more abundant, being especially predominant in Neuromus. The labrum of Neuromus often has a deflexed anterior margin with a feeble indentation.

The mandibles are subfalciform, triangular in cross section, and vary in length from one half to three quarters the length of the head. In female Acanthacorydalis the mandible is as long as the head, while it is longer in male Acanthacorydalis and most male Corydalis (figs. 60, 63). The inner margin of the mandible is entire basally, dentate distally, with one apical and three inner teeth. The dorsal and ventral surfaces are flattened, and exhibit feeble longitudinal depressions. The cuticle is smooth ventrally near the condyle, rugose elsewhere. Mandibular articulation occurs near the anterior margin of the eye.

The maxilla articulates at the lateral margin of the submentum, with the triangular cardo bearing several short setae on the outer margin. The subcylindrical stipes, one and a half to two times as long as wide, bears several setae on its outer margin. These setae are normally inconspicuous, but are well developed in Neurhermes and Protohermes (fig. 12). The triangular lacinia is fused basally with the stipes, closely paralleling the stipes and galea distally. Lacinia vestiture consists of stout setae; three long apical setae are present in all but Neuromus, Acanthacorydalis, and Corydalis (fig. 13). Membrane and two bandlike subgaleal sclerites separate the galea from the stipes,

with the lower sclerite often being divided by membrane. Microsculpture of the galeal base and stival membrane consists of diagonal series of acuminate scales. The galea is densely covered with short and long setae, many of the long setae in Neurhermes and Protohermes being flattened lanceolate. The apex, rounded in Protohermes and Neurhermes, acute in other genera, usually bears a sensory peg with five to seven microsetae. The sensory peg is poorly developed in Neuromus and Neoneuromus, absent in Neurhermes. The cylindrical five segmented maxillary palp (four segmented in Corydalus) arises from a distinct palpifer. The penultimate segment bears an apical crown of alternating longer and shorter setae; basal segments usually have similar crowns obscured by additional setae. The terminal segment is conical (fig. 12) or broadly rounded apically (fig. 13), and has one or two membranous areas densely covered with microsetae.

The labium, broadly joined to the submentum, consists of a nearly quadrate mentum, a short prementum, a pair of three or four segmented palps, and a bilobate ligula. Sclerotization of the mentum is most evident basally; numerous short setae are present dorsally. The rectangular prementum is weakly sclerotized, with the lateral palpifers more heavily sclerotized. The membranous ligula is moderately setose; the labial palp is usually similar to the maxillary palp, although the terminal segment is triangular in some Corydalus.

The submentum and gula are vested with microsetose shallow depressions. The posterior tentorial pits extend obliquely forward from the gular sutures, diverging anteriorly. They are linear in Protohermes and Neurhermes (fig. 3), linear in other genera (fig. 2).

Thorax

The thorax is fairly homogeneous throughout the Corydalinae, and has been amply detailed by Kelsey (1954, 1957). The prosternum of some Corydalis and Platyneuromus bears a pair of small antero-median acuminations.

The elliptical forewing is three to four times as long as wide and a quarter to half again longer than the body; the hindwing is slightly wider and about four fifths as long. Color varies from nearly hyaline in Chloronia, Neuromus, many Protohermes, and some Neoneuromus to brownish or light gray with darker markings in Corydalis, Platyneuromus, Acanthacorydalis, and Neoneuromus or to black with white maculations in Neurhermes and some Protohermes.

Wings are densely covered with grayish or brownish microtrichia and are fringed with longer macrotrichia. Fine black bristlelike macrotrichia are present dorsally on radial and medial veins and scattered in the anal area. Several rows of short, stout macrotrichia occur on the costa.

The costal vein tapers to the apex of the wing, while a fine vein continues around the wing. The subcosta, closely paralleled by and distally fused with R_1 , reaches the wing margin slightly before the apex. The radial sector contains four to sixteen veins, the last bifurcate in all Corydalinae except Corydalis (fig. 15) and Chloroniella. The number of sectorial veins varies within a species, and some individuals may have additional veins or vein bifurcations involving only one of a pair of wings.

The medial vein is nearly fused basally with the radius, diverging approximately one sixth of its length distally. M_{1+2} and M_{3+4} separate slightly distal to the base of Rs. Vein M_{1+2} may consist of two branches (Chloronia, Chloroniella, Platyneuromus, and some Corydalus) (figs. 14, 16), two bifurcate branches (many Neuromus and some Neoneuromus), or four to nine branches (Protohermes and many Neoneuromus). Vein M_{3+4} may be undivided (Chloroniella, Chloronia, and Corydalus), bifurcate (Acanthacorydalis, Neuromus, Neoneuromus, Neurhermes, and Platyneuromus), or consist of up to four branches (Protohermes).

The cubitus diverges from the media basally; Cu_2 separates from Cu_1 slightly past the point of divergence of the media in the forewing, basally in the hindwing. Cu_1 has one to six accesories, Cu_2 is unbranched.

Though veination in the anal area of fore and hindwing is similar, the anal area of the hindwing is much larger, forming a small anal fan. Vein 1A is normally two branched; it is three branched in Neurhermes and Protohermes (figs. 18, 19). Vein 2A is bifurcate, the upper branch approaching 1A and occasionally appearing to be a branch of 1A due to a short crossvein. Vein 3A is often sinuate and, due to a short crossvein, occasionally appears two branched, with the upper branch being the lower branch of 2A. Extra longitudinal veins may also be present.

Costal crossveins are extremely variable in number; there may be anywhere between 18 and 60 veins, with numbers varying among wings of

an individual. Crossveins may be contiguous basally, especially in Corydalus and Protohermes, or in a reticulate pattern (restricted to male Acanthacorydalis) (fig. 17).

Three crossveins connect R_1 and R_s in Corydalus, Chloronia, Chloroniella, and Platyneuromus; other Corydalinae have at least four crossveins. There are one to four crossveins between each sectoral branch. Chloronia and Platyneuromus have three crossveins between the radial sector and M_1 , Neuromus and Neurhermes have four, and other genera have three to eight. The basal r-m crossvein in the hindwing is long and oblique, connecting R_s with the base of M.

There are two medial crossveins in Platyneuromus and Chloronia, three in Neurhermes, Neuromus, and many Neoneuromus, while Corydalus, Acanthacorydalis, and Protohermes have as many as eight. There are usually one to three crossveins between branches of M, rarely up to seven. Three crossveins are often present between M_4 and Cu_1 , with a fourth connecting M and Cu, though Neurhermes and Protohermes have two; Acanthacorydalis and, rarely, Corydalus have as many as eight crossveins.

There is one cubital crossvein, except for Acanthacorydalis, which may have two or three. The cubital accesories are linked by a single crossvein in Neuromus and Neoneuromus (figs. 20, 21), two to five in Acanthacorydalis. Often one crossvien occurs between Cu and 1A, though extras are occasionally present. Anal crossveins are as described in the discussion of the anal area, though Acanthacorydalis often has extra anal area crossveins.

Abdomen

Non-genital segments in Corydalinae are similar to those of Chauliodinae, as described by Maki (1936) for Neochauiodes formosanus. However, Platyneuromus, Chloronia, and some Corydalis females have a sternal pouch on the sixth abdominal sternum (fig. 43). This structure is membranous, semicircular, and opens in the intersegmental membrane. It has previously been reported only for Chloronia (Weele, 1910; Flint, 1970), and its function remains unknown.

Male genitalia

Male genitalia consists of elements from the ninth and tenth segments, though much controversy exists over the exact homologies of these structures. The terminology used here is adapted from Acker (1960).

The ninth tergum is slightly more heavily sclerotized than preceding segments, and has an internal inflection basally which may be arched (figs. 30, 32, 34, 36) or inverted V-shaped (figs. 23, 24, 26, 28). In Neurhermes the tergum is much wider than long, with a shallow postero-median incision (fig. 36), while it is nearly quadrate in other genera.

The ninth gonocoxites are fused with the ninth tergite; in Neoneuromus the dorsal incisions of the tergum (fig. 32) may be vestiges of the ancestral line of fusion between tergum and gonocoxite (Acker, 1960). In all other Corydalinae fusion is complete.

The ninth gonostyli (inferior appendages of Weele, 1910; subgonopods of Crampton, 1918; lower lobes of the cerci of Chandler, 1956; ventral arms of the basimere of Snodgrass, 1957; catoprocesses of Tjeder, 1970) articulate at the postero-ventral margins of the ninth tergum, and may be unguiform or clavate. The clavate stylus (Acanthacorydalis, Platyneuromus, Chloronia, Corydalis) (figs. 22, 25, 27, 29) is densely setose, directed postero-medially, and terminates in a small chitinous claw, the claw being absent in many Corydalis. Unguiform styli are directed medially and may be glabrous or sparsely setose with a glabrous tip (figs. 31, 33, 35, 37). The gonostylus of Neurhermes

(fig. 37) is directed postero-medially in the basal half, dorsally in distal half. The apodeme of the ninth gonostylus usually parallels the lateral margin of the ninth tergum, though it is directed medially in Protohermes and Neurhermes (figs. 35, 37).

The ninth sternite or genital valve is generally quadrate, though it is attenuate in Neoneuromus (fig. 33), broadly and deeply incised medially in Protohermes (fig. 35). Neurhermes display a median projection (fig. 37), sometimes with a median incision; Acacanthacorydalis have postero-lateral lobes (fig. 22); Chloronia bear long setae on feebly to well developed lateral lobes (fig. 27). The setae of Acanthacorydalis are short and stout while those of Chloronia are fine.

The tenth tergites (superior appendages of Weele, 1910; surgonopods of Crampton, 1918; dorsal arms of basimere of Snodgrass, 1957; anoproceses of Tjeder, 1970) are generally tubular or clavate, slightly sigmoid, and about the length of the ninth tergum. The tenth tergites of Chloronia are two to three times as long as the ninth (figs. 26, 27), while those of some Neuromus are flattened (figs. 30, 31). Neurhermes exhibits a biramous tergite with the dorsal arm shorter than the ventral (figs. 36, 37); some Protohermes have a short ventral and a long dorsal arm, though most are uniramous (figs. 34, 35).

The tenth sternite is represented by the fused gonocoxites (penis of Weele and Crampton, parameres of Tjeder, aedeagus of Chandler and others) and the gonostyli (mamilliform processes of Weele, penis hooks of Crampton). The gonocoxites normally form a bandlike sclerite, though a postero-median projection is present in Neoneuromus (fig. 39). The styli are sparsely setose and usually digitiform. In most genera

they are paired antero-medially; they are located lateral to the median projection in Neoneuromus, while they are broadly fused in many Neuromus (fig. 31). In Corydalis and Chloronia the gonostyli are shorter and papilliform (figs. 40, 41).

A pair of genital papilli (figs. 22, 37, 38) (utriculi of Tjeder) may be present lateral to the genital opening, and possibly represent tenth sternal apophyses (Acker, 1960), or may be of ninth sternal origin. They may be present in all members of a genus (Protohermes, Neurhermes, Acanthacorydalis), some members of a genus (Platyneuromus, Neuromus), or unknown in any members (Corydalis, Chloronia, Neoneuromus).

The cerci are located between the tenth tergites and ninth gonostyli, and are small, hemispherical, and setiferous. A sclerite over the anus of Neoneuromus (fig. 32) may represent the eleventh tergum (Acker, 1960).

Female genitalia

The eighth sternite is quadrate or with convex margins, moderately sclerotized, and sparsely to moderately setose. The area between the sternite and ovipositor is generally membranous, though two weak, setose sclerites are present in Neurhermes (fig. 44).

The ninth tergum is moderately sclerotized and usually membranous dorsally. The tenth tergum is divided dorsally by the anus, and is bilobed, nearly divided by the round, setiferous cercus. The ovipositor of Corydalis has been described by Mickoleit (1973), and is similar to that of other Corydalinae, major variations being development of the lateral sclerite and articulation of the ninth gonostylus.

The lateral sclerite (fig. 43), strengthening the ninth gonocoxite, is usually well sclerotized, though it is only weakly to moderately sclerotized in Chloronia. The gonostylus is articulated with the posterior tip of the gonocoxite in Neurhermes and Protohermes (fig. 44), while it is fused in other genera.

The genital opening is in the membrane at the base of the ovipositor, and opens into a membranous saclike (fig. 45) or muscular tubular (figs. 46, 47) bursa copulatrix. The spermathecal duct is short and biramous T-shaped in genera with a saclike bursa, while in genera with a tubular bursa (Neuromus and Neoneuromus) it is long, twisting, and continuous with the bursa. The paired, ovoid spermathecae are located at the end of the spermathecal duct, on either arm of the T-shaped duct, though only one spermatheca is present in Neuromus. The common oviduct enters the saclike bursa near the opening of the

spermathecal duct, while it enters in the anterior third of the bursa - spermathecal duct complex of Neuromus and Neoneuromus.

A pair of glands located on the ovipositor immediately behind the genital opening may be homologous to the accesory glands of Sialidae as described by Heberdey (1931). These glands are absent in Corydalus, Chloronia, and Platyneuromus, while they are longer than the bursa - spermathecal duct complex in Protohermes and Neurhermes (figs. 48, 49) and one fourth to one half as long in Neuromus, Neoneuromus, and Acanthacorydalis (figs. 50 - 52). They are nearly linear in Neuromus and Neoneuromus, sigmoid in Protohermes, Neurhermes, and Acanthacorydalis.

The colleterial gland, opening near the center of the ovipositor, is membranous and nearly as long as the abdomen. This gland secretes a chalky substance used in coating the eggs at oviposition.

CLADISTIC ANALYSIS

As confidence in evolutionary analyses increases with number and diversity of character sources investigated, it would be ideal to investigate all possible sources, including internal and external morphological, physiological and biochemical, karyological, life history, and ecological sources. However, lack of living specimens and life history data often precludes such thorough investigations, necessitating reliance on morphological characters. Moreover, lack of suitably preserved material may prevent thorough examination of internal structures, restricting character investigation to integumental characteristics.

Such is the case in this study - little is known about life histories of most Corydalinae and lack of fluid preserved material prevents comparisons of delicate internal structures. I have partially alleviated this problem by thorough investigation of available integumental sources, including previously overlooked or underutilized sources.

Sources investigated include mouthparts and internal female genitalia, which have never been incorporated into Corydalinae evolutionary hypotheses, and male genitalia and wing venation. While male genitalia and general appearance have been used by many authors, including Weele (1910), wing venation has been used sparingly by most authors except Lestage (1927).

For any of these characters to be useful we must know the variation within each taxon and the polarity, or relative apotypy or

plesiotypy of each character state. Variation was determined by examination of as many species of each genus as available, although lack of Chloroniella specimens necessitated reliance on literature references. Character polarities were determined by the outgroup method, whereby joint possession of a character state by the ingroup (taxon under investigation) and the outgroup (sister group or next highest taxon) is considered indicative of inheritance from a primitive common ancestor rather than independent derivation. Polarity determinations for character states not present in the outgroup were accomplished by using other characters to establish monophyletic units within the Corydalinae to serve as ingroups and outgroups.

Assuming monophyly of the Corydalidae, I looked outgroup to the Chauliiodinae, which must either be, or contain, the sister group of Corydalinae. The Sialidae, the probable sister group of Corydalidae, were also examined. Taxa examined include Chauliodes pectinicornis, C. rastricornis, Neochauliodes simplex, Neochauliodes spp., Neohermes concolor, Neohermes spp., Nigronia fasciatus, N. serricornis, Protochauliodes cinerascens, and Sialis spp. Wing venation and genitalia for additional Chauliiodinae genera were analyzed by reference to works by Esben-Petersen (1924) and Barnard (1931) (Platychauliodes, Taeniochauliodes), Kimmins (1938, 1954) (Anachauliodes, Archichauliodes, Ctenochauliodes), Munroe (1953) and Chandler (1956) (Dysmicohermes), and Ponomarenko (1976) (Cretochaulus).

Characters used in the cladogram and discussion are listed in Table 1, with references to illustrations in parentheses. Numbers in parentheses in the discussion and cladogram refer to apotypic character states.

Table 1 - Character States

Character	Plesiotypic	Apotypic
1. Gular setation	conspicuously setose	microsetose
2. Postocular ridge	absent	present (fig. 1)
3. Postocular plane	absent	present (fig. 1)
4. Head shape	robust	flattened
5. Postocular flange	absent	present (fig. 61)
6. Postocular spine	feebly developed (figs. 56, 57)	moderately to well developed (figs. 58 - 63)
7. Posterior tentorial pits	linear (fig. 3)	arcuate (fig. 2)
8. Cranial disk	without spines	with spines (fig. 60)
9. Antennae	feebly subserrate (figs. 56, 57)	filiform
10. Clypeal margin	entire (figs. 4, 5)	incised medially (figs. 6 - 11)
11. Male mandibles	not enlarged	enlarged (figs. 60, 63)
12. Female mandibles	three fourths head length or shorter	length of head
13. Labrum shape	triangular (figs. 4 - 7)	ovoid (figs. 8, 9)
13'		broadly truncate (figs. 10, 11)
14. Labral position	over mandibles	between mandibles
15. Labral anterior margin	sparsely setose	fimbriate (fig. 9)
16. Maxilla shape	short and broad (fig. 12)	relatively elongate (fig. 13)
17. Lacinia apex	with three elongate setae (fig. 12)	without elongate setae (fig. 13)
18. Stipal setae	conspicuous (fig. 12)	inconspicuous (fig. 13)
19. Galeal setae	flattened, lanceolate	bristlelike
20. Galeal sensory peg	well developed (figs. 12, 13)	poorly developed
20'		absent

Table 1 (cont.)

21. Maxillary palp	five segmented (fig. 12)	four segmented (fig. 13)
22. Maxillary palp apex	conical (fig. 12)	broadly rounded (fig. 13)
23. Maxillary palp setae	long	short
24. Maxillary palp sensory areas	one at apex	two at apex
25. Labial palp	four segmented	three segmented
26. Labial palp sensory areas	one at apex	two at apex
27. Last branch of radial sector	bifurcate (figs. 14, 15, 17 - 21)	not bifurcate (fig. 16)
28. M_{1+2} branches	two (figs. 14 - 17)	four or more (figs. 18 - 21)
29. M_{3+4} branches	two (figs. 16 - 21)	one (figs. 14, 15)
30. 1A branches	two (figs. 14 - 17, 20, 21)	three (figs. 18, 19)
31. R_1 -Rs crossveins	three (figs. 14 - 16)	four or more (figs. 17 - 21)
32. Medial crossveins	two (figs. 14, 16, 18)	three or more (figs. 15, 17, 19 - 21)
33. M-Cu crossveins	three (fig. 18)	four (figs. 14 - 17, 20, 21)
33'		six or more (fig. 17)
34. Cubital accesory crossveins	absent (figs. 14 - 16, 18, 19)	present (figs. 17, 20, 21)
35. Costal crossveins	verticle or oblique	reticulate (fig. 17)
36. Male ninth sternum	hind margin not as in fig. 35	hind margin as in fig. 35
37. Male ninth sternum	more or less quadrate	attenuate (fig. 33)
38. Male ninth sternum	without median projection	with median projection (fig. 37)
39. Male ninth sternum	without postero- lateral lobes	with postero-lateral lobes (fig. 22)
40. Male ninth sternum	without setiferous lateral protuberances	with setiferous lateral protuberances
41. Male ninth sternum	with normal setae	with short, stout setae
41'		with fine setae

Table 1 (cont.)

42. Male ninth sternum	not sclerotized dorsally	sclerotized dorsally (fig. 37)
43. Male ninth sternum	without internal ridges	with internal ridges (figs. 31, 33)
44. Male ninth sternum	not locking with tenth sternite	locking with tenth sternite
45. Male ninth tergum	more or less quadrate	short, with broad median incision (fig. 36)
46. Male ninth tergum	with dorso-lateral incisions (fig. 32)	without dorso-lateral incisions
47. Ninth tergal internal inflection	without median fossa	with median fossa (figs. 30, 32)
48. Ninth tergal internal inflection	arched (figs. 30, 32, 34, 36)	inverted V-shaped (figs. 23, 24, 26, 28)
49. Membrane between ninth and tenth sternites	thin	thickened, bilobate
49'		thickened, regularly convoluted
50. Genital papilli	present (figs. 22, 37, 38)	absent
51. Tenth gonocoxites	without median projection	with median projection (fig. 39)
52. Tenth gonocoxites	antero-lateral corner without acute projection (figs. 36, 39, 42)	antero-lateral corner with acute projection (figs. 40, 41)
53. Tenth gonostylus	digitiform (figs. 38, 39, 42)	short, broad (fig. 31)
53'		papilliform (figs. 40, 41)
54. Ninth gonostylus	unguiform (figs. 31, 33, 35, 37)	clavate (figs. 22, 25, 27, 29)
55. Ninth gonostylus	relatively short	long, bent (fig. 37)
56. Ninth gonostylus	sparsely setose	densely setose
57. Ninth gonostylus apodeme	parallels ninth tergum (figs. 22, 25, 27, 29, 31, 33)	directed medially (figs. 35, 37)
58. Tenth tergites	short	long, thin (figs. 26, 27)
59. Tenth tergites	not as in figs. 36, 37	biramous as in figs. 36, 37

Table 1 (cont.)

60. Eleventh tergum	present (fig. 32)	absent
61. Lateral sclerite of ovipositor	well sclerotized	weakly sclerotized
62. Gonostylus	articulated with gonocoxite (fig. 44)	fused with gonocoxite (fig. 43)
63. Sternal pouch	absent	present (fig. 43)
64. Sclerites between eighth sternum and gonopore	absent (fig. 43)	present (fig. 44)
65. Bursa copulatrix	not saclike (figs. 46, 47)	saclike (fig. 45)
66. Number of spermathecae	two (figs. 45, 46)	one (fig. 47)
67. Spermathecal duct	continuous with bursa (figs. 46, 47)	separate from bursa, T-shaped (fig. 45)
68. Accesory glands	present	absent
69. Accesory glands	short	long
70. Accesory glands	sigmoid (figs. 48 - 50)	linear (figs. 51, 52)

Character phylogeny

The presence of a postocular ridge (2) and postocular plane (3) is regarded as autapotypic for the Corydalinae as neither structure is present in the Chauliodinae or Sialidae. The microsetose gular region (1) of Corydalinae is considered autapotypic; the gular region of Sialidae and Chauliodinae is conspicuously setose.

Dorso-ventral compression of the head (4) within Corydalinae is apotypic as indicated by the robust condition in the primitive Neurhermes and Protohermes, the Chauliodinae, and Sialidae. Expansion of the lateral margin of the cranium into a flange (5), unique to Platyneuromus, is considered autapotypic, as are the spines on the cranial disk of Acanthacorydalis (8). Development of the postocular spine varies from feeble expression in Neurhermes and Protohermes to well developed (6) in other genera. Linear posterior tentorial pits, subserrate antennae, and an entire clypeal margin are primitively found in Neurhermes and Protohermes as well as in the Chauliodinae; apotypic arcuate tentorial pits (7), filiform antennae (9), and incised clypeal margin (10) indicate the other genera form a monophyletic group.

Enlarged male mandibles (11) and a deflexed labrum (14) are convergent apotypies in Acanthacorydalis and most Corydalis, while female mandibles the length of the head (12) are restricted to Acanthacorydalis. Enlarged male mandibles in Corydalis are not considered apotypic for the genus as C. cephalotes, probably the most primitive species, has normal length mandibles. A triangular labrum is considered plesiotypic as indicated by the identical condition in Chauliodinae. In

Neuromus and Neoneuromus the labrum is ovoid (13), with a fimbriate anterior margin (15) autapotypic for Neuromus. A broadly truncate labrum (13') may have been independently derived in Platyneuromus and Chloronia, or may have evolved in the common ancestor to the New World lineage, and has undergone reversal of this character state in Corydalus.

The maxilla of Neurhermes and Protohermes, as in Chauliodinae and Sialidae, is relatively short and broad with conspicuous stipal setae and flattened galeal setae. The more elongate maxilla (16) with inconspicuous stipal setae (18) and bristlelike galeal setae (19) indicates the common ancestry of the rest of Corydalinae. The lacinia bears three elongate apical setae in most Corydalidae; independent loss of these setae (17) has occurred in Acanthacorydalis, Neuromus, and Corydalus. The well developed sensory peg at the tip of the galea has been reduced in the Neuromus - Neoneuromus lineage (20) and lost in Neurhermes (20').

The maxillary and labial palps have five and four segments respectively in most Corydalinae; the four segmented maxillary (21) and three segmented labial (25) palps of Corydalus are autapotypic. Terminal palp segments of most Corydalidae are conical, and the broadly rounded apex in the New World genera indicates monophyly. Reduction of the setae on the last two palp segments has occurred in all Corydalinae except Neurhermes; this may have occurred twice, once in Protohermes and again in the ancestor to the other genera, or may have occurred several different times. One sensory area is primitively present at the tips of the palps as indicated by the homologous state in Chauliodinae; two

areas (24, 26) have evolved in the Protohermes - Neurhermes lineage and the New World lineage, with possible secondary loss of one maxillary palp sensory area in Chloronia.

Most Corydalinae wings exhibit a bifurcate last branch of the radial sector, while that of Corydalis is unbranched (27). As presumably primitive Chauliodinae (Dysmicohermes, Chandler, 1956; Cretochaulus, Ponomarenko, 1976) display the bifurcate condition, and Corydalis is a highly derived genus, the non-bifurcate condition is considered apotypic.

In most Corydalinae, Sialidae, and presumed primitive Chauliodinae M_{3+4} consists of two branches, while these have fused (29) in the ancestor of Corydalis and Chloronia. The opposite trend is apparent in M_{1+2} - again the primitive state is two branched, but the derived state, present in the Protohermes - Neurhermes and Neuromus - Neoneuromus lineages, consists of four or more branches (28). An additional 1A branch (30) is shared by Protohermes and Neurhermes, other Corydalinae, most Chauliodinae, and Sialidae having 1A two branched.

As indicated by comparison with the Chauliodinae and Sialidae, crossvein addition has been a general trend. Three crossveins between R_1 and R_s and two medial crossveins are primitive states, while four or more crossveins between R_1 and R_s (31) and three or more medial crossveins have evolved in the Protohermes - Neurhermes and Neuromus - Neoneuromus lineages and in Acanthacorydalis. Alternatively, the apparent plesiotypies in the New World genera may be secondarily derived. Medial crossvein number has also increased in Corydalis. Three crossveins are plesiotypically present between M and Cu in Protohermes and Neurhermes, while the other genera have four (33), except for Acanthacorydalis,

with six or more (33'). Crossveins between cubital accesories have evolved in the Neuromus - Neoneuromus lineage and in Acanthacorydalis, while a reticulate costal crossvein pattern (35) is autapotypic for Acanthacorydalis.

A more or less quadrate male ninth sternum is plesiotypic, as indicated by this state in Chauliodinae and Sialidae. The broad, deep medial incision of Protohermes (36), attenuate shape of Neoneuromus (37), postero-median projection and sclerotized dorsal surface of Neurhermes (38, 42) are autapotypies, as are the short, stout setae of Acanthacorydalis (41) and the fine setae of Chloronia (41'). Internal longitudinal ridges (43) are shared by Neuromus and Neoneuromus, while these ridges are deep and platelike in Neuromus (44), forming a coupling mechanism with the tenth sternite.

The male ninth tergum of both Chauliodinae and Corydalinae is nearly quadrate, except for the autapotypically shortened tergum of Neurhermes (45). If the dorso-lateral slit of Neoneuromus represents remnants of the division between tergum and ninth gonocoxite (Acker, 1960), then complete fusion (46) has occurred in all other genera.

The internal inflection at the anterior margin of the ninth tergum is primitively a simple arch in Protohermes and Neurhermes, similar to that of Chauliodinae. The deeper arch with a median fossa (47) is shared by Neuromus and Neoneuromus, while an inverted V-shaped inflection (48) indicates the monophyly of Acanthacorydalis and the New World genera.

The membrane immediately behind the ninth sternum, primitively thin, is thickened (49) in the New World genera. Two distinct lobes are

formed in Platyneuromus and Chloronia, and regular convolutions are present in Corydalus (49'). As more characters indicate a sister group relationship between Chloronia and Corydalus than between Chloronia and Platyneuromus, the regularly convoluted state is regarded as more derived.

As the genital papilli are present throughout the primitive Protohermes - Neurhermes lineage and in Acanthacorydalis, the most plesiotypic of the Acanthacorydalis - New World lineage, these are regarded as primitive. Presence of these papilli in the most primitive Neuromus and Platyneuromus species is further evidence of their plesiotypy; they have been lost in (50) in Neoneuromus, Chloronia, and most Neuromus and Platyneuromus.

The tenth gonocoxites are generally without median projections; presence of a broad median projection (51) in Neoneuromus is inferred as autapotypic. Pointed antero-lateral projections (52) and papilliform tenth gonostyli (53') have evolved in the relatively derived Corydalus - Chloronia sister pair, as indicated by the small anterior projections and elongate, digitiform styli of other Corydalinae lineages. The short, broad gonostyli of Neuromus are autapotypic.

As the ninth gonostylus of the Acanthacorydalis - New World lineage is clavate (54) while those of the more primitive Protohermes - Neurhermes and Neuromus - Neoneuromus lineages are unguate, the clavate state is regarded as apotypic. Correlated with this, but also present in advanced Neuromus species, is dense setation (56). The extremely elongate, bent stylus (55) of Neurhermes is autapotypic, while the

apodemes of the ninth gonostylus are directed mesad (57) in Protohermes and Neurhermes, functioning as support for the membranous genital area.

The tenth tergites of Corydalinae are relatively short and cylindrical; tergites at least five times as long as wide (58) and biramous tergites (59) are autapotypic for Chloronia and Neurhermes respectively. The structure interpreted as the eleventh tergite (Acker, 1960) is present only in Neoneuromus, with loss of this structure (60) occurring at least three times (in Neuromus and the Protohermes - Neurhermes and Acanthacorydalis - New World lineages).

The weakly developed lateral sclerite of the ovipositor of Chloronia (61) is considered autapotypic as this sclerite in other Corydalidae and Sialidae is well developed. The gonostylus is freely articulated with the tip of the gonocoxite in Sialidae and many Chauliodinae, while fusion of these structures (62) indicates at least two lineages in Corydalinae, with that lineage excluding Protohermes and Neurhermes being monophyletic.

Autapotypic setiferous sclerites between the gonopore and eighth sternum (64) are unique to Neurhermes, while the sternal pouch (63) is restricted to the New World genera. Monophyly of the New World genera is further indicated by lack of accessory glands (68), while glands much longer than those of any other Megalopteran (69) are shared by Protohermes and Neurhermes. As these glands are sigmoid in Acanthacorydalis and the Protohermes - Neurhermes lineage, the linear state (70) in the Neuromus - Neoneuromus lineage is considered apotypic.

A separate saclike bursa copulatrix (65) has evolved independently in the Protohermes - Neurhermes and Acanthacorydalis - New World

lineages, as indicated by the plesiotypic state of Chauliodinae, Sialidae, and the Neuromus - Neoneuromus lineage. A biramous T-shaped spermathecal duct non-continuous with the bursa (67) is correlated with the saclike bursa, while a single spermatheca (66) is autapotypic for Neuromus.

No discussion was given for size and color characters as polarities remain uncertain. The large size of Acanthacorydalis is possibly apotypic, but due to lack of knowledge on ecology and influence on size, this remains unsure. Luteus coloration occurs in some members of all major lineages, and may be due to plesiotypies or adaptive convergencies. Likewise, dark coloration in the Protohermes - Neurhermes lineage may be synapotypic, with the lighter color of many Protohermes autapotypic for those species, or autapotypic for Neurhermes and convergently autapotypic in several Protohermes species.

Phylogenetic considerations

Although species level cladograms do not rule out ancestor - descendent relations among extant taxa, and therefore are not necessarily representations of the true phylogeny, but rather, representations of several possible phylogenetic trees (Platnick, 1977), supraspecific cladograms can be interpreted as representing phylogeny. As each supraspecific taxon on the cladogram is presumed monophyletic, and only individual species within each taxon can give rise to new taxa, ancestor - descendent relations among supraspecific taxa are impossible (Wiley, 1979a).

Therefore I consider the genus level cladogram of fig. 53 a logical hypothesis of Corydalinae phylogeny, based on 70 characters investigated in eight non-monotypic genera. Although no ancestors are represented on the cladogram, an early dichotomy into two ancestral species is suggested, one of these leading to the Protohermes - Neurhermes lineage, the other eventually giving rise to all the other genera. A dichotomy of this species led to the Neuromus - Neoneuromus and the Acanthacorydalis - New World lineages, with subsequent speciation events leading to the ancestors of each genus.

The probable position of Chloroniella (not shown in fig. 53 or discussed previously) can best be resolved after examination of actual specimens; characters deciphered from previous descriptions indicate inclusion in the Acanthacorydalis - New World lineage, but conflicting character states indicate relationship with either Acanthacorydalis, the most plesiotypic member of this lineage, or Corydalis, the most apotypic.

A well developed postocular spine (6) and four m-cu crossveins (33) are shared with all genera except Protohermes and Neurhermes, the male ninth tergal internal inflection (48) indicates placement in the Acanthacorydalis - New World lineage, an unbranched M_{3+4} (29) is shared with Corydalis and Chloronia, and a non-bifurcate last radial sector branch (27) indicated Corydalis is the sister genus. However, postero-lateral lobes of the male ninth sternite (40) indicate affinity with Acanthacorydalis.

The actual relationship may be somewhere between Acanthacorydalis and Platyneuromus, in which case Chloroniella should share at least some of the apotypies defining the monophyly of the New World lineage, such as a thickened membrane behind the male ninth sternite (49), presence of a sternal pouch (63), or absence of accessory glands (68) in females. Presence of all these apotypies plus those indicating the sister group relationship of Corydalis and Chloronia would indicate common ancestry with Corydalis, especially if any other apparent autapotypies of Corydalis are shared.

Biogeographic considerations

As readily seen in figures 54 and 55, the distribution of Corydalinae is mainly tropical Asian and American, although Chloroniella is restricted to South Africa, Corydalus cornutus ranges to southern Canada, and Protohermes grandis is present in Japan. The Neuromus - Neoneuromus and Protohermes - Neurhermes lineages are Asian, while the Acanthacorydalis - New World lineage has one genus in Asia, one in South Africa, and three in the New World.

Many Neoneuromus occupy Asian montane regions and are restricted to the mainland, while its sister genus, Neuromus, is apparently lowland and occurs on some Malaysian and Indonesian islands. Neurhermes and its sister group, Protohermes, may have both montane and lowland species, and occur on islands and the mainland. Acanthacorydalis has a similar distribution to Neoneuromus.

The New World lineage is most diverse in tropical South America, although Platyneuromus is restricted to Central America. The ancestral Platyneuromus probably diverged from an ancestral South American stock after a vicariant event between Central and South America.

Because of the diversity and presence of the most primitive species of Corydalus and Platyneuromus in the Amazonian region, I hypothesize this as the ancestral range of the common ancestor of these genera, with subsequent range extension into Central America after divergence of Chloronia and Corydalus. Chloronia mexicana, the northernmost Chloronia species, appears to be highly derived, as do Corydalus cornutus and C. lutea, the northernmost Corydalus species.

Taxonomic conclusions

Before conversion of the cladogram into a phyletic sequence classification a suprageneric category must be established for the three major lineages. Although this category is between genus and subfamily, making tribal status appear logical, I believe such a designation adds little to predictability of the classification. Tribal status should imply significant difference between lineages. However, the difference between the three major lineages of Corydalinae is no greater than that between genera. Therefore I am assigning each of these lineages the informal status of genus assemblage, this category being merely for taxonomic convenience and without nomenclatural significance.

The classification I propose for Corydalinae (Table 2) reflects the phylogeny of the subfamily with minimum nomenclatural change. Two of the eleven genera recognized by Lestage, Doeringia and Allohermes, do not appear in this classification due to new synonymies. As Doeringia appears to be a rather derived member of the Platyneuromus lineage, exclusion from Platyneuromus would require recognition of Platyneuromus as paraphyletic. Likewise Allohermes is an apparently derived member of the Protohermes lineage, necessitating synonymy. As I have been unable to satisfactorily establish the position of Chloroniella I list it at the end of the classification under "placement uncertain."

Table 2 - Classification of Corydalinae

Protohermes assemblage

Protohermes

Neurhermes

Neuromus assemblage

Neuromus

Neoneuromus

Corydalus assemblage

Acanthacorydalis

Platyneuromus

Chloronia

Corydalus

Chloroniella - placement uncertain

SYSTEMATICS SECTION

Subfamily Corydalinae

Corydalinae Davis, 1903: 443. (type genus Corydalus Latreille, 1802: 290). Tilyard, 1918: 820. Lestage, 1927: 75, 93. Banks, 1940: 179 (as Corydalini).

Neurominae Weele, 1909: 250; 1910: 8 (as Neuromini) (type genus Neuromus Rambur, 1842: 441). Barnard, 1931: 170. Kuwayama, 1962: 327.

Diagnosis. Quadrate head with postocular ridge, spine, and plane; microsetose gular region; males with well developed ninth gonostyli.

Description. Size: length 15 - 70 mm; wingspan 45 - 170 mm. Coloration: often luteus or stramineus with piceus markings, sometimes fuscus to piceus; wings nearly hyaline with darker markings, sometimes smoky or black with lighter maculations. Head: quadrate, robust to flattened, slightly rugose with smooth dendriform patterns; gular region microsetose; posterior tentorial pits oblique, linear or arcuate; postocular ridge and plane present, postocular spine feebly to well developed; ocelli centered between posterior margins of eyes, hind margin of median ocellus rarely anterior to lateral ocelli; antenna near anterior of eye, with 30 - 85 articles, usually filiform, about length of forebody; clypeal margin entire or incised medially; labrum triangular, ovoid, or broadly truncate, usually partly covering mandibles; mandibles usually half to three fourths length of head, with three inner teeth, rarely greatly enlarged, without distinct teeth. Thorax: prothorax rectangulate or trapezoidal, slightly narrower than head, about length of meso- plus metathorax; meso- and metathorax

quadrate, about equal sized, slightly wider than hind margin of pronotum; legs about length of forebody, femur about length of tibia, tibial apex with two ventral spines, tarsi with five articles, first and fifth about equal in length, articles two through four combined about length of first, tarsal claws feebly dilated basally. Wings: elongate elliptical, forewing half again length of body, hindwing four-fifths length of forewing, with small anal fan; Rs four to 16 branched, M_{1+2} two to nine branched, M_{3+4} one to four branched, Cu_1 with one to six accessories, Cu_2 one branch, 1A two or three branches, 2A two branches, 3A one or more branches; 3, or 4 - 14 R_1 - Rs crossveins, three to eight Rs - M crossveins, basal one in hindwing long, oblique, two to eight medial crossveins with one to seven between branches of M, three to eight m-cu's, one (rarely up to three) cu's with zero, one, or two to five crossveins between accessories, costal crossveins 18 - 60, verticle or oblique, rarely in reticulate pattern. Males: ninth sternite and tergite usually quadrate; ninth gonostyli well developed; clavate or unguate, apodeme usually paralleling margin of ninth tergum; tenth gonocoxites fused medially; tenth gonostyli sparsely setose, usually digitiform. Females: eighth sternum usually quadrate; ovipositor composed of ninth gonocoxites, reinforced by usually well sclerotized lateral sclerite; gonostylus fused or articulate with gonocoxite; genital opening near anterior of ovipositor; spermathecae ovoid, usually paired, rarely single; spermathecal duct usually about length of bursa; accessory glands immediately behind genital opening when present; colleterial gland large, opening at midlength of ovipositor.

Distribution: temperate and tropical North and South America, South Africa, temperate and tropical Asia (India to China and Indonesia, Japan).

Natural history: Larvae are aquatic and long lived, while adults are often collected at lights, many being found in montane regions.

Remarks: Due to great intraspecific variation within this subfamily, some genera contain many nominal species, yet the total number of species in Corydalinae may be less than fifty. Relatively little material is available for Asian genera, making generic revisions difficult.

Key to genera of Corydalinae

1. Three crossveins between R_1 and R_s (figs. 14 - 16) 2
- 1'. Four or more crossveins between R_1 and R_s (figs. 17 - 21) 5
- 2(1). M_{3+4} bifurcate (fig. 16); postocular region explanate (fig. 61);
Central America Platyneuromus Weele
- 2'. M_{3+4} a single branch (figs. 15, 15); postocular region not explanate 3
- 3(2'). Last branch of radial sector branched (fig. 14); South America
..... Chloronia Banks
- 3'. Last branch of radial sector unbranched (fig. 15) 4
- 4(3'). Male ninth gonostylus clavate (fig. 29); males usually with
enlarged mandibles; North to South America . Corydalis Latreille
- 4'. Male ninth gonostylus clawlike; South Africa
..... Chloroniella Esben-Petersen
5. (1'). Occipital disk with two prominent spines (fig. 60); males with
enlarged mandibles; large, dark species; Asia
..... Acanthacorydalis Weele
- 5'. Occipital disk without spines; males never with enlarged mandibles
..... 6
- 6(5'). Posterior tentorial pits arcuate (fig. 2); postocular tooth
well developed; 1A two branched (figs. 20, 21) 7
- 6'. Posterior tentorial pits linear (fig. 3); postocular tooth poorly
developed; 1A three branched (figs. 18, 19) 8

Key to genera (cont.)

- 7(6) Male ninth sternite attenuate (fig. 33); female with two spermathecae (fig. 46); labral margin with few setae (fig. 8); mostly large, dark species; Asia Neoneuromus Weele
- 7'. Male ninth sternite quadrate (fig. 31); female with one spermatheca (fig. 47); clypeal margin fimbriate (fig. 9); moderate sized, pale species; Asia Neuromus Rambur
- 8(6'). Male tenth tergites always biramous, ventral arm slightly longer than dorsal (figs. 36, 37); head and body black, pronotum often orange, wings black with light maculations; galea without sensory peg; Asia Neurhermes Navas
- 8'. Male tenth tergites simple (figs. 34, 35) or with dorsal arm much longer than ventral; body usually pale, wings hyaline to smoky, sometimes with lighter markings; galea with sensory peg; Asia ..
..... Protohermes Weele

Genus Protohermes Weele (figs. 4, 12, 19, 34, 35, 49, 55, 56)

Protohermes Weele, 1907: 243. (type species Protohermes anticus Weele, 1907: 243, not Hermes anticus Walker, 1853: 207; designation by Weele, 1910); 1909: 251; 1910: 35. Banks, 1908: 28; 1940: 179. Lestage, 1927: 99. Kimmins, 1948: 52.

Allohermes Lestage, 1927: 100. (type species Protohermes davidi Weele, 1909: 254; original designation). New synonymy.

Diagnosis. Linear posterior tentorial pit; galeal sensory peg well developed; usually lighter than Neurhermes; male ninth sternite broadly incised; male tenth tergite uniramous, or with short ventral and long dorsal arm.

Description. Size: length 20 - 60 mm; wingspan 60 - 130 mm. Coloration: stramineus to fulvus, two piceus prothoracic vittae, often with head maculations, rarely entire body dark; wings stramineus, veins often darker, wings occasionally smoky with lighter maculations. Head (fig. 56): robust; posterior tentorial pit linear; postocular spine feebly developed; antennae feebly subserrate, about length of forebody, of 35 - 50 articles; clypeal margin entire, labrum triangular (fig. 4); maxilla (fig. 12) relatively short and broad; stipes with conspicuous setae; lacinia with three elongate apical setae; galeal sensory peg well developed; maxillary palp five segmented, labial palp four segmented; terminal palp segments conical, with two sensory areas. Wings (fig. 19): radial sector eight to eleven branches, last branch bifurcate; M_{1+2} four to nine branched; M_{3+4} two to four branches; Cu_1 with two or three accessories; 1A three branches; six to fourteen crossveins between R_1

and Rs, four or five (rarely three) between Rs and M; two to five medial crossveins, with one to three between branches (rarely up to eight, with up to seven between branches); three to seven m-cu's, one cubital crossvein, 24 - 58 costal crossveins. Males: ninth sternite (fig. 35) broadly and deeply incised medially; genital papilli present; internal inflection of ninth tergum arched; ninth gonostyli unguate, nearly glabrous, apodemes directed mesad, occasionally uniting; tenth tergites short, tubular with setal brush directed medially (figs. 34, 35), or flattened triangular, occasionally with long dorsal and short ventral arm; tenth gonostyli sparsely setose, long, digitiform. Females: without sternal pouch; gonostylus setose, articulated with gonocoxite; bursa saclike, separate from spermathecal duct; accessory glands sigmoid, longer than bursa plus spermathecal duct (fig. 49).

Distribution: Northeastern India to Indonesia and China, Japan (fig. 55).

Natural history: Label data indicate adult emergence year round in some localities, with some species seasonal or present in montane regions.

Remarks: Although there are many nominal species, many names may require synonymizing, reducing the number of valid species to around a dozen.

Lestage's Allohermes is placed in the Protohermes lineage by the apotypic incised male ninth sternite. Lestage based his genus on the complex venation of P. davidi, though other species, such as P. grandis, have similar venation. As there are no major genitalic

differences, and P. davidi may be a relatively derived species of the Protohermes lineage, separation of Allohermes from Protohermes may result in a paraphyletic group. Therefore I place Allohermes in synonymy with Protohermes.

Genus Neurhermes Navas (figs. 3, 5, 18, 36, 37, 44, 48, 55, 57)

Neurhermes Navas, 1915: 391. (type species Hermes maculipennis Gray, 1832: 331; original designation). Lestage, 1927: 96.

Hermes Gray, 1832: 331. (type species Hermes maculipennis Gray, 1832: 331; by monotypy). (not Hermes Montfort, 1810: 398, in Molluska).

Walker, 1853: 20. Weele, 1906: 208; 1909: 251; 1910: 40. Banks, 1908: 29; 1940: 179. Okamoto, 1910: 258.

Diagnosis. Linear posterior tentorial pit; galeal sensory peg absent; dark color, usually with orange prothorax; male tenth tergite biramous, lower arm slightly longer than upper.

Description. Size: length 15 - 30 mm; wingspan 45 - 85 mm. Coloration: black, prothorax usually orange, rarely black or with black maculations; wings black with white maculations. Head (fig. 57): robust; posterior tentorial pit linear (fig. 3); postocular spine feebly developed; antennae feebly suberrate, about length of forebody, of 40 - 55 articles; clypeal margin entire, labrum triangular (fig. 5); maxilla relatively short and broad; stipes with conspicuous setae; lacinia with three elongate apical setae; galeal sensory peg absent; maxillary palp five segmented, labial palp four segmented; terminal palp segments conical, with two sensory areas; palp setae relatively long. Wings (fig. 18): radial sector seven or eight branches, last bifurcate; M_{1+2} four branches; M_{3+4} two (rarely three) branches; Cu_1 with two accessories; 1A three branches; five to eight crossveins between R_1 and Rs, four between Rs and M; three medial crossveins, with one between branches; one cubital crossvein, 25 - 46 costal crossveins. Males: ninth sternite

with prominent (fig. 37) or short, notched median projection, upper surface sclerotized; genital papilli present; internal inflection of ninth tergum arched, ninth tergite short, broadly incised posteriorly (fig. 36); ninth gonostyli elongate, setose, distal half narrower, directed dorsally, apodemes directed mesad, occasionally uniting; tenth tergites biramous, dorsal arm slightly shorter than ventral (figs. 36, 37); tenth gonostyli sparsely setose, long, digitiform. Females: without sternal pouch; gonostylus setose, articulated with gonocoxite (fig. 44); setiferous sclerites present between eighth sternite and gonopore; bursa saclike, separate from spermathecal duct; accesory glands sigmoid, longer than bursa plus spermathecal duct (fig. 48).

Distribution: Northeastern India to Indonesia (fig. 55).

Natural history: Label data indicates specimens were collected from late March to May at altitudes of 2000 - 3500 feet. Weele (1910) mentions specimens collected between October and February.

Remarks: Navas's Neurhermes is a replacement name for Gray's Hermes, homonomous with a gastropod genus. Of the six nominal species of Neurhermes, four are based on color pattern of females, and may be variations of the other two.

Genus Neuromus Rambur (figs. 9, 20, 30, 31, 47, 51, 54, 58)

Neuromus Rambur, 1842: 441. (type species Neuromus testaceus Rambur, 1842: 442; designation by Weele, 1907: 235). Brauer, 1868: 400. MacLachlan, 1869: 36. Davis, 1903: 465. Weele, 1906: 208; 1907: 235; 1910: 27. Banks, 1908: 29; 1940: 179. Lestage, 1927: 96.

Diagnosis. Smaller and paler than most Neoneuromus; no spines on cranial disk; labral margin fimbriate; male ninth sternite quadrate; female with one spermatheca.

Description. Size: length 30 - 35 mm; wingspan 75 - 100 mm. Coloration: luteus; antennae, tips of mandibles, four spots on pronotum piceus; wings nearly hyaline, with piceus forewing veins. Head (fig. 58): moderately flattened; posterior tentorial pit arcuate; postocular spine moderately developed; antenna filiform, about length of forebody, of 45 - 65 articles; clypeal margin incised medially, labrum ovoid, anterior margin deflexed and fimbriate (fig. 9); maxilla relatively long and narrow; stipes with indistinct setae; lacinia without elongate apical setae; galeal sensory peg moderately developed; maxillary palp five segmented, labial palp four segmented; terminal palp segments conical, with one sensory area. Wings (fig. 20): radial sector eight to ten branches, last bifurcate; M_{1+2} two or three branches; M_{3+4} two branches; Cu_1 with two or three accesories; 1A two branches; four or five crossveins between R_1 and Rs , four between Rs and M and between M and Cu ; three medial crossveins, with one or two between branches; one cubital crossvein, with one crossvein between accesories, 28 - 35 costal

crossveins. Males: ninth sternite (fig. 31) nearly quadrate, slightly incised medially, narrower than eighth sternite, with two longitudinal, flangelike dorsal ridges; genital papilli present or absent; internal inflection of ninth tergum arched, with median fossa; ninth gonostyli unguate, sparsely to moderately setose; tenth tergites cylindrical, feebly sigmoid, or flattened triangular (figs 30, 31); tenth gonostyli setose, broadly fused to gonocoxite, often fused medially. Females: without sternal pouch; gonostylus fused with gonocoxite; bursa tubular, fused with spermathecal duct; spermathecal duct short (fig. 47) or extremely long, coiled; one spermatheca; accessory glands linear, half length of bursa (fig. 51).

Distribution: Northeastern India to Indonesia (fig. 54).

Natural history: Label data indicates specimens were collected in September at 450 feet.

Remarks: Neuromus contains three nominal and at least one undescribed species. Two of the nominal species are probably synonymous.

Genus Neoneuromus Weele (figs. 8, 21, 32, 33, 39, 46, 52, 54, 59)

Neoneuromus Weele, 1909: 252. (type species Neuromus fenestralis MacLachlan, 1869: 42; designation by Weele, 1910); 1910: 24. Lestage, 1927: 96.

Diagnosis. Usually larger and darker than Neoneuromus; no spines on cranial disk; labral margin sparsely setose; male ninth sternite attenuate; female with two spermathecae.

Description. Size: length 35 - 50 mm; wingspan 80 - 140 mm. Coloration: ferruginus to fuscus, rarely luteus; often with fuscus or piceus vittae on head and prothorax; wings fulvus to fuscus, usually with darker tessellations. Head (fig. 59): moderately flattened; posterior tentorial pit arcuate; postocular spine well developed; antenna filiform, about length of forebody, of 45 - 65 articles; clypeal margin incised medially, labrum ovoid, anterior margin sparsely setose (fig. 8); maxilla relatively long and narrow; stipes with inconspicuous setae; lacinia with three elongate apical setae; galeal sensory peg moderately developed; maxillary palp five segmented, labial palp four segmented; terminal palp segments conical, with one sensory area. Wings (fig. 21): radial sector ten to thirteen (usually eleven) branches, last bifurcate; M_{1+2} three to eight branches; M_{3+4} two branches; Cu_1 with two to four accesories; $1A$ two branches; four to seven crossveins between R_1 and Rs , four (rarely five or six) between Rs and M ; three (rarely four) medial crossveins, with one to three between branches; four m-cu's; one cubital crossvein, with one between accesories, 30 -

50 costal crossveins. Males: ninth sternite (fig. 33) attenuate, extending to tip of tenth tergites, slightly incised medially, with two longitudinal ridges internally; internal inflection of ninth tergum arched, with median fossa; poster margin of tergum dorsolaterally incised; ninth gonostylus unguate, sparsely setose; tenth tergites clavate, feebly sigmoid (figs. 32, 33); tenth gonocoxites with postero-median projection (fig. 39); tenth gonostyli lateral to projection, sparsely setose, digitiform; eleventh tergite present over anus. Females: without sternal pouch; gonostylus fused to gonocoxite; bursa tubular, continuous with spermathecal duct (fig. 46); accessory glands linear, half length bursa plus spermathecal duct (fig. 52).

Distribution: Northeastern India to Malay Peninsula and China (fig. 54).

Natural history: Label data indicates most specimens were collected in June or July, one at 4400 feet. Banks (1940) indicates collection in July and August at altitudes ranging from 2000 to 8000 feet.

Remarks: Only eight nominal species have been described, and the number of actual species may be two or three.

Genus Acanthacorydalis Weele (figs. 6, 17, 22, 23, 50, 54, 60)

Acanthacorydalis Weele, 1907: 228. (type species Corydalis asiatica Wood-Mason, 1884: 110; present designation); 1909: 250; 1910: 22. Banks, 1908: 29; 1940: 179. Lestage, 1927: 95.

Diagnosis. Large size; spines on cranial disk; male mandibles enlarged.

Description. Size: length 60 - 80 mm; wingspan 140 - 175 mm. Coloration: piceus, often with testaceous to ferrugineous markings on head, thorax, and abdomen; wings smoky, with darker veins and tessellations. Head (fig. 60): moderately flattened; posterior tentorial pit arcuate; postocular spine well developed; one pair spines on cranial disk; antenna filiform, about length of forebody, of 70 - 85 articles; clypeal margin deeply incised medially, labrum triangular (fig. 6), deflexed between mandibles; male mandibles up to length of body; female mandibles length of head; maxilla relatively long and narrow; stipes with indistinct setae; lacinia without elongate apical setae; galeal sensory peg well developed; maxillary palp five segmented, labial palp four segmented; terminal palp segments conical, with one sensory area. Wings (fig. 17): radial sector eight to eleven branches, last bifurcate; M_{1+2} and M_{3+4} bifurcate (M_{3+4} of hindwing rarely with three branches); Cu_1 with two to four accesories; 1A two branches; usually six crossveins between R_1 and Rs , four to eight between Rs and M and between M_{1+2} and M_{3+4} ; three to five crossveins between branches of media; six to eight m-cu's; one to three cubital crossveins, with two to five between accesories; 25 - 45 costal crossveins, median ones forming reticulate

pattern in males. Males: ninth sternite ovoid, with lateral lobes (fig. 22), setae short, stout; genital papilli present; internal inflection of ninth tergite inverted V-shaped; ninth gonostyli clavate, densely setose, with terminal chitinous claw; tenth tergites clavate or tubular, weakly sigmoid (figs. 32, 33); tenth gonostyli sparsely setose, long, digitiform. Females: without sternal pouch; gonostylus fused with gonocoxite; bursa saclike, separate from spermathecal duct; accessory gland sigmoid, half length bursa plus spermathecal duct (fig. 50).

Distribution: Northeastern India to Viet Nam and China (fig. 54).

Natural history: Label data indicates specimens were collected late March to May at 1800 - 3500 feet.

Remarks: Weele (1907: 230) lists the types of Acanthacorydalis as Corydalis asiatica Wood-Mason and C. orientalis MacLachlan. I am designating C. asiatica, the first described species, as the type of the genus. Only three other nominal species have been described, and there may be only two or three valid species.

Genus Platyneuromus Weele (figs. 2, 11, 16, 24, 25, 42, 54, 61)

Platyneuromus Weele, 1909; 252 (type species Corydalis soror Hagen, 1861: 193; by monotypy); 1910: 23. Lestage, 1927: 94.

Doeringia Navas, 1925: 207. (type species Doeringia christel Navas, 1925: 209; by monotypy). Lestage, 1927: 94. New synonymy.

Diagnosis. Presence of postocular flange, Central American distribution.

Description. Size: length 20 - 50 mm; wingspan 50 - 110 mm.
 Coloration: luteus to fulvus; pronotum with fuscus to piceus vittae, vittae often on head; wings fulvus with darker tessellations. Head (fig. 61): broad, flattened; posterior tentorial pit arcuate (fig. 2); postocular flange at least width of eye; postocular spine usually prominent, occasionally fused with postocular flange; antenna filiform, about length of forebody, of 40 - 55 articles; clypeal margin feebly incised medially, labrum broadly truncate, rounded at corners (fig. 11); maxilla relatively long and narrow; stipes with indistinct setae; lacinia with three apical elongate apical setae; galeal sensory peg well developed; maxillary palp five segmented, labial palp four segmented; terminal palp segments broadly rounded, with two sensory areas. Wings (fig. 16): radial sector eight to ten (usually ten) branches, last bifurcate; M_{1+2} and M_{3+4} each two branches; Cu_1 with four or five accessories; 1A two branches; three crossveins between R_1 and R_s and between R_s and M ; two medial crossveins, four m-cu's; one cubital crossvein, 18 - 35 costal crossveins; first R_1 cell one to one and a half times length of third. Males: ninth sternite quadrate

(fig. 25), membrane behind sternite thickened, bilobate; genital papilli present or absent; internal inflection of ninth tergum inverted V-shaped; ninth gonostyli clavate or nearly unguiform, with terminal chitinous claw; tenth tergites clavate, sometimes with crenulate inner margin (figs. 24, 25); tenth gonocoxites broad (fig. 42); gonostyli long, digitiform, sparsely setose. Females: with sternal pouch; gonostylus fused with gonocoxite; bursa saclike, separate from spermathecal duct; accessory glands absent.

Distribution: Central America (fig. 54).

Natural history: Species in Panama are highly seasonal (Wolda, personal communication) and label data from Mexican specimens indicates adult emergence from May to July. The larvae may inhabit slow moving rivers (Adams, personal communication).

Remarks: Navas's Doeringia christel appears to be a highly derived member of the Platyneuromus lineage, having male genitalia similar to those of P. soror, and an extremely developed postocular flange. To avoid recognition of Platyneuromus as paraphyletic I place Doeringia in synonymy with Platyneuromus. Besides these two species, Platyneuromus contains one additional nominal species and one variety, and at least one undescribed species.

Genus Chloronia Banks (figs. 10, 14, 26, 27, 40, 43, 55, 62)

Chloronia Banks, 1908: 30 (type species Hermes corriprens Walker, 1860: 180; designation by Weele, 1909: 252); 1943: 60. Weele, 1909: 252; 1910: 30. Lestage, 1927: 94.

Diagnosis. Usually smaller and paler than Corydalis; third R_1 cell longer than first; last branch Rs forked; South and Central American distribution.

Description. Size: length 20 - 40 mm; wingspan 50 - 90 mm. Coloration: luteus, with four piceus markings on pronotum, occasionally with other markings on head and mesothorax; wings nearly hyaline, luteus or stramineus, often with darkened veins and maculations. Head (fig. 62): moderately flattened; posterior tentorial pit arcuate; postocular spine moderately developed; antenna filiform, of 35 - 60 articles; clypeal margin feebly incised medially, labrum broadly truncate or feebly pointed anteriorly (fig. 10); maxilla relatively long and narrow; stipes with indistinct setae; lacinia with three elongate apical setae; galeal sensory peg well developed; maxillary palp five segmented, labial palp four segmented; terminal palp segments broadly rounded, labial palp with two sensory areas, maxillary with one. Wings (fig. 14): radial sector seven to nine (usually eight) branches, last bifurcate; M_{1+2} two branches, M_{3+4} one; Cu_1 with one to four (usually three) accessories; 1A two branches; three crossveins between R_1 and Rs and between Rs and M; two medial crossveins; four m-cu's; one (rarely two) Cu crossveins, 22 - 36 costal crossveins; third R_1 cell at least as long as first. Males: ninth sternite more or less quadrate (fig. 27),

with long, fine setae, often on lateral projections, membrane behind sternite thickened, bilobate; internal inflection of ninth tergum inverted V-shaped; ninth gonostyli clavate, with terminal chitinous claw; tenth tergites elongate tubular, three to eight times longer than wide (figs. 26, 27); tenth gonostyli sparsely setose, papilliform (fig. 40). Females: with sternal pouch (fig. 43); lateral sclerite of ovipositor weakly sclerotized; gonostylus fused with gonocoxite; bursa sac-like, separate from spermathecal duct; accesory glands absent.

Distribution: Central and South America (fig. 55).

Natural history: Label data and field work (Wolda, personal communication) indicate a high degree of seasonality in at least some tropical areas. Mexican specimens were collected from May to August, Panamanian specimens from May to June, and South American specimens from December to January.

Remarks: Banks (1908) originally proposed Chloronia as a subgenus for the New World species then placed in Neuromus. Eleven nominal species have been described.

Genus Corydalus Latreille (figs. 7, 13, 15, 28, 29, 45, 54, 63)

Corydalus Latreille, 1802: 290. (type species Hemerobius cornutus Linnaeus, 1758: 551; by monotypy). Weele, 1909: 251; 1910: 9. Lestage, 1927: 94. Comstock, 1940: 287. Banks, 1943: 60. Chandler, 1956: 232. Gurney and Parfin, 1959: 976. Evans, 1978: 138.

Corydalis Latreille, 1804: 44. "Lapsus calami." Palisot, 1821: pl. 1, fig. 1. Olivier, 1825: 59. Burmeister, 1839: 950. Rambur, 1842: 534. Hagen, 1861: 192. MacLachlan, 1869: 36. Davis, 1903: 470. Banks, 1908: 29. Needham, 1918: 935. Townsend, 1935: 27. Imms, 1957: 492.

Diagnosis. Three and four segmented labial and maxillary palps respectively; last branch of radial sector not bifurcate; first R_1 cell much longer than third; males usually with enlarged mandibles; New World distribution.

Description. Size: length 20 - 60 mm; wingspan 70 - 150 mm. Coloration: fuscus to fulvus, occasionally with lighter head and pronotum markings; wings usually fuscus with darker markings, often with white dots in forewing cells. Head: moderately flattened; posterior tentorial pit arcuate; postocular spine prominent; antenna filiform and length of forebody in female, usually stouter, filiform to subserrate or denticulate in male, may be as long as entire body; clypeal margin feebly to moderately incised medially, labrum triangular (fig. 7), deflexed between mandibles; male mandibles usually without conspicuous teeth, may be length of body (fig. 63); maxilla relatively long and narrow (fig. 13); stipes with indistinct setae; galeal sensory peg well developed; maxillary palp four segmented, labial palp three

segmented; terminal palp segments broadly rounded, with two sensory areas. Wings (fig. 15): radial sector six to fourteen branches, last not bifurcate; M_{1+2} two to five (usually three) branches, M_{3+4} one; Cu_1 with three to six accessory veins; 1A two branches; three crossveins between R_1 and Rs , three to six between Rs and M ; three to seven medial crossveins, one to three between M_1 and M_2 ; four to eight m-cu;s; one (rarely two) cubital crossveins, 30 - 60 costal crossveins; first R_1 cell one and a half to two and a quarter times length of third. Males: ninth sternite quadrate (fig. 29), rarely with median projection, membrane behind sternite thickened, regularly convoluted; internal inflection of ninth tergum inverted V-shaped; ninth gonostyli clavate, rarely with terminal chitinous claw; tenth tergites cylindrical or clavate, often uncinata or dilated basally (figs. 26, 27); tenth gonostyli sparsely setose, papilliform (fig. 41). Female: sternal pouch present or absent, rarely feebly developed; gonostylus fused with gonocoxite; bursa saclike, separate from spermathecal duct (fig. 45); accessory glands absent.

Distribution: North, Central, and South America (fig. 54).

Natural history: Larvae of some species, such as C. cornutus, are common in unpolluted riffles of small streams. Adults of some species may be collected nearly year round in tropical areas, while others emerge in spring and summer.

Remarks: Much intraspecific variation is evident in Corydalis; consequently species limits are poorly defined. Of the 35 nominal species and subspecies, only about a dozen appear valid (Glorioso, in prep.).

Genus Chloroniella Esben-Petersen

Chloroniella Esben-Petersen, 1924: 151. (type species Chloroniella peringueyi Esben-Petersen, 1924: 152; by monotypy). Lestage, 1927: 93. Barnard, 1931: 171.

Diagnosis. Last branch of radial sector not bifurcate; ninth gonostylus unguate; South African distribution.

Description. Size: forewing 33 mm. Coloration: luteus to fulvus, with piceus dorsolateral head and pronotal vittae; wings hyaline with fuscus veins. Head: moderately flattened, postocular spine present; male antenna serrate, three fourths length of forewing; labrum triangular. Wings: radial sector five branches, last not bifurcate; M_{1+2} two branches, M_{3+4} one; Cu_1 with one accessory; 1A two branches; three crossveins between R_1 and Rs, four between Rs and M; two medial crossveins, four m-cu's; one cubital crossvein, 22 - 26 costal crossveins. Males: ninth sternite moderately incised medially, with lateral lobes; internal inflection of ninth tergum inverted V-shaped; ninth gonostyli unguate; tenth tergites obtusely conical, convex dorsally, slightly concave ventrally.

Distribution: South Africa (Stellenbosch; Wellington) (fig. 55).

Natural history: Adults and one pupa were collected in mountains in November, one specimen at 3000 feet. Larvae were collected in March.

Remarks: I have been unable to obtain specimens of the only known species due to its scarcity in collections, and base this description on those of Esben-Petersen and Barnard.

Barnard states that the ninth gonostyli arise from the tenth tergites, but without examination of a specimen I can't ascertain whether this is true, or is an artifact of preservation. If Barnard examined dried material without clearing the genitalia, the ninth gonostyli may appear distorted and fused with the tenth tergites.

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APPENDIX A: Material Examined

Acanthacorydalis Weele. 2 species.

A. fruhstorferi Weele. 2 specimens.

TONKIN (North Viet Nam). (MNHN); Montes Mauson (ZMHU).

A. orientalis (MacLachlan). 6 specimens, including type of A. kolbei Weele (CHINA. SZECHWAN: Mt. Omei Shan - ZMHU).

CHINA. HUPEH: Ichang (MCZC). SZECHWAN: Kuanshien (MCZC, USNM).
Kouy Tcheou (MNHN).

INDIA. ASSAM: United Jaintia Khasi Hills, Mynso (CNCC).

Chloronia Banks. 6 species.

C. mexicana Stitz. 19 specimens.

MEXICO. CHIAPAS: Chiapa de Corzo (CNCC); 20 - 25 miles N Huixtla (CNCC); Palenque (CNCC, MCZC); 32 miles W San Cristóbal (CNCC). SAN LUIS POTOSI: El Salto (SEMK). VERA CRUZ: Cordoba (CNCC).

C. pallidus (Davis). type in USNM.

Chloronia spp. 39 specimens.

BOLOVIA. Rio Longa (MCZC).

BRAZIL. SÃO PAULO: Salisopolis (CASC). Annapolis (MCZC).

COLOMBIA. META: Villavicencio (MCZC).

COSTA RICA. CARTAGO: (MCZC).

GUATEMALA. SOLOLA: Olas de Moka (MCZC).

PANAMA. CHIRIQUI: Bugaba (MCZC); Fortuna (MJGC); Lino (MCZC).

PERU. HUANACA: Tingo Maria (SEMK); Manson Valley (CASC).

VENEZUELA. Guaquíra (MCZC); Northern Range (MCZC).

Corydalis Latreille. 13 species.

C. affinis Burmeister. 40 specimens.

ARGENTINA. BUENOS AIRES: (MCZC). MISSIONES: Arroyo Coati, 15 km. E. San José (USNM); Arroyo Liso, 8 km. W. Gal Guemes (USNM); Arroyo Piray Guazu, N San Pedro (USNM); Arroyo Piray Mini, W. Dos Hermanas (USNM); Panambi (PAAC). TUCUMÁN: Ciudad Universitaria (USNM); Tafi de Valle (USNM).

BRAZIL. (MCZC, USNM). MIMAS GERAIS: Vigosa (CASC, USNM). PARANA: (BMNH). RIO DE JANEIRO: Itatiaia, N. Park (PAAC). SANTA CATARINA: Nova Bremen (CUNY). SÃO PAULO: Salesopolis (CNCC); São Jose dos Campos (CUNY).

COLOMBIA: Medellin (CASC).

PARAGUAY (MCZC).

C. armatus Hagen. Around 400 specimens.

ARGENTINA. JUJUY: (CUNY, LACM). TUCUMAN: LACM); Quebrada de Lules (USNM). Salto Pocitos (FSCA).

BOLIVIA. COCHABAMBA: (PAAC); Chappare (PAAC, FSCA). LA PAZ: Chulumani (USNM); Coroico Exp. Sta., N Yungas Prov. (USNM).

COLOMBIA. (LACM). ANTIOQUIA: Jerico (USNM). META: Villavicencio (MCZC). VALLE DE CUACA: (CASC); Altaflor (BMNH); Anchicaya (CNCC); Cali (MCZC); Costa Rica (CASC); La Esperanza (CASC). Buena Vista (USNM); Medellín (USNM); Monterredondo (PAAC); Praetera (MCZC); San Augustin (MCZC) San José (MCZC); San Vicente (MCZC); St. Antonio (MCZC).

COSTA RICA. (MCZC, USNM). CARTAGO: (MCZC, USNM); Piedra Negra (USNM); Turrialba (LACM, USNM); Volcan de Turrialba (GEKI).

GUANANCASTE: (SEMK). LIMÓN: Guapiles (SEMK); Los Diamantes (LACM).

PUNTARENAS: Monte Verde (LACM, USNM); 4 miles E Palmar (SEMK); Rincon de Osa (LACM); San Vito de Java (FSCA).

ECUADOR. (BMNH). EL ORO: 9 miles S Santa Rosa (CASC). GUAYAS: Guayanquil (USNM). MORONA-SANTIAGO: (BMNH). NAPO: Puyo (CUNY, USNM); Tena (USNM). PASTAZA: (CUNY, USNM). PICHINCHA: Quito (MCZC); Santo Domingo de los Colorados (CASC); Tandapi (SEMK). ZAMORA-CHINCHIPE: Rancho Allegro, 15 miles below Zamora (CASC). Balzapamba (USNM); Banos (MCZC); Nanegalito (UIDC); Playas de Montalva (MCZC).

GUATEMALA. CHIMALTENANGO: Yepocapa (USNM). SACATEPÉQUEZ: Finca Moca (USNM); Finca Paraxé (USNM). El Cacao (USNM); Price Aguas (USNM); San Marcos (CASC).

HONDURAS. Middlesex, Stann Cr. Distr. (LACM).

MEXICO. CHIAPAS: (PAAC). VERA CRUZ: Cordoba (LACM); Dos Amates (PAAC).

PANAMA. CHIRIQUÍ: Bugaba (MCZC, USNM); Fortuna (MJGC); Miramar (MJGC); Potrerillos (FSCA); Volcan de Chiriqui (BMNH, CASC).

PERU. (MNHN, SEMK). AMAZONAS: 5 km. N Pomacocha (CASC). CAJAMARCA: Jaén Pucara (CASC). HUÁNUCO: 10 miles N Huanta (CASC); Tingo Maria (CASC, USNM); Yurac, 67 miles E Tingo Maria (CASC). LIMA: Verrugas (USNM). PASCO: (LACM): Chontilla, 22 km. SE Iscozazin (LACM); Pan de Azucar (LACM). Chanchamayo (USNM, CASC); Chauchorango (MCZC); Chosica (SEMK); Paltaybamba (USNM); San Miguel (USNM), Sinchono (USNM).

VENEZUELA. (BMNH, MCZC). ARAGUA: Rancho Grande (CUNY, USNM). MERIDA: (BMNH, MCZC, MNHN, USNM); Paranos (MCZC). MIRANDA: Caracas (MCZC). El Valle (USNM).

C. batesi MacLachlan. 15 specimens, including holotype (BRAZIL.

AMAZONAS: Ega - BMNH).

BRAZIL. AMAZONAS: Manaus (INPA), Reserva Campinas (INPA), Reserva
Duke (USNM).

BOLIVIA. SANTA CRUZ: (MCZC). COCHABAMBA: (CUNY).

ECUADOR. NAPO: Lago Agrio (USNM).

GUYANA. (BMNH). ESSEQUIBO: 6 miles S Winniperu, Picrenana Island
(USNM).

C. bolivari Banks. 29 specimens, including types (VENEZUELA. Appun -
MCZC).

COLOMBIA. (PAAC).

VENEZUELA. ARRAGUA: Rancho Grande (CUNY, PAAC, USNM). MERIDA: La
Mucuy (CUNY). Appun (MCZC); Los Canales, Naiguata (MCZC); Páramo la
Negra (MCZC); San Felipe Yara (CUNY).

C. cephalotes Rambur. 12 specimens.

BRAZIL. (MCZC). Chapada (BMNH, MCZC); Espirito Santo (BMNH);
Sabara-Bello-Horizonte, Rio das Velhao (BMNH).

C. cornutus (Linnaeus). Around 900 specimens.

CANADA: Ontario (CNCC); Quebec (CNCC).

MEXICO: Baja California Sur (CASC); Colima (USNM); Distrito
Federal (USNM); Durango (OSUC, USNM); Guerrero (USNM); Jalisco (CUNY,
MCZC); Morelos (CUNY, SEMK, USNM); Puebla (SEMK); Sinaloa (CNCC);
Sonora (CUNY).

UNITED STATES: Arizona (CASC, CNCC, CUNY, FMNH, MCZC, SEMK, UIDC, USNM); Arkansas (CUNY, MJGC, NWBR, UIDC, USNM); California (CASC, USNM); Connecticut (USNM); District of Columbia (USNM); Florida (CNCC, CUNY, FSCA, MCZC, USNM); Georgia (CNCC, USNM); Illinois (CNCC, FMNH, USNM); Indiana (CNCC, MCZC, USNM); Iowa (UIDC, USNM); Kansas (CUNY, MCZC); Kentucky (CNCC, OSUC, USNM); Louisiana (CASC); Maine (USNM); Massachusetts (MCZC, USNM); Michigan (CUNY, FMNH); Mississippi (FSCA, USNM); Missouri (CASC, CNCC, FMNH, NWBR, OSUC, USNM); New Hampshire (CNCC); New Jersey (USNM); New Mexico (MCZC); New York (CUNY, MCZC, USNM); North Carolina (SEMK, USNM); Ohio (CUNY, MJGC, NWBR, USNM); Oklahoma (CUNY, FMNH, MCZC, UOKL, USNM); Pennsylvania (MCZC, USNM); Rhode Island (MCZC); Tennessee (FMNH); Texas (CASC, CUNY, FMNH, MCZC, TAMU, USNM); Utah (MCZC, USNM); Virginia (CUNY, MCZC, NWBR, USNM).

C. ecuadorianus Banks. 5 specimens, including holotype (ECUADOR: Banos - MCZC).

COLOMBIA: Anchicaya (CNCC); St. Antonio (MCZC).

C. flavicornis Stitz. 32 specimens, including type (PANAMA: CHIRIQUI - ZMHU).

COLOMBIA. ANTIOQUIA: Jerico (USNM). Buena Vista (USNM).

COSTA RICA. LIMON: Hacienda Tapezco, 29 km. W Tortuguero (LACM).

PUNTARENAS: 1.8 miles W. Rincon Oso Peninsula (LACM).

ECUADOR. Los Rios Quevedo (USNM); 29 km. W St. Domingo, Manabi (USNM); Quevedo (MCZC, USNM).

C. lutea Hagen. Around 500 specimens.

COSTA RICA. GAUNACASTE: 5 km. N Cañas (TAMU). near Guápiles (CUNY); 7 miles NW Liberia (USNM); Rio Corbici, Las Canas (USNM).

EL SALVADOR. Lomas Verde (TAMU); San Nicolas Lempa (USNM).

GUATEMALA. CHIMALTENANGO: Yepocapa (USNM). GUATEMALA: E SE Guatemala City (USNM). SAN MARCOS: Puente Talisman (CUNY). SUCHITEPÉQUEZ: Cuyotenango (USNM). Atta Vera Paz, Trece Aguas (USNM).

HONDURAS. Belize (USNM); El Zamarano (OSUC); Middlesex, Stann Cr. Distr. (PAAC); Siguatepeque, Escuela Sup. Cienc. For. (PAAC).

MEXICO: Chiapas (CASC, TAMU, USNM); Colima (USNM); Durango (OSUC); Guerrero (FSCA); Hidalgo (SEMK); Morelos (FSCA, SEMK); Nayarit (SEMK); Nuevo Leon (CUNY, FSCA, TAMU, USNM); Oaxaca (TAMU); Puebla (USNM); Querétaro (TAMU); San luis Potosi (FSCA, SEMK, TAMU, USNM); Sinaloa (CNCC); Tamaulipas (CUNY); Vera Cruz (CASC, CNCC, PAAC, SEMK, TAMU, USNM); Zacatecas (OSUC).

NICARAGUA. Matagalpa (USNM).

PANAMA. CANAL ZONE: Barro Colorada Island (CASC, CNCC, CUNY, INPA, MCZC, MJGC, SEMK, USNM). CHIRIQUI: Miramar (MJGC). COLÓN: Santa Rita Ridge (INPA). PANAMA: Pearl Island (USNM).

UNITED STATES. TEXAS: Bexar Co. (MCZC); Gillespie Co. (TAMU); Hays Co. (MCZC); Hidalgo Co. (USNM); Kimble Co. (OSUC); Kleburg Co. (CUNY); Sabine Co. (USNM); Uvalde Co. (USNM); Webb Co. (TAMU).

C. nubilus Ehrichson. 2 specimens, including holotype (BRITISH GUYANA - ZMHU).

FRENCH GUYANA. Saut-Maripa Oyapock (MNHN).

C. primitivus Weele. 12 specimens.

ARGENTINA. CATAMARCA: Rio Portrero, near Andalgala (USNM). JUJUY: (CUNY). MISSIONES: Campo Viera (PAAC). TUCUMÁN: Quebrada de Lules (USNM).

BOLIVIA. Rio Longa (USNM).

BRAZIL. Chapada (MCZC).

PARAGUAY. 2 km. S Cerro Cora (USNM).

PERU. PASCO: Chontilla, 22 km. SE Iscozazia (USNM).

C. tridentatus Stitz. 18 specimens, including type (BRAZIL - ZMHU).

BRAZIL. (MCZC).

ARGENTINA. MISSIONES: Arroyo Piray Mini, W Dos Hermanos (USNM); Piray Guazu (USNM).

Corydalis sp. 16 specimens.

BOLIVIA. Cavinás Beni (USNM); Guayarin (MCZC).

BRAZIL. AMAZONAS: Manaus (INPA); Para Urúá, 65 km. SW Itaituba (INPA); Porto Velho, Rio Madieros (MCZC); Reserva Campines (INPA).

COLOMBIA. Buena Vista (USNM); Puerto Berrio (MCZC).

ECUADOR. Huigra (MCZC).

FRENCH GUYANA. Saut-Maripa-Oyapock (MNHN); Sikini-Oyapock (MNHN).

GUYANA. Bartica (BMNH); Rockstone, Essequibo River (USNM).

PARAGUAY. (MCZC).

PERU. Huallaga, Aguatia (PAAC).

Ithaca, New York (CUNY) - mislabeled

Neoneuromus Weele. 2 or three species

N. sikkimensis Weele. 2 specimens, including type (INDIA. SIKKIM - ZMHU).

INDIA. ASSAM: Khasia Hills (MCZC).

Neoneuromus spp. 27 specimens, including types of N. fenestralis
maclachlani (Weele) (TONKIN. Montes Mauson - MCZC) and N. latratus
tonkinensis (Weele) (CHINA. SZECHWAN: Mt. Omei Shan - MCZC).

CHINA. HUPEH: Suisap, Lichuan Distr. (CASC). KIANGSI : Hong San
(MCZC). KWANGTUNG: Tsin Leongshan (CASC). Mohkanshan (CASC); Yim Na
San, E Ewantung (MCZC); Yuman Fou, Tau-Nin Kai (MNHN).

INDIA. ASSAM: Kameng (Bhareli River), Dirdmq Dzong (CNCC), Nakha
(CNCC), Salar (CNCC). MANIPUR: Chatrick (CNCC); Khamassom (CNCC).
SIKKIM: Monqang (CNCC); Simqhik (CNCC); Yugang (CNCC).

Neurhermes Navas. 2 or 3 species.

N. maculipennis (Gray). 9 specimens.

INDONESIA. SUMATRA: Medan (MCZC). JAVA: (MCZC); Mont Gedeh (MNHN).

MALAYSIA. KEDAH: Kedah Peak (MCZC). SABAH: Mt. Kinabalu (MNHN).

SELANGOR: Ulu Langat (MCZC).

No data (MCZC).

N. costatostriata (Weele). 2 specimens.

INDIA. ASSAM: United Jaintia Khasi Hills, Mawpran (CNCC), Mowshun
(CNCC).

Neurhermes spp. 6 specimens.

INDIA. MANIPUR: Kambiron (CNCC); Lagairong (CNCC); Luaglang Kunov
(CNCC).

TONKIN (North Viet Nam). Montes Mauson (MCZC).

Neuromus Rambur. 3 species.

N. intimus MacLachlan. 11 specimens.

INDIA. ASSAM: Lushai (Hills), Sonai (CNCC).

NEPAL. near Birganj Lothar (CNCC).

SOUTH VIET NAM. Pleiku Prov., Nui Hong Kong (UIDC).

N. testaceus Rambur. 5 specimens.

INDONESIA. JAVA: Saeka Poemi (MNHN). SUMATRA: (MCZC): Fort Dekoch (MCZC); Redjang-Lebong (ZMHU).

Neuromus sp. 1 specimen.

MALAYSIA. SABAH: Mt. Kinabalu (USNM).

Platyneuromus Weele. 4 or 5 species.

P. auritus Kimmins. 10 specimens.

GUATEMALA. Cayuga (USNM).

HONDURAS. (BMNH); La Lima (USNM).

MEXICO. CHIAPAS: Chiapa (CASC); Ocozoautla (CASC); Tuxtla Gutierrez (MCZC, PAAC).

P. christel (Navas). 9 specimens, including type (COSTA RICA, Turialba - IFPK).

MEXICO. VERA CRUZ (USNM); CHIAPAS: Tuxtla Gutierrez (USNM).

PANAMA. CHIRIQUI: Fortuna (MJGC); Santa Clara (INPA).

No data. (BMNH, CASC).

P. soror (Hagen). 40 specimens, including types (MEXICO. Koppe - MCZC).

COSTA RICA. Heredia, Finca la Selva (USNM).

HONDURAS. (BMNH).

MEXICO. CHIAPAS: 6 miles S Puebla Nueva (CASC); Tuxtla Gutierrez (MCZC). MORELOS: Cuernavaca (MCZC). PUEBLA: Villa Juarez (MCZC). SAN LUIS POTOSI: El Salto (CASC, MCZC, SEMK, USNM); El Naranjo (USNM); Palitla (USNM). VERA CRUZ: Ciudad Mendoza (CASC); Fortun de las Flores (NWBR); 5 miles N Huatusco (TAMU); Misantla (BMNH); Teacalco (USNM); Tuxtla (USNM). Jalapa (BMNH); Rinconada (BMNH); Temescaltepec (CASC); Xilitla (USNM).

PANAMA. CHIRIQUI: Fortuna (MJGC); Santa Clara (INPA); Volcan de Chiriqui (BMNH).

Platyneuromus spp. 10 specimens.

GUATEMALA. Panzos (USNM); Quirigua (USNM); Trece Aguas (USNM).

HONDURAS. Lombardia (USNM).

MEXICO. CHIAPAS: Palenque (CNCC). VERA CRUZ (USNM).

Protohermes Weele. 8 or 9 species.

P. costalis (Walker). 3 specimens.

CHINA. HUPEH: Suisap, Lichuan Distr. (CASC). Kwaysi, Pui Liaw (MCZC).

INDIA. ASSAM: Khasia Hills (MCZC).

P. davidi Weele. Type (NORTH VIET NAM. Mou Pin - MNHN).

P. grandis (Thunberg). 9 specimens.

JAPAN. HOKKAIDO: (MCZC); Sapporo (MCZC). HONSHU: Kofu (CASC); Nikko (CASC); Nippon Moyon, env. Tokyo (MNHN). KYUSHU: Ashiya (CASC).

Protohermes spp. 43 specimens.

CHINA. HUPEH: Suisapa, Lichuan Distr. (CASC). SZECHWAN: (MCZC); Chengtu (CASC, MCZC); Chiang Nsien (MCZC); Mt. Omei Shan (MCZC). Ta Hao, Haipa (MCZC).

INDIA. ASSAM: Kameng (Bhareli River), Bilo La (CNCC), Domkha (CNCC), Nakhu (CNCC), Nyukmadong (CNCC), Rupa (CNCC), Salar (CNCC), Shergaon (CNCC); United Jaintia Khasi Hills, Mawja (CNCC). MANIPUR: Chimasao (CNCC); Khangoi (CNCC); Mapum (CNCC). WEST BENGAL: Lingsoka (CNCC).

INDONESIA. BORNEO: (MCZC).

TAIWAN (FORMOSA). Hori (MCZC); Rokki (MCZC).

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Fig 1. Corydalinae head, showing postocular ridge, spine, and plane.

Figs. 2, 3. Gular region of Corydalinae. 2. Platyneuromus auritus.

3. Neurhermes maculipennis.

Figs. 4 - 11. Labrum and clypeal margin of Corydalinae. 4. Protohermes
sp. 5. Neurhermes maculipennis. 6. Acanthacorydalis orientalis.
7. Corydalis cornutus. 8. Neoneuromus sikkimensis. 9. Neuromus
testaceus. 10. Chloronia sp. 11. Platyneuromus soror.

Figs. 12, 13. Maxillae of Corydalinae. 12. Protohermes sp.

13. Corydalis cornutus.

Figs. 14 - 17. Wings of Corydalinae. Scale bar represents one centimeter. 14. Chloronia mexicana. 15. Corydalis cornutus. 16. Platyneuromus soror. 17. Acanthacorydalis orientalis.

Figs. 18 - 21. Wings of Corydalinae. 18. Neurhermes maculipennis.
19. Protohermes davidi. 20. Neuromus intimus. 21. Neoneuromus
sp.

Figs. 22, 23. Acanthacorydalis orientalis, male genitalia. 22. Ventral view. 23. Dorsal view.

Figs. 24, 25. Platyneuromus soror, male genitalia. 24. Dorsal view.

25. Ventral view.

Figs. 26, 27. Chloronia sp., male genitalia. 26. Dorsal view.

27. Ventral view.

Figs. 28, 29. Corydalis cornutus, male genitalia. 28. Dorsal view.

29. Ventral view.

Figs. 30, 31. Neuromus intimus, male genitalia. 30. Dorsal view.

31. Ventral view.

Figs. 32, 33. Neoneuromus sp., male genitalia. 32. Dorsal view.

33. Ventral view.

Figs. 34, 35. Protohermes costalis, male genitalia. 34. Dorsal view.

35. Ventral view.

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Figs. 36, 37. Neurhermes maculipennis, male genitalia. 36. Dorsal view.

37. Ventral view.

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Figs. 38 - 42. Male tenth sternites. 38. Protohermes costalis, showing genital papilli. 39. Neoneuromus sp. 40. Chloronia sp. 41. Corydalis cornutus. 42. Platyneuromus soror.

Figs. 43, 44. Female abdomens. 43. Chloronia sp. 44. Neurhermes maculipennis.

Figs. 45 - 47. Bursa and spermathecae. 45. Corydalis cornutus.

46. Neoneuromus sp. 47. Neuromus intimus.

Figs. 48 - 52. Female accesory glands. 48. Neurhermes maculipennis.

49. Protohermes sp. 50. Acanthacorydalis fruhstorferi.

51. Neuromus intimus. 52. Neoneuromus sp.

Fig. 53. Cladogram showing relationships of Corydalinae genera.

Pro = Protohermes, Nrh = Neurhermes, Nnr = Neoneuromus,

Neu = Neuromus, Aca = Acanthacorydalis, Pla = Platyneuromus,

Chl = Chloronia, Cor = Corydalus.

Fig. 54. Distribution of Corydalinae. Abbreviations as in Fig. 53.

Fig. 55. Distribution of Corydalinae. C11 = Chloroniella, other abbreviations as in Fig. 53.

Fig. 56. Protohermes sp., forebody.

Fig. 57. Neurhermes maculipennis, forebody.

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Fig. 58. Neuromus testaceus, forebody.

Fig. 59. Neoneuromus sp., forebody.

Fig. 60. Acanthacorydalis orientalis, forebody.

Fig. 61. Platyneuromus soror, forebody.

Fig. 62. Chloronia sp., forebody

Fig. 63. Corydalis cornutus, habitus.