Systematics of the dobsonfly subfamily Corydalinae (Megaloptera: Corydalidae)

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ABSTRACT. The genera of Corydalinae are redefined, and representative characters are figured for each genus. New character sources, such as mouthparts and internal female genitalia, are investigated, as well as traditional male genitalia and wings. Allohermes is synonymized with Protohermes, Doeringia with Platyneuromus. Intergeneric relationships are hypothesized on the basis of a cladistic analysis. Acanthacorydalus and the New World genera form a monophyletic group, as do Protohermes and Neurhermes, and Neuromus and Neoneuromus. Chloroniella belongs in the Acanthacorydalus — New World lineage, but exact placement is uncertain. A phyletic sequence classification is proposed on the basis of the cladistic analysis.

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, Corydalinae and Chauliodinae. The Corydalinae are restricted to North and South America, South Africa and Asia, while the Chauliodinae also occur in Australia and New Zealand.

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

While not as spectacular, the larvae may be of Specialized importance. Those of the North American Corydalis cornutus are excellent angling bait, while 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 are poorly defined. 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 Neuromini, while Tillyard (1918) and many subsequent authors called this group the Corydalinae. Lestage (1927) noted the name should be based on Corydalis, reducing Neuromini to a junior synonym.

Some early authors (Tillyard, 1918;
Lestage, 1927; Barnard, 1931) considered the Sialidae and Corydalidae distinctive enough to merit familial status, with Weele's tribes elevated to subfamilies, while others followed 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 the Corydalinae, recognizing eight genera and thirty-four species and postulated affinities based on wing venation. Since 1927 work on Corydalinae has been mainly species description, though Banks (1940) included a key to Chinese genera, Kimmins (1948) reviewed the Protocorydalinae in the British Museum, and Penny (1977) listed the New World species.

**Natural history**

With the exception of Corydalus cornutus, the natural history of Corydalinae is poorly known, though the larvae are probably all lotic inhabitants. Larval lifespan varies from 1 to 5 years (Evans, 1978), this being correlated with latitude in C. cornutus (Brown & Fitzpatrick, 1978). Some species have been observed occupying specific microhabitats within a stream (Geijskes, personal communication), while label data indicate a correlation between species and stream type or altitude.

Adults are crepuscular or nocturnal and readily collected at lights. Though some evidence exists indicating feeding on liquids (Parfin, 1952), adult life is generally short, ranging from 3 to 13 days for C. cornutus (Davis, 1903; Parfin, 1952). Adult emergence of some species is seasonal in certain regions, while little seasonality is observed in other localities. Seasonality may be influenced by temperature or rainfall, but also occurs in regions with no distinct seasons.

**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 (Natural History), London, England (BMNH); D. H. Kavanaugh, California Academy of Sciences, San Francisco, California (CASC); G. Ekis, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CMNH); 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. Kethley, Field Museum of Natural History, Chicago, Illinois (FMNH); L. A. Stange, Florida State Collection of Arthropods, Gainesville, Florida (FSAC); N. D. Penny, Instituto Nacional de Pesquisas da Amazônia, 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 (MCZ); M. J. Glorioso, Columbus, Ohio (MJGC); J. Legrand, Muséum National d'Histoire Naturelle, Paris, France (MNHN); C. A. Triplehorn, Ohio State University, Entomology, Columbus, Ohio (OSUC); N. W. Brit, 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 (UKOL); O. S. Flint, Jr, P. J. Spangler, United States National Museum of Natural History, Entomology, Smithsonian Institution, Washington, D.C. (USNM); K. K. Gunther, Zoologisches Museum, Humboldt-Universität, Berlin, Germany (ZMUH).

**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, but in the sense of Hennig (1965, 1966), and, ideally, genera should be 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 is not essential, major monophyletic lineages based on synapomorphies 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 distant lineages (defined by autapomorphies) can be given categorial 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 autapomorphies 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, b).

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 descriptions, 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 1 mm 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 imaginal 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 rugously 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 and 57), moderately developed in *Chlororhina* and *Neurornus* (Figs. 58 and 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

![Diagram of Corydalinae head, showing postocular ridge, spine, and plane.](image)
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 thirty-five to seventy-five articles, and are generally about as long as the head plus prothorax, though in male Corydalus 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

FIGS. 4–11. Labrum and clypeal margin of Corydalinae: 4, Protohermes sp.; 5, Neurhermes maculipennis; 6, Acanthacorydalis orientalis; 7, Corydalus cornutus; 8, Neoneuromus sikkimensis; 9, Neuromus testaceus; 10, Chloronia sp.; 11, Platyneuromus soror.
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 and 5), or medially incised to varying degrees, ranging from the shallow notch in Chlorononia (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 and 9) the short setae are more abundant, being especially predominant in Neuromus. The labrum of Neuromus often has a deflexed anterior margin with a slight 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 and 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 weak 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 carido bearing several short setae on the outer margin. The subcylindrical stipes, one-and-a-half to twice as long as wide, bears several setae on the 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 band-like subgaleal sclerites separate the galea from the stipes, with the lower sclerite often being divided by membrane. Microsculpture of the galeal base and stipal 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 Corydalis) 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 palpigers 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 Corydalis.

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), arcuate in other genera (Fig. 2).

Thorax

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

The elliptical forewing is 3–4 times as long as wide and a half again longer than the body; the hindwing is slightly wider and about four-fifths as long. Colour varies from nearly hyaline in Chloronia, Neuromus, many Protohermes, and some Neoneuromus to brownish or light grey with darker markings in Corydalis, Platynemus, Acanthacorydalis and Neoneuromus or to black with white maculations in Neurhermes and some Protohermes.

Wings are densely covered with greyish 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 R1, 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. M1+2 and M3+4 separate slightly distal to the base of Rs. Vein M1+2 may consist of two branches (Chloronia, Chloroniella, Platynemus and some Corydalis) (Figs. 14 and 16), two bifurcate branches (many Neuromus and some Neoneuromus) or four to nine branches (Protohermes and many Neoneuromus). Vein M3+4 may be undivided (Chloroniella, Chloronia and Corydalis), bifurcate (Acanthacorydalis, Neuromus, Neoneuromus, Neurhermes and Platynemus) or consist of up to four branches (Protohermes).

The cubitus diverges from the media basally; Cu2 separates from Cu1 slightly past the point of divergence of the media in the forewing, basally in the hindwing. Cu1 has one to six accessories, Cu2 is unbranched.
Though venation in the anal area of fore and hindwing is similar, the anal area of the hindwing in much larger, forming a small anal fan. Vein 1A is normally two-branched; it is three-branched in Neurhermes and Protocorix (Figs. 18 and 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 eighteen and sixty veins, with numbers varying between wings of an individual. Crossveins may be contiguous basally, especially in Corydalus and Protocorix, or in a reticulate pattern (restricted to male Acanthacorixalis) (Fig. 17).

Three crossveins connect R₁ and Rs in Corydalus, Chloronia, Chloroniella and Platyneuromus; other Corydalinae have at least four crossveins. There are one to four crossveins between each sectorial branch. Chloronia and Platyneuromus have three crossveins between the radial sector and M₁, Neurromus and Neurhermes have four, and other genera have three to eight. The basal r-m crossvein in the hindwing is long and oblique, connecting Rs with the base of M.

There are two medial crossveins in Platyneuromus and Chloronia, three in Neurhermes, Neurromus and many Neoneuromus, while Corydalus, Acanthacorixalis and Protocorix 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 M₄ and Cu₁, with a fourth connecting M and Cu, though Neurhermes and Protocorix have two; Acanthacorixalis and, rarely, Corydalus have as many as eight crossveins.

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

**Abdomen**

Non-genital segments in Corydalinae are similar to those of Chauliodinae, as described by Maki (1936) for Neochaullodes formosanus. However, Platyneuromus, Chloronia and some Corydalus 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 consist 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
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FIGS. 22 and 23. Acanthacorydalis orientalis, male genitalia: 22, ventral view; 23, dorsal view.

an internal inflection basally which may be arched (Figs. 30, 32, 34 and 36) or inverted V-shaped (Figs. 23, 24, 26 and 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, Corydalus) (Figs. 22, 25, 27 and 29) is densely setose, directed postero-medially, and terminates in a small chitinous claw, the claw being absent in many Corydalus. Unguiform styli are directed medially and may be glabrous or sparsely setose with a glabrous tip (Figs. 31, 33, 35 and 37). The gonostylus of Neurhermes (Fig. 37) is directed postero-medially in the basal half, dorsally in the 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 and 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 displays a median projection (Fig. 37), sometimes with a median incision; Acanthacorydalis has postero-lateral lobes (Fig. 22); Chloronia bears 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; anoprocesses of Tjeder, 1970) are generally tubular or clavate, slightly sigmoid, and about the length of the ninth tergum. The tenth tergites of Chloronia are 2–3 times as long as the ninth (Figs. 26 and 27), while those of some Neurormus are flattened (Figs. 30 and 31). Neurhermes exhibits a biramous tergite with the dorsal arm shorter than the ventral (Figs. 36 and 37); some Protohermes have a short ventral and a long dorsal arm, though most are uniramous (Figs. 34 and 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 (mammiliform 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 and 41).

A pair of genital papilli (Figs. 22, 37 and 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 and 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 accessory glands of Sialidae as described by Heberdey (1931). These glands are absent in Corydalis, Chloronia and Platyneuromus, while they are longer than the bursa–spermathecal duct complex in Protohermes and Neurhermes (Figs. 48 and 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.

FIGS. 24 and 25. Platyneuromus soror, male genitalia: 24, dorsal view; 25, ventral view.
The colleteral gland, opening near the centre 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 investigations of

**FIGS. 26 and 27. Chloronia sp., male genitalia: 26, dorsal view; 27, ventral view.**

**FIGS. 28 and 29. Corydalus comutus, male genitalia: 28, dorsal view; 29 ventral view.**
TABLE 1. Character states.

<table>
<thead>
<tr>
<th>Character</th>
<th>Plesiotypic</th>
<th>Apotypic</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Gular setation</td>
<td>Conspicuously setose</td>
<td>Microsetose</td>
</tr>
<tr>
<td>2. Postocular ridge</td>
<td>Absent</td>
<td>Present (Fig. 1)</td>
</tr>
<tr>
<td>3. Postocular plane</td>
<td>Absent</td>
<td>Present (Fig. 1)</td>
</tr>
<tr>
<td>4. Head shape</td>
<td>Robust</td>
<td>Flattened</td>
</tr>
<tr>
<td>5. Postocular flange</td>
<td>Absent</td>
<td>Present (Fig. 61)</td>
</tr>
<tr>
<td>6. Postocular spine</td>
<td>Feebly developed (Figs. 56 and 57)</td>
<td>Moderately to well developed (Figs. 58-63)</td>
</tr>
<tr>
<td>7. Posterior tentorial pits</td>
<td>Linear (Fig. 3)</td>
<td>Arcuate (Fig. 2)</td>
</tr>
<tr>
<td>8. Cranial disk</td>
<td>Without spines</td>
<td>With spines (Fig. 60)</td>
</tr>
<tr>
<td>9. Antennae</td>
<td>Feebly suberrate (Figs. 56 and 57)</td>
<td>Filiform</td>
</tr>
<tr>
<td>10. Clypeal margin</td>
<td>Entire (Figs. 4 and 5)</td>
<td>Incised medially (Figs. 6-11)</td>
</tr>
<tr>
<td>11. Male mandibles</td>
<td>Not enlarged</td>
<td>Enlarged (Figs. 60 and 63)</td>
</tr>
<tr>
<td>12. Female mandibles</td>
<td>Three-fourths head length or shorter</td>
<td>Length of head</td>
</tr>
<tr>
<td>13. Labrum shape</td>
<td>Triangular (Figs. 4-7)</td>
<td>Ovoid (Figs. 8 and 9)</td>
</tr>
<tr>
<td>13'.</td>
<td></td>
<td>Broadly truncate (Figs. 10 and 11)</td>
</tr>
<tr>
<td>14. Labral position</td>
<td>Over mandibles</td>
<td>Between mandibles</td>
</tr>
<tr>
<td>15. Labral anterior margin</td>
<td>Sparsely setose</td>
<td>Fimbriate (Fig. 9)</td>
</tr>
<tr>
<td>16. Maxilla shape</td>
<td>Short and broad (Fig. 12)</td>
<td>Relatively elongate (Fig. 13)</td>
</tr>
<tr>
<td>17. Lacinia apex</td>
<td>With three elongate setae (Fig. 12)</td>
<td>Without elongate setae (Fig. 13)</td>
</tr>
<tr>
<td>18. Stidal setae</td>
<td>Conspicuous (Fig. 12)</td>
<td>Inconspicuous (Fig. 13)</td>
</tr>
<tr>
<td>19. Galeal setae</td>
<td>Flattened, lanceolate</td>
<td>Bristellike</td>
</tr>
<tr>
<td>20. Galeal sensory peg</td>
<td>Well developed (Figs. 12 and 13)</td>
<td>Poorly developed</td>
</tr>
<tr>
<td>20'.</td>
<td></td>
<td>Absent</td>
</tr>
<tr>
<td>21. Maxillary palp</td>
<td>Five-segmented (Fig. 12)</td>
<td>Four-segmented (Fig. 13)</td>
</tr>
<tr>
<td>22. Maxillary palp apex</td>
<td>Conical (Fig. 12)</td>
<td>Broadly rounded (Fig. 13)</td>
</tr>
<tr>
<td>23. Maxillary palp setae</td>
<td>Long</td>
<td>Short</td>
</tr>
<tr>
<td>24. Maxillary palp sensory areas</td>
<td>One at apex</td>
<td>Two at apex</td>
</tr>
<tr>
<td>25. Labial palp</td>
<td>Four-segmented</td>
<td>Three-segmented</td>
</tr>
<tr>
<td>26. Labial palp sensory areas</td>
<td>One at apex</td>
<td>Two at apex</td>
</tr>
<tr>
<td>27. Last branch of radial sector</td>
<td>Bifurcate (Figs. 14, 15, 17-21)</td>
<td>Not bifurcate (Fig. 16)</td>
</tr>
<tr>
<td>28. M₄₁₂ branches</td>
<td>Two (Figs. 14-17)</td>
<td>Four or more (Figs. 18-21)</td>
</tr>
<tr>
<td>29. M₄₄₁ branches</td>
<td>Two (Figs. 16-21)</td>
<td>One (Figs. 14 and 15)</td>
</tr>
<tr>
<td>30. A₁ branches</td>
<td>Two (Figs. 14-17, 20 and 21)</td>
<td>Three (Figs. 18 and 19)</td>
</tr>
<tr>
<td>31. R₄₃₉ crossveins</td>
<td>Three (Figs. 14-16)</td>
<td>Four or more (Figs. 17-21)</td>
</tr>
<tr>
<td>32. Medial crossveins</td>
<td>Two (Figs. 14, 16 and 18)</td>
<td>Three or more (Figs. 15, 17, 19-21)</td>
</tr>
<tr>
<td>33. M-Cu crossveins</td>
<td>Three (Fig. 18)</td>
<td>Four (Figs. 14-17, 20 and 21)</td>
</tr>
<tr>
<td>33'.</td>
<td></td>
<td>Six or more (Fig. 17)</td>
</tr>
<tr>
<td>34. Cubital accessory crossveins</td>
<td>Absent (Figs. 14-16, 18-19)</td>
<td>Present (Figs. 17, 20 and 21)</td>
</tr>
<tr>
<td>35. Costal crossveins</td>
<td>Vertical or oblique</td>
<td>Reticulate (Fig. 17)</td>
</tr>
<tr>
<td>36. Male ninth sternum</td>
<td>Hind margin not as in Fig. 35</td>
<td>Hind margin as in Fig. 35</td>
</tr>
<tr>
<td>37. Male ninth sternum</td>
<td>More or less quadrate</td>
<td>Attenuate (Fig. 33)</td>
</tr>
<tr>
<td>38. Male ninth sternum</td>
<td>Without median projection</td>
<td>With median projection (Fig. 37)</td>
</tr>
<tr>
<td>39. Male ninth sternum</td>
<td>Without postero-lateral lobes</td>
<td>With postero-lateral lobes (Fig. 22)</td>
</tr>
<tr>
<td>40. Male ninth sternum</td>
<td>Without setiferous lateral protuberances</td>
<td>With setiferous lateral protuberances</td>
</tr>
<tr>
<td>41. Male ninth sternum</td>
<td>With normal setae</td>
<td>With short, stout setae</td>
</tr>
<tr>
<td>41'.</td>
<td></td>
<td>With fine setae</td>
</tr>
<tr>
<td>42. Male ninth sternum</td>
<td>Not sclerotized dorsally</td>
<td>Sclerotized dorsally (Fig. 37)</td>
</tr>
<tr>
<td>43. Male ninth sternum</td>
<td>Without internal ridges</td>
<td>With internal ridges (Figs. 31 and 33)</td>
</tr>
<tr>
<td>44. Male ninth sternum</td>
<td>Not locking with tenth sternite</td>
<td>Locking with tenth sternite</td>
</tr>
<tr>
<td>45. Male ninth tergum</td>
<td>More or less quadrate</td>
<td>Short, with broad median incision (Fig. 36)</td>
</tr>
<tr>
<td>46. Male ninth tergum</td>
<td>With dorso-lateral incisions (Fig. 32)</td>
<td>Without dorso-lateral incisions</td>
</tr>
<tr>
<td>47. Ninth tergal internal inflection</td>
<td>Without median fossa</td>
<td>With median fossa (Figs. 30 and 32)</td>
</tr>
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</table>
TABLE 1 (Continued)

<table>
<thead>
<tr>
<th>Character</th>
<th>Plesiotypic</th>
<th>Apotypic</th>
</tr>
</thead>
<tbody>
<tr>
<td>48. Ninth tergal internal inflection</td>
<td>Arched (Figs. 30, 32, 34 and 36)</td>
<td>Inverted V-shaped (Figs. 23, 24, 26 and 28)</td>
</tr>
<tr>
<td>49. Membrane between ninth and tenth sternites</td>
<td>Thin</td>
<td>Thickenened, bilobate</td>
</tr>
<tr>
<td>49'.</td>
<td></td>
<td>Thickened, regularly convoluted</td>
</tr>
<tr>
<td>50. Genital papillae</td>
<td>Present (Figs. 22, 37 and 38)</td>
<td>Absent</td>
</tr>
<tr>
<td>51. Tenth gonocoxites</td>
<td>Without median projection</td>
<td>With median projection (Fig. 39)</td>
</tr>
<tr>
<td>52. Tenth gonocoxites</td>
<td>Antero-lateral corner without acute projection (Figs. 36, 39 and 42)</td>
<td>Antero-lateral corner with acute projection (Figs. 40 and 41)</td>
</tr>
<tr>
<td>53. Tenth gonostylus</td>
<td>Digitiform (Figs. 38, 39 and 42)</td>
<td>Short, broad (Fig. 31)</td>
</tr>
<tr>
<td>53'.</td>
<td></td>
<td>Papiliform (Figs. 40 and 41)</td>
</tr>
<tr>
<td>54. Ninth gonostylus</td>
<td>Unguiform (Figs. 31, 33, 35 and 37)</td>
<td>Clavate (Figs. 22, 25, 27 and 29)</td>
</tr>
<tr>
<td>55. Ninth gonostylus</td>
<td>Relatively short</td>
<td>Long, bent (Fig. 37)</td>
</tr>
<tr>
<td>56. Ninth gonostylus</td>
<td>Sparsely setose</td>
<td>Densely setose</td>
</tr>
<tr>
<td>57. Ninth gonostylus apodeme</td>
<td>Parallels ninth tergum (Figs. 22, 25, 27, 29, 31 and 33)</td>
<td>Directed medially (Figs. 35 and 37)</td>
</tr>
<tr>
<td>58. Tenth tergites</td>
<td>Short</td>
<td>Long, thin (Figs. 26 and 27)</td>
</tr>
<tr>
<td>59. Tenth tergites</td>
<td>Not as in Figs. 36 and 37</td>
<td>Biramous as in Figs. 36 and 37</td>
</tr>
<tr>
<td>60. Eleventh tergum</td>
<td>Present (Fig. 32)</td>
<td>Absent</td>
</tr>
<tr>
<td>61. Lateral sclerite of ovipositor</td>
<td>Well sclerotized</td>
<td>Weakly sclerotized</td>
</tr>
<tr>
<td>62. Gonostylus</td>
<td>Articulated with gonocoxite (Fig. 44)</td>
<td>Fused with gonocoxite (Fig. 43)</td>
</tr>
<tr>
<td>63. Sternal pouch</td>
<td>Absent</td>
<td>Present (Fig. 43)</td>
</tr>
<tr>
<td>64. Sclerites between eighth sternum and gonopore</td>
<td>Absent (Fig. 43)</td>
<td>Present (Fig. 44)</td>
</tr>
<tr>
<td>65. Bursa copulatrix</td>
<td>Not saclike (Figs. 46 and 47)</td>
<td>Saclike (Fig. 45)</td>
</tr>
<tr>
<td>66. Number of spermathecae</td>
<td>Two (Figs. 45 and 46)</td>
<td>One (Fig. 47)</td>
</tr>
<tr>
<td>67. Spermathecal duct</td>
<td>Continuous with bursa (Figs. 46 and 47)</td>
<td>Separate from bursa, T-shaped (Fig. 45)</td>
</tr>
<tr>
<td>68. Accessory glands</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>69. Accessory glands</td>
<td>Short</td>
<td>Long</td>
</tr>
<tr>
<td>70. Accessory glands</td>
<td>Sigmoid (Figs. 48–50)</td>
<td>Linear (Figs. 51 and 52)</td>
</tr>
</tbody>
</table>

available integumental sources, including previously overlooked or under-utilized 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 plesiotypic 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 Chaulioidinae, 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 Chauliodinae genera were analysed by reference to works by Esben-Petersen (1924) and Barnard (1931) (Platycheilidae, Taeniochauliodes), Kimmins (1938, 1954) (Anachauliodes, Archichauliodes, Ctenochauliodes), Munroe (1953) and Chandler (1956) (Dysmicothermes), and Ponomarenko (1967) (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.

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, sub serrate 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 apot ypies in Acanthacorydalis and most Corydalus, while female mandibles the length of the head (12) are restricted to Acantha corydalis. Enlarged male mandibles in Corydalus 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 Chloronra, 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 Neur Hermes and Proto Hermes, as in the 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 the Corydalinae. The lacinia bears three elongate apical setae in most Corydalidae; independent loss of these setae (17) has occurred in Acanthocorydalis, 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 Neur Hermes (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 Neur Hermes; this may have occurred twice, once in Proto Hermes and again in the ancestor to the other genera, or may have occurred several times. One sensory area is primitively present at the tips of the palps as indicated by the homologous state in Chauliodinae; two areas (24 and 26) have evolved in the Proto Hermes–Neur Hermes lineage and the New World genera.
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 *Corydalus* is unbranched (27). As presumably primitive Chauliodinae (*Dysmicokerrnc*, Chandler, 1956; *Cretochaulus*, Ponomarenko, 1976) display the bifurcate condition, and *Corydalus* is a highly derived genus, the non-bifurcate condition is considered apotypic.

In most Corydalinae, Sialidae and presumed primitive Chauliodinae M3+4 consists of two branches, while these have fused (29) in the ancestor of *Corydalus* and *Chloronia*. The opposite trend is apparent in M1+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). In *Protohermes* and *Neurhermes* 1A is three-branched (30), while the primitive two-branched state is present in all other Corydalinae, most Chauliodinae, and Sialidae.

As indicated by comparison with the Chauliodinae and Sialidae, crossvein addition has been a general trend. Three crossveins between R1 and Rs and two medial crossveins are primitive states, while four or more crossveins between R1 and Rs (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 *Corydalus*. 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 accessories 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 and 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.

In 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 papillae 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 papillae in the most primitive Neuromus and Platyneuromus species is further evidence of their plesiotypic; they have been lost (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 anterolateral projections (52) and papilliform tenth gonostyli (58) 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 5 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

FIGS. 38–42. Male tenth sternites: 38, Protohermes costalis, showing genital papillae; 39, Neoneuromus sp.; 40, Chloronia sp.; 41, Corydalus cornutus; 42, Platyneuromus soror.
FIGS. 43 and 44. Female abdomens: 43, Chloronia sp.; 44, Neurhermes maculipennis.
FIGS. 45—47. Bursa and spermathecae: 45, Corydatus cornutus; 46, Neoneuromus sp.; 47, Neuromus intimus.
FIGS. 48—52. Female accessory glands: 48, Neurhermes maculipennis; 49, Protohermes sp.; 50, Acanthacorydalis fruhstorferi; 51, Neuromus intimus; 52, Neuromus sp.
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 gonapophyses 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 Neurhomus–Neoneurhomus lineage is considered autapotypic.

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 the 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 Neurhomus.

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

**Phylogenetic considerations**

Although species level cladograms do not rule out ancestor–descendant 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–descendant 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 seventy 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 Neurhomus–Neoneurhomus 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 Corydalus, 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 M₃₄₄ (29) is shared with Corydalus and Chloronia, and a non-bifurcate last radial sector branch (27) indicates Corydalus 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 Corydalus and Chloronia would indicate common ancestry with Corydalus, especially if any other apparent autapotypies of Corydalus are shared.
Biogeographic considerations

As readily seen in Figs. 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, 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. *Platyneuromus* probably diverged from an ancestral South American stock after dispersal into, and subsequent vicariance in Central 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 does Corydalus cornutus and also 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 synonymes. 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.'

**CORYDALINAE**


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 luteous or stramineous with piceous markings, sometimes fuscous to piceous; 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 thirty to eighty-five articles, usually filiform, about length of head plus prothorax; clypeal margin entire or incised medially; labrum triangular, ovoid, or broadly truncate, usually partly covering mandibles; mandibles usually half to three-quarters length of head and with three prominent inner teeth, rarely greatly enlarged and without distinct teeth. Thorax: prothorax rectangular or trapezoidal, slightly narrower than head, about length of meso- plus metathorax; meso- and metathorax quadrate, about equal size, slightly wider than hind margin of pronotum; legs about length of head plus prothorax, femur about length of tibia, tibial apex with two ventral spines, tarsi with five articles, first and fifth about equal in length, articles two to four combined about length of first, tarsal claws feebly

<table>
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<th>TABLE 2. Classification of Corydalinae.</th>
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<td><strong>Protohermes assemblage</strong></td>
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<td>Protohermes</td>
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<td><strong>Neuromus assemblage</strong></td>
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<td><strong>Corydalus assemblage</strong></td>
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<td>Platyneuromus</td>
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<td>Chloronia</td>
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<td>Corydalus</td>
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<td>Chloronella — placement uncertain</td>
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Systematics of the dobsonfly subfamily Corydalinae

Key to genera of Corydalinae

1 Three crossveins between R₁ and Rs (Figs. 14–16) ........................................... 2
   Four or more crossveins between R₁ and Rs (Figs. 17–21) .................................... 5

2 M₃₊₄ bifurcate (Fig. 16); postocular region explanate (Fig. 61); Central America
   Platyneuromus
   – M₃₊₄ a single branch (Figs. 14 and 15); postocular region not explanate ............... 3

3 Last branch of radial sector branched (Fig. 14); South and Central America ........ Chloronia
   – Last branch of radial sector unbranched (Fig. 15) .............................................. 4

4 Male ninth gonostylus clavate (Fig. 29); males usually with enlarged mandibles; North to South America .................. Corydalus
   – Male ninth gonostylus clawlike; South Africa ............................................... Chloroniella

5 Occipital disk with two prominent spines (Fig. 60); males with enlarged mandibles; large, dark species; Asia ........... Acanthacorydalis
   Occipital disk without spines; males never with enlarged mandibles ............................. 6

6 Posterior tentorial pits arcuate (Fig. 2); postocular tooth well developed; 1A two branched (Figs. 20 and 21) .................. 7
   – Posterior tentorial pits linear (Fig. 3); postocular tooth poorly developed; 1A three branched (Figs. 18 and 19) .... 8

7 Male ninth sternite attenuate (Fig. 33); female with two spermathecae (Fig. 46); clypeal margin with few setae (Fig. 8); mostly large, dark species; Asia ........................................... Neoneuromus
   – Male ninth sternite quadrate (Fig. 31); female with one spermatheca (Fig. 47); clypeal margin fimbriate (Fig. 9); moderate sized, pale species; Asia ................................................ Neurorhmes

8 Male tenth tergites always biramous, ventral arm slightly longer than dorsal (Figs. 36 and 37); head and body black, pronotum often orange, wings black with light maculations; galea without sensory peg; Asia ................................................ Neurorhmes
   – Male tenth tergites simple (Figs. 34 and 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

Protohermes Weele (Figs. 4, 12, 19, 34, 35, 49, 55 and 56)


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; wing-span 60—130 mm. Coloration: stramineous to fulvous, two piceous prothoracic vittae, often with head maculations, rarely entire body dark; wings stramineous, veins often darker, wings occasionally smoky with lighter maculations. Head (Fig. 56): robust; posterior tentorial pit linear; postocular spine feebly developed; antennae feebly sub serrate, about length of head plus prothorax, of thirty-five to fifty 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 four-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

FIG. 56. Protohermes sp., head and prothorax.
crossvein, twenty-four to fifty-eight costal crossveins. Males: ninth sternite (Fig. 35) broadly and deeply incised medially; genital papillae present; internal inflection of ninth tergum arched; ninth gonostyli unguate, nearly glabrous, apodemes directed mesad; occasionally unifying; tenth tergites short, tubular with setal brush directed medially (Figs. 34 and 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 that adult emergence occurs all the 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 *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*.

*Neurhermes* Navás (Figs. 3, 5, 18, 36, 37, 44, 48, 55 and 57)


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

Description. Size: length 15–30 mm; wing-span 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 subsegmented, about length of head plus prothorax, of forty to fifty-five articles; clypeal margin entire, labrum triangular (Fig. 5); maxilla relatively short and broad; stipes with conspicuous setae; labrum 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; M4+5 with four branches; M3+4 with two (rarely three) branches; Cu1 with two accessories; 1A with three branches; five to eight crosveins between R1 and R5, four between Rs and M; three medial crosveins, with one between branches; one cubital crosvein, twenty-five to forty-six costal crosveins. Males: ninth sternite with prominent (Fig. 37) or short, notched median projection, upper surface sclerotized; genital papillae 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 unifying; tenth tergites biramous, dorsal arm slightly shorter than ventral (Figs. 36 and 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; accessory glands sigmoid, longer than bursa plus spermathecal duct (Fig. 48).

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

Natural history: Label data indicate that specimens were collected from late March to May at altitudes of 2000–3500 ft. Weele (1910) mentions specimens collected between October and February.
Remarks: Navás's *Neurhermes* is a replacement name for Gray's *Hermes*, homonymous with a gastropod genus. Of the six nominal species of *Neurhermes*, four are based on colour pattern of females, and may be variations of the other two.

*Neuromus* Rambur (Figs. 9, 20, 30, 31, 47, 51, 54 and 58)


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

Description. Size: length 30—35 mm; wingspan 75—100 mm. Coloration: luteous; antennae, tips of mandibles, four spots on pronotum piceous; wings nearly hyaline, with piceous forewing veins. Head (Fig. 58); moderately flattened; posterior tentorial pit arcuate; postocular spine moderately developed; antennal sensory peg moderately developed; antenna filiform, about length of head plus prothorax, of forty-five to sixty-five 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 accessories; $1A$ 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 accessories, twenty-eight to thirty-five costal crossveins. Males: ninth sternite (Fig. 31) nearly quadrate, slightly incised medially, narrower than eighth sternite, with two longitudinal, flangelike dorsal ridges; genital papillae 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 and 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 indicate that specimens were collected in September at 450 ft.

Remarks: *Neuromus* contains three nominal and at least one undescribed species. Two of the nominal species are probably synonymous.
Neoneuromus Weele (Figs. 8, 21, 32, 33, 39, 46, 52, 54 and 59)


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

Description. Size: length 35–50 mm; wing-span 80–140 mm. Coloration: ferruginous to fuscous, rarely luteous; often with fuscous or piceous vittae on head and prothorax; wings fulvous to fuscous, usually with darker tessellations. Head (Fig. 59): moderately flattened; posterior tentorial pit arcuate; postocular spine well developed; antenna filiform, about length of head plus prothorax, of forty-five to sixty-five 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<sub>1+2</sub> three to eight branches; M<sub>3+4</sub> two branches; Cu<sub>1</sub> with two to four accessories; 1A two branches; four to seven crossveins between R<sub>1</sub> 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 accessories, thirty to fifty 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; posterior margin of tergum dorsolaterally incised; ninth gonostylus unguate, sparsely setose; tenth tergites clavate, feebly sigmoid (Figs. 32 and 33); tenth gono-
coxites 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 gonocoxit; bursa tubular, continuous with spermathecal duct (Fig. 46); accessory glands linear, half length of bursa plus spermathecal duct (Fig. 52).

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

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

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

**Acanthacorydalis** Weele (Figs. 6, 17, 22, 23, 50, 54 and 60)


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

Description. Size: length 60–80 mm; wing-span 140–175 mm. Coloration: piceous, often with testaceous to ferruginous 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 of spines on cranial disk; antenna filiform, about length of head plus prothorax, of seventy to eighty-five 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; M₁+₂ and M₃+₄ bifurcate (M₃+₄ of hindwing rarely with three branches); Cu₁ with two to four accessories; 1A two branches; usually six crossoveins between R₁ and Rs, four to eight between Rs and M and between M₁+₂ and M₃+₄; three to five crossoveins between branches of media; six to eight m-cu's; one to three cubital crossoveins, with two to five between accessories; twenty-five to forty-five costal crossoveins, median ones forming reticulate pattern in males. Males: ninth sternite ovoid, with lateral lobes (Fig. 22), setae short, stout; genital papillae 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 and 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 of bursa plus spermathecal duct (Fig. 50).

Distribution: Northeastern India to Vietnam and China (Fig. 54).

Natural history: Label data indicates that specimens were collected from late March to May at 1800–3500 ft.

Remarks: Weele (1907: 230) included in Acanthacorydalis the species Corydalus asiaticus Wood-Mason and C. orientalis McLachlan. I designate C. asiaticus, 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.

Platyneurornus Weele (Figs. 2, 11, 16, 24, 25, 42, 54 and 61)


Diagnosis. Presence of postocular flange, Central American distribution.

Description. Size: length 20–50 mm; wingspan 50–110 mm. Coloration: luteous to fulvous; pronotum with fuscous to piceous vittae, vittae often on head; wings fulvous 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 head plus prothorax, of forty to fifty-five 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 \( Rs \) and between \( Rs \) and \( M \); two medial crossveins, four \( m-cu \)'s; one cubital crossvein, eighteen to thirty-five costal crossveins; first \( R_1 \) cell \( 1-\frac{3}{2} \) times length of third. Males: ninth sternite quadrate (Fig. 25), membrane behind sternite thickened, bilobate; genital papillae 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 and 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 indicate 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.

**Chloronia Banks** (Figs. 10, 14, 26, 27, 40, 43, 55 and 62)


Diagnosis. Usually smaller and paler than *Corydalus*; third \( R_1 \) cell longer than first; last branch \( Rs \) forked; South and Central American distribution.

Description. Size: length 20–40 mm; wing-span 50–90 mm. Coloration: luteous, with four piceous markings on pronotum, occasionally with other markings on head and mesothorax; wings nearly hyaline, luteous or stramineous, often with darkened veins and maculations. Head (Fig. 62): moderately flattened; posterior tentorial pit arcuate; postocular spine moderately developed; antennal filiform, of thirty-five to sixty 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_i 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, twenty-two to thirty-six 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, 3–8 times longer than wide (Figs. 26 and 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 saclike, separate from spermathecal duct; accessory 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 *Neurromus*. Eleven nominal species have been described.

*Corydalus* Latreille (Figs. 7, 13, 15, 28, 29, 45, 54 and 63)


FIG. 63. *Corydalus cornutus*, habitus.
Diagnosis. Three- and four-segmented labial and maxillary palps respectively; last branch of radial sector not bifurcate; first R₁ cell much longer than third; males usually with enlarged mandibles; New World distribution.

Description. Size: length 20–60 mm; wingspan 70–150 mm. Coloration: fuscous to fulvous, occasionally with lighter head and pronotum markings; wings usually fuscous 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 head plus prothorax 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; two to five (usually three) branches, M₃+₄ one; Cu₁ with three to six accessory veins; 1A two branches; three crossveins between R and Rs, three to six between Rs and M; three to seven medial crossveins, one to three between M₁ and M₂; four to eight m-cu’s; one (rarely two) cubital crossvein, thirty to sixty costal crossveins. Males: ninth sternite moderately incised medially, with lateral lobes; internal inflection of ninth tergum inverted V-shaped; ninth gonostylus 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 ft. 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 cannot 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. fruhydrorferi Weele. 2 specimens. TONKIN (North Viet Nam). (MNHN); Montes Mauson (ZMHU).


Chlororia Banks. 6 species.

C. mexicana Stitz. 19 specimens. MEXICO. CHIAPAS: Chiapa de Corzo (CNCC); 20–25 miles N Huixtl (CNCC); Palenque (CNCC, MCZC); 32 miles W San Cristóbal (CNCC). SAN LUIS POTOSI: El Salto (SEM); VERACRUZ: Cordoba (CNCC).

C. pallidus (Davis). type in USNM.


Corydalis Latreille. 13 species.


Carmatus Hagen. Around 400 specimens. ARGENTINA. JUJUY: (CASC); Altaflor (BMNH); CABA: Quebrada de Lules (USNM). Salto Poítos (FSAC). BOLIVIA. COCHABAMBA: (PAAC); Chappare (PAAC, FSCA). LA PAZ: Chulumani (USNM); Coreico Exp. Sta., N Yungas (USNM). COLOMBIA. (LACM). ANTIOQUIA: Jerico (USNM). META: Villavicencio (MCZC). VALLE DE CUACA: (CASC); Altaflor (BMNH); Anchicaya (CNCC); Cali (MCZC); Costa Rica (CAS); La Esperanza (CASC). BUENA VISTA (USNM); Medellín (USNM); Monterredondo (PAAC); Praetra (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 (CMNH). GUANANCASTE: (SEM). LIMÓN: Guapiles.
(SEMK); Los Diamantes (LACM). PUNTARENAS: Monte Verde (LACM, USNM); 4 miles E Palmar (SEM); 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: (CASC, USNM). PICHINCHA: Quito (MCZC); Santo Domingo de Los Colorados (CASC); Tandapi (CUNY, USNM). PICHINCHA: Quito (MCZC); Puyo (CUNY, USNM); Tena (USNM). PASTAZA: Distr. (LACM). MEXICO. CHIAPAS: (PAAC). Cacao (USNM); Trece Aguas (USNM); San Marcos (CASC). BRITISH HONDURAS. Middlesex, Stann Cr. (PAAC). PANAMA. CHIRIQUI: Bugaba (MCZC, SEMK); Los Diamantes (LACM). PUNTARENAS: Monte Verde (LACM, USNM); 4 miles E PERU. (MNHN, SEMK). AMAZONAS: (CASC). HUANUCO: 10 miles N Huanta (CASC); Pan de Azucar (LACM); Pomacocha (CASC). CAJAMAKCA: C.batesi T'ING TING; C. c.batesi (PAAC); C. c. Hagen. ARAGUA: Kancho Grande (CUNY, USNM). PASCO: (LACM): Chontilla, 22 km SE Iscozazin (LACM); Pan de Azucar (LACM), Chanchamayo (USNM, CASC); Chuchorongo (MCZC); Chosica (SEMK); Paltaybamba (USNM); San Miguel (USNM). MERIDA: (BMNH, MCZC, MNHN, USNM). El Sinchono (USNM). VENEZUELA. (BMNH, MCZC). MIKANIIA: Caracas (MCZC). El Rincon Oso Penninsula (LACM). ECUADOR. LOS RIOS: 9 miles W Tortugero (LACM). PUNTARENAS: 1.8 miles W Rincon Oso Penninsula (LACM). EC. (BMNH). CHIMALTENANGO: Yecapica (USNM). SUCATEPEQUEZ: Finca Moca (USNM); Finca Paraxé (USNM). El Cacao (USNM); Trece Agua (USNM); San Marcos (CASC). BRITISH HONDURAS. Middlesex, Stann Cr. Distr. (LACM). MEXICO. CHIAPAS: (PAAC). PANAMA. CHIRIQUI: 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). HUANUCO: 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); Choucharongo (MCZC); Chosica (SEMK); Paltaybamba (USNM); San Miguel (USNM). VENEZUELA. (BMNH, MCZC). ARAGUA: Rancho Grande (CUNY, USNM). MERIDA: (BMNH, MCZC, MNHN, USNM). Paranos (MCZC). MIRANDA: Caracas (MCZC). El Valle (USNM).


C. boliviari Banks. 29 specimens, including types (VENEZUELA. Appun — MCZC). COLOMBIA. (PAAC). VENEZUELA. ARAGUA: 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); Espírito 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 (SEM); 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. eucadorianus Banks. 5 specimens, including holotype (ECUADOR: Banos — MCZC). COLOMBIA: Ancichayna (CNCC); St Antonio (MCZC).

C. flavicornis Stitz. 32 specimens, including type (PANAMA: CHIRIQUI — ZMHU). COLOMBIA. ANTIOQUIA: Jérico (USNM). Buena Vista (USNM). COSTA RICA. LIMON: Hacienda Tapezco, 29 km W Tortugero (LACM). PUNTARENAS: 1.8 miles W Rincon Oso Penninsula (LACM). EC. (BMNH). LOS RIOS: Quevedo (USNM); 29 km W St Domingo, Manabi (USNM); Quevedo (MCZC, USNM).

C. lutea Hagen. Around 500 specimens. COSTA RICA. GUANACASTE: 5 km N Cañas (TAMU). El Salvador. Lomas Verde (TAMU); San Nicolas Leapa (USNM). GUATEMALA. CHIMALTENANGO: Yecapica (USNM). GUATEMALA: E SE Guatemala City (USNM). SAN MARCOS: Puente Talisman (CUNY). SUCHITTEPEQUEZ: Cuyotengo (USNM). ALTA VERA PAZ: Trece Agua (USNM). BRITISH HONDURAS. BELIZE: Belize (USNM). STANN CREEK: Middlesex (PAAC). HONDURAS. El Zamorano (OSUC); Siguatepeque Escuela Sup. Cienc. For. (PAAC). MEXICO: Chiapas. (CASC, TAMU, USNM); Colima (USNM); Durango (OSUC); Guerrero (FSCA); Hidalgo (SEMK); Morelos (FSCA, SEMK); Nayarat (SEMK); Nuevo Leon (CUNY, FSCA, TAMU, USNM); Oaxaca (TAMU); Puebla (USNM); Querétaro (TAMU); San Luis Potosi (FSCA, SEMK, TAMU, USNM); Sinaloa (CNCC); Tamaulipas (CUNY); Veracruz (CASC, CNCC, PAAC, SEMK, TAMU, USNM); Zacatecas (OSUC). NICARAGUA. Matagalpa (USNM). PANAMA. CANAL ZONE: Barro Colorado Island (CASC, CNCC, CUNY, INPA, MCZC, MJGC, SEMK, USNM). CHIRIQUI: Miramar (MJGC); COLON: 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). WEB Co. (TAMU).

C. rubidus Erikson. 2 specimens, including holotype (BRITISH GUYANA — ZMHU). FRENCH GUYANA: Saut-Maripa (MNHN).

Neurotrneus 18 specimens, including type (BRAZIL – ZMHU). BRAZIL. (MCZC). ARGENTINA. MISSIONES: Arroyo Piray Mini, W Dos Hermanos (USNM); Piray Guazu (USNM).

Neurotrneus Stitz. 18 specimens, including type (BRAZIL – ZMHU). BRAZIL. (MCZC).

Coryalus sp. 16 specimens. BOLIVIA. Cavinas Beni (USNM); Guayarin (MCZC). BRAZIL. AMAZONAS: Manaus (INPA); Para Urúa, 65 km SW Itaituba (INPA); Porto Velho, Rio Madieros (MCZC); Reserva Campines (INPA). COLOMBIA. Bueno 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) – mislabelled. Neurotrneus Wele. 2 or 3 species. Neurotrneus spp. 27 specimens, including types of N.fenestralis maculichani (Weele) (TONKIN, Montes Mauson – MCZC) and N.latratius tonkinensis (Weele) (CHINA. SZECHWAN: Mt. Omei Shan – MCZC). CHINA. HUPEH: Suisap, Lichuan Distr. (CASC). KIANGSI: Hong San (MCZC). KWANGTUNG: Tsin Leongsham (CASC). Mohkanshan (CASC); Yim Na San, E Ewanton (MCZC); Yuman Fou, Tau-Nin Kai (MNHN). INDIA. ASSAM: Kameng (Bharelhi River), Dirdmq Dzong (CNCC), Nakha (CNCC), Salar (CNCC). MANIPUR: Chatrck (CNCC); Khamassom (CNCC). SIKKIM: Monqang (CNCC); Simqhk (CNCC); Yugang (CNCC).


Neurotrneus 1 specimen. MALAYSIA. SABAH: Mt Kinabalu (USNM).

Platyneuromus Wele. 4 or 5 species. P.auritus Kimmins. 10 specimens. GUATEMALA. Cayuga (USNM). HONDURAS. (BMNH); La Lima (USNM). MEXICO. CHIAPAS: Chipas (CASC); Ocozoa Autla (CASC); Tuxtla Gutierrez (MCZC), PAAC.

P.christel (Navás). 9 specimens, including type (COSTA RICA, Turrialba – 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); Paltita (USNM). VERA CRUZ: Ciudad Mendoza (USNM); Fortín 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); Volcán de Chiriquí (BMNH).

Platyneuromus spp. 10 specimens. GUATEMALA. Panzos (USNM); Quirigua (USNM); Trece Aguas (USNM). HONDURAS. Lombardia (USNM). MEXICO. CHIAPAS: Palenque (CNCC). VERA CRUZ (USNM).


P.davidi Wele. Type (NORTH VIET NAM. Mou Pin – MNHN).

P.grandis (Thunberg). 9 specimens. JAPAN. HOKKAIDO: (MCZC); Sapporo (MCZC). HOKSHU: Kofu (CASC); Nikko (CASC); Nippon Moyen, env. Tokyo (MNHN). Kyushu: Ashiya (CASC).

Protohermes spp. 43 specimens. CHINA. HUPEH: Suisap, Lichuan Distr. (CASC). SZECHWAN: (MCZC); Chengtu (CASC, MCZC); Chiang Nsian (MCZC); Mt Omei Shan (MCZC). Ta Hao, Haipa (MCZC). INDIA: ASSAM: Kameng (Bharelhi River), Bilo La (CNCC), Domkja (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). Horii (MCZC); Rokki (MCZC).
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