AN ABSTRACT OF THE THESIS OF

ELWIN D. EVANS for the DOCTOR OF PHILOSOPHY
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Title: A STUDY OF THE MEGALOPTERA OF THE PACIFIC COASTAL REGION OF THE UNITED STATES

Abstract approved: N. H. Anderson

Nineteen species of Megaloptera occurring in the western United States and Canada were studied. In the Sialidae, the larvae of Sialis arvalis Ross, S. californica Banks, S. cornuta Ross, S. hamata Ross, S. nevadensis Davis, S. occidens Ross and S. rotunda Banks are described with a key for their identification. The female of S. arvalis is described for the first time. Descriptions of the egg masses, hatching, and the egg bursters and first instar larvae are given for some species. Data are given on larval habitats, life cycles, distribution and emergence of the adults. An evolutionary scheme for the Sialidae in the study area and the world genera is hypothesized.

In the Corydalidae, Orohermes gen. nov. and Protochauliodes cascadius sp. nov. are described. The adults of Corydalus cognatus Hagen, Dysmicohermes disjunctus Munroe, D. ingens Chandler, Orohermes crepusculus (Chandler), Neohermes filicornis
(Banks), *N. californicus* (Walker), *Protochauliodes aridus* Maddux, *P. spenceri* Munroe, *P. montivagus* Chandler, *P. simplus* Chandler, and *P. minimus* (Davis) are also described. The larvae of all but three species are described. Keys are presented for identifying the adults and larvae. Egg masses, egg bursters and the mating behavior are given for some species. Pre-genital scent glands were found in the males of the Corydalidae. Data are given on the larval habitats, distribution and adult emergence. Life cycles of five years are estimated for some intermittent stream inhabitants and the cold stream species, *O. crepusculus*. The life cycles of *O. crepusculus* and *N. californicus* were studied in detail. The latter species was reared from the egg to the adult stage. An evolutionary scheme for the species of Corydalidae in the study area and for the Chauliodinae of the world is hypothesized.

Data are presented on heat tolerance of a number of species. Carbon dioxide is shown to be released ventrally on the abdomen and thorax. Oxygen consumption data are given for *Sialis occidentis*, *S. californica* and *S. rotunda*. 
A Study of the Megaloptera of the Pacific Coastal Region of the United States

by

Elwin D. Evans

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INTRODUCTION

The order Megaloptera is composed of two families, the Sialidae or alderflies, and the Corydalidae or dobsonflies. This small order consists of about 200 species at the present time. Some consider this taxon to be the most generalized order of holometabolous insects. Both families are worldwide in distribution. The larvae are predaceous and aquatic, while the exarate pupae, eggs, and adults are terrestrial. Some species are among the largest of aquatic insects, the larvae attaining a length of 75+ mm and give rise to adults with a wing expanse of over 150 mm.

The Sialidae include six genera and about 50 species. The 21 Nearctic species are placed in a single genus, Sialis Latreille. The Corydalidae are divided into two sub-families, the Corydalinae with 11 genera, and the Chauliodinae with 12 genera. About 150 species and sub-species have been described in this family. Within the Nearctic Region, 7 genera and 18 species are known to occur. In addition, a new genus and and a new species are described here.

This study was undertaken when it was found that the seven named species of Protochauliodes Weele of the Corydalidae occurring in the Pacific Coastal Region could not be identified accurately. Another species, Orohermes crepusculus (Chandler), was found to
have been provisionally placed in the genus *Dysmicothermes* Munroe. When this research began, the larvae of only two of the 13 named species of Corydalidae occurring in the Pacific Coastal Region could be identified. *Protochauliodes aridus* Maddux was the only species on which a biological study had been undertaken and the larvae of five species of Sialidae known from the region had not been associated with the adult forms. The female of *S. arvalis* Ross was undescribed.

Besides solving the taxonomic problems indicated and associating the adult and larval forms, information regarding habitats, distribution, life cycles, eggs, mating behavior and physiology was obtained to better understand how and why these insects are able to live where they do. Finally, this study was undertaken to gain some idea as to their possible evolutionary history.
LITERATURE REVIEW

The most recent work encompassing the order Megaloptera is that of Wee (1910) who offered keys for the adult forms. Lestage (1927) divided the Corydalidae into two sub-families, the Corydalinae and the Chauliodinae. In this work, keys to the genera of the adult Corydalinae and Sialidae were given. Kimmins (1954) provided a key to the genera of the adult Chauliodinae. A generic key to the larvae of the Megaloptera as they are now known has not been published.

The basic work dealing with the adult Nearctic Sialidae was that of Ross (1937), wherein 12 new species of Sialis were described and a confused taxonomic situation was clarified. Townsend (1939) described a new species and Flint (1965) described three more making a total of 21 known species in the United States. The larvae have often been described and figured but Azam and Anderson (1969) were the first to associate the larva and the adult of any Nearctic species. Furthermore, they provided a detailed life history study of two species of Sialis. Davis (1903) gave a life history of what was thought to be a single species, S. infumata Newman. This "species" was subsequently divided into 16 species by Ross (1937); therefore, Davis' study has no specific validity.

The most valuable work on the Nearctic Corydalidae to date is that of Chandler (1956), with generic keys to the adults and larvae
and a key to the California adults. Previously, Munroe (1953) described a new genus and a new species from the Pacific Coastal Region. Caudell (1933), Van Dyke (1945) and Maddux (1954) each described a new species from the same region. Chandler (1954) described four new species making a total of 13 named species for the region. Flint (1967) revised the transcontinental genus, Neohermes Banks and described a new species and designated a new allotype.

Biological investigations of the Corydalidae have been carried out by several authors. Riley (1873), Davis (1903), Barnard (1931), Hamilton (1940), Maddux (1954), Cuyler (1958, 1965), Neunzig (1966) and Smith (1970) have all contributed to a general understanding of life cycles and habitats.

The larvae of only five species of Nearctic Corydalidae have been described. Cuyler (1956) described the larvae of the two species of Chauliodes Latreille and the larva of Nigronia fasciatus Walker in 1965). Neunzig (1966) described the larvae of both N. fasciatus and N. serricornis (Say). The larva of Corydalus cornutus (L.) has been described by many authors but most recently and completely by Peterson (1960). Chandler (1956) recognized the larva of Orohermes crepusculus (Chandler) but gave no description. Therefore, at least 14 species of Nearctic corydalid larvae remain undescribed. Baker and Neunzig (1968) described the eggs, egg masses and first instar
larvae of five species of Corydalidae occurring in eastern North America.
METHODS

Material Examined

During this study over 1500 adults and 1000 larvae of Corydalidae from North America were examined. Over 1000 adults and 1000 larvae of the Sialidae were examined. Type specimens were examined from the Museum of Comparative Zoology, Harvard University; the California Academy of Science and the United States National Museum. A few specimens of Megaloptera were examined from Asia, Europe, South Africa, South America and Australia.

Collection records will be kept in my personal files with duplicate copies remaining at the Department of Entomology, Oregon State University, Corvallis, Oregon 97331.

Study Area

The study area is chiefly within the boundaries of California and Oregon. In these states, certain areas presumed or known to have various species of Megaloptera were visited at various times. The extent of the collecting trips is shown in Figure 124. Collections were made in numerous streams and some lakes along the way. These ranged as far south as the San Jacinto Mountains west of Palm Springs, California and as far north as Pullman in southeastern Washington. The Sierra Nevada Mountains of California and their surrounding
foothills were collected extensively. The coastal mountains of western California and Oregon and the Siskiyou Mountains were also visited. Numerous collections were made in the Cascade Mountains of Oregon. Trips were made in eastern Oregon to the Steens, Wallowa and Blue Mountains. The Willamette Valley was an area in which numerous collections were made.

**Collecting**

Field collecting was done with standard aerial and aquatic nets. A black light was used to collect adult specimens. Handpicking for larvae worked very well in many stream situations. Eggs were simply scraped from the substrate into large plastic pill bottles or the substrate was brought back to the laboratory. Live larval specimens were transported in styrofoam coolers. Larger corydalid larvae were placed in individual 1/4 pint plastic containers, while smaller larvae were placed in 10 dram plastic pill bottles.

**Preservation**

The importance of proper preservation of larvae cannot be over-emphasized as color and body distension are critical for proper (accurate) identification. The K. A. A. D. solution was modified from that of Peterson (1959). The following proportions of chemicals were used in the modified formulation: kerosene - 1 part; ethyl alcohol -
20 parts; glacial acetic acid - 4 parts; dioxane - 2 parts. Sialid larvae were placed directly in this killing solution while the larger corydalid larvae were orally injected with the killing solution before immersion. Adult specimens were preserved in 95% ethyl alcohol. Larvae and pupae were killed and fixed using a K.A.A.D. solution before final storage in 95% ethyl alcohol.

**Illustrations and Photographs**

All drawings of larvae were made from material preserved in KAAD. Larval length measurements were taken from live specimens. Genitalia drawings were made from material cleared with a KOH solution. Wing drawings were from projected images of mounted wings. Either a camera lucida or an ocular grid was used in making drawings when a dissection or compound microscope was necessary. Photographs were made using a 35 mm Pentax-Spotmatic with extension tubes or a Zeiss compound microscope and the attached camera.

**Slide Mounts**

All permanent slide mounts were made using Hoyer's mounting media (Peterson, 1964). Whole mounts of small larvae were cleared with lactic acid and phenol mixed at a 1:1 ratio. Eggs were also cleared if unhatched or if hatching had occurred the shells were simply wet with alcohol before placing them in the mounting media.
Rearing

Cages were constructed from acrylic plastic 2.5 mm thick. The outside dimensions were 8 cm wide, 6.5 cm high and 28.5 cm long. This was divided into 10 equal subunits each having a 2 cm hole on each side for water circulation. The holes were covered with .333 mm Nitex cemented in place with waterproof plastic cement. The tight-fitting top was also of the same plastic. These cages were used in artificial streams when several hundred specimens were being reared at once. Many specimens were raised in small plastic containers with a small amount of water in them but these required frequent cleaning.

Sialid larvae were also mass-reared using wooden boxes or large pans. One or two inches of organic substrate was placed in the bottom and covered with a few inches of water. Air was bubbled into each unit. At regular intervals all larvae were fed oligochaete worms commonly known as "tubifex."

Sialid larvae were placed in small dishes of moist soil to pupate. The soil was kept damp. For the corydalids, a moist sand clay mixture was lightly packed in the dish, an impression was made to hold the larva which was covered by a flat stone. After the pupal cell was completed, the cover was removed and a plastic screen covering was substituted in its place. The screen allowed the sand to dry out and retained the adult on emergence.
Eggs secured in the laboratory or the field were allowed to hatch over large pans filled with water and organic debris. After a few instars, the corydalid larvae were put in individual cages because of their cannibalistic behavior. Sialids were usually placed in the large containers described above.

Mating Behavior

Mating was observed using several kinds of cages. Gallon glass jars were adequate for the smaller species. A cage with clear acetate sides, measuring 30 cm x 40 cm x 60 cm, was constructed to observe crepuscular corydalid mating behavior. A red darkroom bulb was used for illumination. The insects were easily visible against one end of the cage which was white styrofoam.

Physiology

Oxygen consumption by sialid larvae was measured using a Gilsen respirometer. Carbon dioxide release sites were determined by immersing larvae in the pH indicator Brom-Thymol blue. Larvae used in two heat tolerance experiments were acclimated at 13 and 21°C for 7-10 days. Testing was done in artificial streams and temperatures were maintained within 1°C by the heating units. The first test lasted 590 hours; the second 525 hours. Tests were run at 35, 33, 30.5, 28.5 and 27°C. All larvae were assumed dead when no response occurred when pinched with forceps.
ORDER MEGALOPTERA

The order Megaloptera can be distinguished from other orders of insects on the basis of the following combination of characters: holometabolous; aquatic larvae; exarate terrestrial pupae; terrestrial adults and eggs. **Adults** - large, soft-bodied, short-lived, non-feeding; broad flattened head, chewing mouth parts; long, many-segmented antennae; large, bulging compound eyes; pronotum, large and subquadrate; two pairs similar membranous wings held roof-like over the body in repose; all major wing veins present, many cross veins; all veins well sclerotized, not bifurcating at wing margins, hind wings with folded anal areas; tarsi five-segmented with paired apical claws; abdomen lacking cerci. **Egg masses** laid above larval habitat; long axes of eggs parallel or angled to substrate, eggs cylindrical with a tassel-like micropylar projection; egg bursters present, either V-shaped or a single ridge, located at apex of labrum and shed at eclosion. **Larvae** - elongate, predaceous, resembling adults. Head well sclerotized, mandibles long and toothed; antennae four- or five-segmented; six lateral stemmata. **Thorax** - sclerotized dorsally, pronotum quadrate, the meso- and meta-notum together wider than long; legs elongate, five-segmented, coxa, trochanter, femur, tibia, tarsus with two claws; meso- and metathoracic spiracles. **Abdomen** - soft, with seven or eight pairs of lateral filaments and spiracles on segments 1-8.
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Key to the Families of Megaloptera

1. Adults less than 25 mm in length; ocelli absent; fourth tarsal segment bilobed. Larvae with seven pairs of 4-5 segmented lateral filaments and a single, long, caudal filament. . . . . . . . . . . . Sialidae (p. 20)

2. Adults over 25 mm in length; ocelli present, fourth tarsal segment not bilobed. Larvae with eight pairs of two-segmented lateral filaments, two anal prolegs with a pair of apical claws . . . . . . . . . Corydalidae (p. 63)
The following genera have been described on the basis of the shape and venation of the wings: **Austrosialis** Tillyard (1919), from Australia and Tasmania; **Indisialis** Lestage (1927), from India, the Malayan Peninsula, Borneo, and Java; **Leptosialis** Ebsen-Petersen (1920), from Madagascar; **Nipponsialis** Kuwayama (1962), from Japan; **Protosialis** Van der Weele (1909), from South and Central America; and **Sialis** Latreille (1802), which is Holarctic. Species descriptions are based mainly on genitalic characters but these are sometimes supplemented with other distinctive features (Ross, 1937). A comparative study of the larvae at the generic or species level has not been undertaken.

The larvae of **Sialis** have been known since Roesel (1749) described the unnamed larvae of **S. fuliginosa** Picket. Lestage (1919) indicated that several European workers had described the larvae of **S. lutaria** (L.) in the 19th Century. Ross (1937) and Peterson (1960) gave generic characters for the larvae of **Sialis** from unassociated material. Azam and Anderson (1969) gave the first descriptions of North American sialids based on positively associated larvae and adults. The tentative descriptions by Cuyler (1956) were not based on reared and associated specimens and are therefore subject to question.
Biology

Azam and Anderson (1969) summarized the previous knowledge of the biology of Sialis and furthered this knowledge with their work on S. rotunda Banks and S. californica Ross. A resumé of this work supplemented by my observations must serve as representative of the Sialidae, as biological studies of the other genera have not been undertaken.

Sialis larvae are found in the substrates of a variety of permanent fresh water habitats, ranging from small springs and seepage areas to large rivers, and from ponds to large lakes. The habitat can be equally variable for a single species, although certain species are found in restricted habitats. The burrowing larvae are usually found where the substrate is soft and composed of organic detritus. Sometimes they are found in gravel or among rocks in the current or among the roots of aquatic vegetation. They feed on almost any other animal they can overpower, including their own kind. The prey is seized by the elongate mandibles and forelegs and worked into the mouth with the aid of labrum, maxillae and labium. Sometimes, only the softer abdominal parts of prey are eaten.

Sialid larvae are eaten by only a few predators. In streams, the larvae are seldom preyed upon by fish (Warren et al., 1966), but Davis (1903) listed corydalids as a predator of Sialis. I have caught bluegills, Lepomis macrochirus Rafinesque, through the ice of
northern Michigan lakes with their stomachs gorged with sialid larvae.

The life cycle takes one or two years depending on the physical and biological conditions of the larval habitat. The colder and less productive habitats such as trout streams and mountain lakes lengthen the period of larval life while rapid development occurs in warm productive habitats such as ponds, warm lakes and muddy rivers. The length of the life cycle may vary for a single species.

During early spring, the fully developed larvae leave the water and dig an unlined chamber in the soil or debris near the shoreline. The adults emerge after a pupal instar of two or more weeks. Adults are most active during mid-day. In mating, the male crawls beneath the female's abdomen from the rear and raises his abdomen upward and forward to couple the genitalia. A spermatophore is passed to the female within a few minutes, copulation is terminated and oviposition occurs within a day.

The eggs are laid on a variety of substrates above the larval habitat in masses of 300-900 eggs. Each egg is about 0.7 mm in length and 0.3 mm in diameter. Two types of egg masses have been observed for this genus. In one, the long axis of the egg is almost parallel to the substrate and in the other it is almost upright. The incubation period is from 10 days to two weeks (8-12 days) (Azam and Anderson, 1969). Almost all the eggs in a mass hatch together during the night and the young larvae fall or crawl into the water. Eggs are sometimes
parasitized by a tiny wasp, *Trichogramma semblidis* (Aurivillius).

Parasitized eggs turn black as the wasps develop and those which have been parasitized may be distinguished by the circular opening made by the emerging wasp.

I have observed the hatching of sialid eggs on several occasions. The larva pushes its head against the chorion below the micropylar projection creating a slight bulge and stretching the chorion. The toothed, V-shaped egg burster, with apex of the V in the slight indentation of the labrum, then ruptures the chorion, initiating the jagged tear through which the larva emerges. After the chorion is punctured, a slight amount of amniotic fluid leaks out and a swallowing or pulsing action is evident at the site. The swallowing of air at this point increases the volume of the larva and aids the larva in tearing the chorion further (Smith, 1920). This is the first report of the occurrence of egg bursters in the Sialidae. As the larva leaves the egg, the post-embryonic molt occurs and the egg burster and embryonic membrane are left attached to the egg. After this, all the body appendages and filaments are expanded and free, and the larva becomes very active. The swallowed air is easily seen in the gut at this time. Azam (1968) erred in his observations of hatching of sialid eggs. His statement that the egg is torn by the legs of the larva never occurred during my observations. On reaching water, the larva is quickly wetted, passes through the surface film and swims to the bottom. The
larva passes through ten larval stadia before pupating.

**Genus Sialis Latrielle (1802)**

_Sialis_ may be distinguished from the other genera by the following: Wings similar in size and shape, about three times as long as wide; usually two accessory veins reaching the wing margin between veins $R_2$ and $R_3$; $M_{1+2}$ simple; $M_{3+4}$ forked; Holarctic in distribution.

Ross (1937) divided the Nearctic species into four groups on the basis of the male genitalia: the _aequalis_ group, the _americana_ group, the _californica_ group, and the _infumata_ group. Only the latter two groups were found in the study area. The _californica_ group was represented by five species: _Sialis arvalis_ Ross (1937), _S. californica_ Banks (1920), _S. cornuta_ Ross (1937), _S. hamata_ Ross (1937), and _S. occidens_ Ross (1937). The _infumata_ group was represented by _S. nevadensis_ Davis (1903) and _S. rotunda_ Banks (1920). Descriptions of all except one adult sialid found in the study area were adequately presented by Ross (1937) and will not be included here. The following taxonomic portion will deal mainly with larval descriptions.

The larvae of one other genus of Sialidae has been described. Crass (1949) described _Leptosialis africana_ Ebsen-Petersen from South Africa. From the description there is little apparent morphological difference between _Leptosialis_ and _Sialis_.

In general, the elongate larvae (Figure 1) resemble certain predaceous beetle larvae such as those of the Gyrinidae and some genera of the Dytiscidae and Hydrophilidae. The head, legs and the dorsal surface of the thorax are heavily sclerotized. The abdomen and the ventral thoracic surface are soft and lightly sclerotized. Mature larvae, 12 to 20+ mm, not including the caudal filament; head, and dorsum of the thorax patterned, smooth and shining; abdomen variously colored and patterned. Head quadrate, flattened, and prognathous; antenna distinct and four-segmented, segment I shortest and widest, II longest and wider than III and IV, III and IV are sub-equal in length; six lateral stemmata; clypeus very narrow and transverse; labrum triangular, crenulate laterally, produced apically and covering mouthparts; mandibles pointed and elongate, two inner teeth near midpoint; maxilla with a cardo, stipes, palpifer, four-segmented palpus, conical galea and pointed lacinia; labium with submentum, ligula, and three-segmented palpus. Thorax with pronotum quadrate, longer than the mesonotum which is longer than metanotum; legs elongate, five-segmented with two apical claws and many rows of long and short setae; mesothoracic spiracle distinct, metathoracic spiracle minute. Abdomen ten-segmented, a small transverse dorsal sclerite on anterior portion of segment I, last segment ending in a long tapering caudal filament; first seven segments with segmented filaments, longer than width of abdomen, filaments of segment I usually
four-segmented, II either four- or five-segmented, III-VII five-
segmented, with marginal setae; small spiracles present on segments
I-VIII, located anterior to base of filament and in a similar position
on VIII; anus dorsal, anterior to base of caudal filament.

First instar larva (Figure 17) - 1.2± mm from apex of caudal
filament to labrum; very lightly pigmented and resembling fully
developed larva. Head slightly roughened with variable patterned
areas dorsally; antenna three-segmented, segment I short and wide,
II and III sub-equal in length, narrower than I, apex of II and III with
long setae; labrum semi-oval, slightly emarginate anteriorly with a
few short setae and projections, apex of egg burster fitting into the
emargination; mandibles serrate on inner margin before first tooth
and between first and second tooth; setae of dorsum of head in distinc-
tive patterns. Thorax lightly sclerotized; legs with a few scattered
setae and relatively long claws. Abdomen - dorsum and venter lightly
pigmented and finely spiculate, a few short setae on the dorsum and
venter of each segment, lateral setae on each segment, longer than
lateral filaments; lateral filaments apparently unsegmented, slightly
swollen basally with apical setae longer than filament, segments VIII
and IX with a whorl of long setae; anal filament more heavily sclero-
tized than abdomen with long sub-apical setae.

A range of colors from yellow to reddish brown to purple, with
distinctive patterns both on the head, thorax and abdomen serves as
the main character to distinguish mature larvae. The shape and crenulation of the labrum are of some taxonomic value. The setal patterns of the legs are too variable to be of taxonomic value. The mouth parts do not have easily observable characters by which the larvae may be separated. Some variation in color and color patterns occurs. Larvae about to pupate lose the distinct patterns of the head and thorax as the muscle insertions that create these patterns are detached prior to pupation. First instar larvae may be identified by the setal patterns and color patterns on the dorsum of the head. Faulty preservation may cause the loss of color or patterns, or both. If correct species determination is desired, proper preservation techniques should be used.

Key to the Mature Larvae of *Sialis* of the Pacific Coastal Region of the United States and Canada

<p>| | |</p>
<table>
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<tr>
<td>1.</td>
<td>Abdomen yellow to reddish brown.  .  .  .  .  .  .  .  .  2</td>
</tr>
<tr>
<td>1'</td>
<td>Abdomen lavender to purple or black  .  .  .  .  .  .  .  .  .  4</td>
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<tr>
<td>2(1)</td>
<td>Pronotum with large lateral brownish parenthesis-like markings, head pattern reduced laterally (Figure 2); venter of abdomen lighter along meson. West of Sierra Nevada Mountains from southern California north to southern Oregon (Figure 22)  .  .  .  .  .  .  .  .  .  arvalis Ross</td>
</tr>
<tr>
<td>2'</td>
<td>Pronotum lacking distinctive lateral brown markings, head pattern distinct laterally (Figure 3); venter of abdomen lacking a lighter area along meson.  .  .  .  .  3</td>
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3(2'). Southern California north to southern British Columbia
and western Alberta (Figure 23) . . . . . . . . . . . . californica Banks

3'. Sierra Nevada Mountains of California from Lassen to
Tulare County (Figure 22) . . . . . . . . . . . . occidens Ross

4(1'). Dorsum of abdomen with a distinctive median white
stripe (Figure 1). Northern counties of California north
to British Columbia (Figure 22) . . . . . . . . . . . . rotunda Banks

4'. Dorsum of abdomen lacking a median white stripe . . . . 5

5(4'). Venter of abdomen with a lighter area along the
meson (Figure 8); northeastern Oregon, eastern
Washington and British Columbia, Alberta, Montana,
Idaho, and Utah (Figure 22) . . . . . . . . . . . . ? cornuta Ross

5'. Venter of abdomen lacking a lighter area
along the meson. . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6

6(5'). Lateral filaments pigmented purple (Figure 9);
Sierra Nevada, Siskiyou and Coast Range Mountains
south to Santa Cruz County in California
(Figure 23) . . . . . . . . . . . . . . . . . . . . . . . . . . nevadensis Davis

6'. Lateral filaments white and sometimes slightly pig-
mented at their base (Figure 4); northwestern Nevada,
eastern Oregon, Washington and British Columbia,
and Alberta, Idaho, Utah and Wyoming
(Figure 23) . . . . . . . . . . . . . . . . . . . . . . . . . . hamata Ross

The californica Species Group

The californica group has been characterized by the relatively
simple male genitalia which has no part greatly enlarged. In all the
species where egg masses were found, the eggs were laid with their long axis parallel to the substrate (Figure 6). The larvae apparently lack morphological characters to separate them from other groups.

*Sialis arvalis* Ross
(Figures 2, 5, 22, 26)

*Sialis arvalis* Ross, 1937:68 (male description); Chandler, 1956:230

**Female** - General structure and color as in the male. Length 11-14 mm. Genitalia as in Figure 5. Resembling *S. californica* with the following differences: eighth sternite recurved along posterior lateral margins with a small triangular, posterior, mesal projection. Lateral setae of eighth segment short, seventh sternite slightly incurved medially on posterior margin. Bursa copulatrix triangular from dorsal view, slightly sclerotized laterally, apex membranous and slightly up-turned from lateral aspect.

**Allotype** - female. Ventura Co., Calif., Los Pardes Nat'l. For., Sespe Ck., Sespe Gorge Campground, Hwy. 33, Alt. 3400'.


**Larvae** - Mature larvae 12-20 mm long; dorsum of head and pronotum patterned light yellowish-brown (Figure 2). **Head** - anterior darker yellowish brown with pattern reduced laterally; labrum with 10-14 fine crenulations on each side. **Thorax** - pronotum with a large
brown parenthesis-like marking on each side; meso- and meta-notum shading to reddish brown with yellow markings. Abdomen - reddish brown, sometimes lighter along the meson, venter of abdomen lighter with a light area along meson, lateral filaments white. Earlier instars lighter in color and usually yellow on abdomen but pattern of head and pronotum distinct.

During this study, 11 males, 23 females and over 50 later instar larvae were examined. Five adults were reared from late instar larvae. Two male paratypes were examined. The female of this species has not been described and the description is included here.

Distribution - From Los Angeles Co. in southern California north to Jackson, Josephine and Curry Cos. in southwestern Oregon; east to the foothills of the Sierra Nevada Mountains (Figure 22).

Larvae - California: Napa Co.: Soda Ck., 0.3 mi. above jct. Capell Ck.; Child's Ck., 1.7 mi. N. of Hwy. 128. San Benito Co.: Pinnacles Nat'l. Mon. Sonoma Co.: Mill Ck. nr. Healdsburg.


Adults emerge from February through May with peak emergences occurring in April.

Biology - Adults have been collected with *S. californica* at the following places in California: Mill Creek near Healdsburg, 15 April 1950 and Adobe Creek, 22 mi. W. Patterson, 23 April 1949. Larvae of these same species have been collected together at Mill Creek near Healdsburg, 15 April 1950 and at Soda Creek, 0.3 mi. above jct. Capell Creek, 30 August 1954 in California.

I have collected the larvae only in warm streams (Figure 26). The life cycle may take two years, as late instar larvae were collected at Sespe Gorge Campground, Los Padres National Forest, Ventura County, California on 11 July 1969 and 26 June 1967. Some of these specimens were reared in the laboratory and did not pupate until the following spring. Larvae too small to mature but too large to have developed that year were collected at the same location on 24 March 1968.
Sialis californica Banks
(Figures 3, 6, 12, 19, 23, 24)


Larvae - Mature larvae 16-22 mm long; dorsum of head and thorax yellowish brown with a yellow pattern (Figure 3). Head - anterior portion darker brown, labrum with 11-13 fine crenulations on each side. Abdomen - brownish red, venter lighter with intersegmental areas white, lateral filaments white, slightly pigmented at base.

First Instar Larvae - with pigmented area of head and abdomen very light red; two setae midway on dorso-lateral aspect of head, labrum with four setae on each side (Figure 19).

Eggs - yellow, becoming pinkish or brownish before hatching (Figure 6). Egg burster as in Figure 12.

During this study over 300 adults were examined, about a third were males. More than 50 larvae were reared to adulthood. The lectotype was not seen but 19 specimens identified by H. H. Ross were examined. This species is closely related to S. occidens. The female and mature larvae of these two species cannot be reliably distinguished by morphological characters.

Distribution - Known from Los Angeles Co. in California north to southern British Columbia and Alberta and not east of these states at the present (Figure 23). This is the most common and widely
distributed sialid in the Pacific Coastal Region.


and 0.2 mi. N. O'Brien, Lake Co.: Chandler State Park, N. Lakeview, 5.5 mi. W. Silver Lake; Bridge Ck.; E. Quartz Mt. Summit, E. Lakeview; Long Ck., 12 mi. NE Bly; Salt Spgs. Ck., 13.7 mi. NE Bly; Camp Ck., 18 mi. NE Bly, Fremont Nat'l. For. Union Co.: 45 mi. S. LaGrande, Hwy. 30; Phillips Ck. Rd. jct. 204, N. Elgin; Medical Spgs.

Locations given for unreared specimens from the Sierra Nevada Mountains are based mainly on adult distribution data. While not completely reliable, these records are given here to serve future investigators as a point of departure in any attempts to understand the relationship between S. californica and S. occidens.

Adults have been collected from February to September. Emergence peaks occur earlier at lower latitudes and altitudes. In the San Francisco Bay area, peak emergences occur in April and May. About 500 miles further north in the vicinity of Corvallis, in the Willamette Valley of western Oregon, peak emergences occur from mid-May through June. East of Corvallis, in the Cascade Mountains, adult collection records indicate that June and July are times of peak emergence.

**Biology** - Azam and Anderson (1969) studied the biology of this species in the vicinity of Corvallis and found it to be a stream inhabitant. Adults have been collected at Paulina Lake, Deschutes Co., and at Diamond Lake, Klamath Co., Oregon, and at Lake Cowichan,
Vancouver Island, British Columbia. The life cycle usually takes two years but under optimum conditions a one-year life cycle may be possible. From the numerous collections I have made at various times of the year, it was always apparent from the sizes involved that two generations of this univoltine species were present, as larvae smaller than mature larvae were always present.

This wide-ranging species is frequently sympatric with other sialids. Adult collecting records show that *S. californica* has been collected at the following times and locations with the following species (not included are records previously mentioned for *S. arvalis*): *S. rotunda* and *S. californica* - Oregon: Paulina Lake, Deschutes Co., 14 July 1962; Marion Forks, Linn Co., 30 July 1962; 3 mi. W. Philomath, Benton Co., 26 May 1960; and Diamond Lake, Klamath Co., 21 June 1962. At Chandler State Park, N. Lakeview, Lake Co., Oregon, three species have been collected but not at the same time. I collected the eggs of *S. rotunda* and the larvae of *S. californica*. The adults of *S. hamata* had previously been collected there by S. G. Jewett, 26 May 1957.

Other than those larval collections of *S. arvalis* and *S. californica* mentioned previously, I have collected *S. californica* at the following locations in the same habitats as the species indicated below: Oregon: *S. rotunda* and *S. californica*: Berry Ck. Experimental Stream, 9 mi. NW Corvallis, Benton Co.; 0.5 mi. W. and 0.2 mi.
S. nevadensis and S. californica: California: 2.5 mi. S. Child's Resort, Hwy. 36 (reared; Figure 24), Gurnsey Ck., S. Child's Resort, Hwy. 36, Tehama Co.; N. Comptonville, Hwy. 49 (not reared), Yuba Co.  
S. hamata and S. californica: Oregon: Medical Springs and 3 mi. S. LaGrande, Hwy. 30, Union Co.  
At these locations the effects of current flow were sometimes apparent. If the stream flow was very slow, larvae other than S. californica predominated. At Berry Creek, which has a moderate flow in the pools, only an occasional specimen of S. rotunda was found. South of Child's Resort, in areas where there was more current, the substrate was sand or gravel and S. californica was more abundant. In slow areas with organic substrates S. nevadensis was more abundant. From these observations it seems apparent that these species are generally isolated in their micro-habitats even though in certain locations like Paulina and Diamond lakes this separation may not be as definite.

_Sialis cornuta_ Ross  
(Figures 8, 23)

_Sialis cornuta_ Ross, 1937:69
Larvae - Mature larvae 14-22 mm long. Head and thorax - light yellowish brown dorsally and patterned with light yellow, pattern differing from S. hamata; labrum with 8-10 fine lateral crenulations on each side. Abdomen - lavender to purple, venter with a distinctive median white area as in Figure 8.

The larva of this species was not reared and positively associated with the adults because the larvae were not collected. The larva described is distinctly different from all the others that were reared from the study area. It is possible that this description could be of the larvae of S. velata Ross, a species that occurs in the north and eastern part of the range of S. cornuta.

During this study, 28 males, 30 females and 6 larvae were examined. Included were five specimens determined by H. H. Ross.

First instar larvae and eggs unknown.

Distribution - This species occurs east of the Cascade Mountains in Alberta, Idaho, Montana, Oregon, Washington, Wyoming and Utah (Figure 22). Adults - Alberta: Turnerville. Idaho: Caribou Co.: Wyan. Clearwater Co.: Elk R.; Orofino. Idaho Co.: Lolo Pass. Latah Co.: Robinson Lake; Moscow, Viola Grade; Moscow; Meadow Ck.; Section 9 pond; Viola; Laird Park, 4 mi. W. Harvard. Montana: Gallatin Co.: Belgren (Belgrade). Glacier Co.: Swift Current Ck., Glacier Cpgd., Glacier Nat'l. Park; Grinnel Lake, Glacier Nat'l.


The rather meager collecting data indicate an emergence period from late March through July with May and June the months of most frequent collection. Local conditions probably influence peak emergence as those at Glacier National Park occur in June and July. In the vicinity of Moscow, Idaho, May is the peak month. This could be more a reflection of collecting than actual emergence patterns.

Biology - The larvae occur in streams and lakes. The life cycle is probably two years, as large but not mature larvae were collected in the N. Platte River, Carbon Co., Wyoming in June 1961, and are considerably smaller than those collected there in March 1961. Adults of this species and S. hamata have been collected together at Robinson Lake, Latah Co., Idaho, 15 May 1954, and at Grinnell Lake, Glacier National Park, Glacier Co., Montana 11 July 1964.
**Sialis hamata** Ross (Figures 4, 11, 14, 15, 16, 21, 23)

**Sialis hamata** Ross, 1937:70

**Larvae** - Mature larvae 14-22 mm in length. **Head and thorax** - similar in color to *S. cornuta* but patterned as in Figure 4, head pattern sometimes indistinct laterally; labrum with 11-14 lateral crenulations on each side. **Abdomen** - lavender to purple, venter lighter with intersegmental areas and lateral filaments white; venter lacking a median white area.

**First instar larvae** - light gray, frons with a slightly darkened and roughened bell-shaped area with a lateral triangular patch on each side; mid-labral setae in groups of four; lateral head setae in triangular groups of three (Figure 21).

**Eggs** - grayish pink becoming brownish pink before hatching.

Egg burster (Figures 11, 14, 15).

During this study 41 males, 31 females, five paratypes and over 200 larvae were examined. Five adults were reared from late instar larvae.

**Distribution** - The distribution of this species is similar to that known for *S. cornuta*. *S. hamata* has been collected in Alberta, British Columbia, Idaho, Montana, Nevada, Oregon, Utah, Washington and Wyoming (Figure 23).


Collecting records indicate an emergence period from April to July. In Washington and Idaho most of the specimens have been collected in May and June. At Glacier National Park, Montana, the meager records indicate June and July as peak emergence times. In general, this parallels the collecting data for S. cornuta. Collecting may again be a factor.

Biology - The larvae have been found in streams and lakes. As mentioned previously, the larvae of S. hamata have been collected with those of S. californica. The life cycle usually takes two years as indicated from my field collecting experience and laboratory rearings from eggs. In the field large but immature larvae were collected in July 1967, south of La Grande, Oregon. At this same location in April 1968, I collected large numbers of small larvae that did not mature until the following year. Laboratory rearings from eggs collected at the above location in June 1970 and reared in large containers gave three mature and 67 immature larvae on 25 April 1971. This indicates that it is possible for this insect to have a one- or two-year life cycle but usually the latter.

Sialis occidens Ross (Figures 13, 20, 22)

Sialis occidens Ross, 1937:69; Chandler, 1956:230

Larvae - The mature larvae of this species cannot be
distinguished with any certainty from that of *S. californica*.

**First instar larvae** - similar to *S. californica*; labral setae in two triangular groups of three, lateral head setae diagonal to long axis of head (Figure 20).

**Eggs** - Yellow when laid, becoming pinkish gray when mature. Egg burster (Figure 13).

The females and mature larvae of this species cannot be reliably distinguished on a morphological basis from those of *S. californica*. Material examined during this study included 51 males, 124 females, 6 paratypes, and over 100 larvae.

**Distribution** - This species is known only from the Sierra Nevada Mountains of California and Nevada (Figure 22).

**Adults** - California: Alpine Co.: Winnemuca Lake; Hope Valley; Woodfords; Woods Lake. El Dorado Co.: trib. to Gilmore Lake, Tahoe; Wright Lake; China Flat; Echo Lake; Taylor Ck.; Riverton; Angora Lake; Alpine Ck., Tahoe; Fallen Leaf Lake, Tahoe. Fresno Co.: Hume Lake; Marie Lake; 60 Lake Basin. Inyo Co.: Frog Lake, Kings Cyn. Nat'l. For. Lassen Co.: Crater Lake Mt. Mariposa Co.: Mosquito Ck., Yosemite Nat'l. Park; S. Fork Tuolumne R., Yosemite Nat'l. Park; 6 mi. E. Miami Ranger Station; Fish Camp; Strawberry; Wawona; Lake Tenaya; 7 mi. NW Fish Camp; Yosemite Village. Mono Co.: Convict Lake. Nevada Co.: Sagehen Ck. nr. Hobart Mills; Nevada City; Vera Lake; Grass Valley; Boca nr.
Keddie. Placer Co.: Cornelian Bay, Lake Tahoe. Plumas Co.: Meadow Valley; Cubks' Lake; Smith Lake. Sierra Co.: Gold Lake; S. Grayeagle; Independence. Tulare Co.: Wolverton, Sequoia Nat'l. Park; Pearl Lake, Sequoia Nat'l. Park; Hamilton Lake, Sequoia Nat'l. Park. Tuolumne Co.: 4 mi. S. Mather; May Lake, Yosemite Nat'l. Park; Yosemite; Vernon Lake, Yosemite Nat'l. Park; Strawberry; Ackerson Mdws., 3 mi. S. Mather; Pinecrest.


The records given here for larvae are mostly based on distributional data derived from the adults and are not to be considered positive identifications. These records are to serve future investigators in any attempts to understand the relationships between *S. occidentes* and *S. californica*.

Collection records show an emergence period from April to August but almost all the records are from June and July. This is probably a result of their higher altitude distribution.
Biology - From the collecting data it is evident that the larvae of *S. occidens* can be found in either lakes or streams and I have collected eggs above both habitats. From my collecting and rearing experience, the life cycle usually takes two years. At Mosquito Creek, Yosemite National Park, California, 24 June 1968, I collected eggs and large, but immature, larvae. A few larvae were reared and pupated the following spring. At Yosemite Creek, Yosemite National Park, California, 16 July 1969, several masses of eggs were collected and brought to the laboratory where they hatched. The larvae were kept in a container so that mature larvae could crawl out and pupate. Only a single female emerged after one year. All the remaining larvae were removed 25 April 1971 and from their size, all were apparently mature. Thirty-four mature larvae and two pupae were placed in a container with damp soil and sawdust and kept at about 20°C. Adults emerged in the following fashion after the number of days given: 2 days - ♀ (pupa); 7 days - ♀ (pupa); 10 days - 3♂, 2♀; 12 days - 4♂, 3♀; 13 days - 3♂, 3♀; 14 days - ♀; 16 days - ♀. Thirteen females and ten males emerged with a survival of 64%. The time from larvae to adult was from 10 to 16 days. Survival may have been affected by the techniques used in separating and transporting the larvae. From these data it is concluded that the life cycle is usually two years.

Collecting data indicate that *S. occidens* probably occurs with *S.*
nevadensis at the following California locations: Echo Lake, El Dorado Co.; Miami Ranger Station, Mariposa Co.; Buck's Lake, Plumas Co.; Grass Valley and Sagehen Creek N. Hobart Mills, Nevada Co.; and Strawberry, Tuolumne Co. I have collected the larvae of what I assumed to be these species, together north of Comptonville along Nwy. 49 near the Yuba County line. As the larvae determined as S. occidens was not reared, an error is possible.

The infumata Species Group

The infumata group has been characterized by the male genital plate having long hooks. S. rotunda and S. nevadensis, the only known species in the study area, form a sub-group in which the ninth segment forms a flap covering the genitalia. The eggs are laid with the long axis at right angles to the substrate (Figure 7).

Sialis nevadensis Davis
(Figures 9, 23, 24)

Sialis nevadensis Davis, 1903:450; Ross, 1937:76; Chandler 1956:230
Sialis morrisoni Davis, 1903:450

Larvae - Mature larvae 14-24 mm long. Head and pronotum - brown, meso- and meta-notum shaded to purple like abdomen, patterned with yellow as in Figure 9; anterior portion of head darker brown. Abdomen - dorsum and venter purple, intersegmental areas
narrow and white; lateral filaments purple.

**First instar larvae** and egg bursters unknown.

**Eggs** - black on the apical half at maturation.

During this study, 34 males, 121 females and over 100 larvae were examined. Twenty of these specimens were determined by H.H. Ross. Thirteen specimens were reared from late instar larvae. The type of this distinctive species was not examined.

**Distribution** - This species is known from the Sierra Nevada Mountains of California and Nevada. In western California, the known range extends from Siskiyou County in the north to Santa Cruz County (Figure 23).


**Larvae - California:** El Dorado Co.: trib. to head of Whaler

Collection data show an emergence period from April to August. Peak emergence occurs in May, June or July.

**Biology** - The adults have been collected along lakes and streams. All larval collections have been made in streams but this is probably the result of larval accessibility and collecting techniques rather than the absence of larvae in lakes. Dubois and Geigy (1935) have shown that the larger larvae are in deeper water until just prior to pupation. As indicated previously, I have collected this species mostly in the slow backwaters of streams with *S. californica* (Figure 24) and *S. occidens*. Although I have not reared this species from eggs, large larvae collected two miles south of Child's Resort, Hwy. 36, in June 1967, and east of Downieville, Hwy. 49, in July 1967 in California, did not pupate and emerge until April and May 1968. This evidence indicates a two-year life cycle, although rearing experience with other species suggests that a one-year life cycle is possible.
Sialis rotunda Banks
(Figures 1, 7, 10, 17, 18, 22, 25)

*Sialis rotunda* Banks, 1920:327; Ross, 1937:75; Chandler, 1956:230; Azam and Anderson, 1969:549-558

**Larvae** - Mature larvae 12-20 mm long. **Head and thorax** - yellowish brown with a yellow pattern dorsally (Figure 1); labrum with 10-12 coarse lateral crenulations on each side. **Abdomen** - dark purple to black with a distinctive dorsal creamy white stripe; venter lighter purple with wide creamy white intersegmental areas, lateral filaments creamy white.

**First instar larvae** - light gray in color. Head with large, darkened, somewhat rounded triangular area occupying most of frons with smaller dark area at each side; labrum grayish with four seta on each side of meson (Figures 17, 18).

**Eggs** - light brownish yellow becoming dark brown at matura-
tion (Figure 7). Egg burster (Figure 10).

During this study, 84 males, 88 females and more than 200 larvae were examined. Fourty-four of the adults were determined by H. H. Ross. Since Azam and Anderson (1969) had reared the distinc-
tive larvae and adults previously, I reared only six adults from larvae. The lectotype was not examined.

**Distribution** - This species is known to occur from Shasta and Del Norte counties in northern California north to southern British
Columbia (Figure 22).

Adults - British Columbia: Blanket; Canim Lake. California:
Shasta Co.: Crystal Lake. Oregon: Benton Co.: Oak Ck. Fisheries
Laboratory, Corvallis; Berry Ck. Experimental Stream, 9 mi. NW
Corvallis; 3 mi. W. Philomath; pond nr. Rock Ck., SW Philomath;
Colorado Lake nr. Corvallis; Wohink Lake nr. Corvallis; Muddy
Ck; 8 mi. N. Corvallis; Alsea Mt. Clatsop Co.: Necanicum R.;
Astoria. Coos Co: Marshfield. Deschutes Co.: East Lake; Paulina
R. Nat'l. For. Jackson Co.: Little Squaw Lake, R3W T4S Sec 2.
Lake; Douglas Ck. nr. Odel Lake, Diamond Lake. Lake Co.:
Chandler State Park, N. Lakeview; Silver Lake. Lane Co.: Scott's
Lake, Three Sisters; Woahink Lake; lake nr. Florence. Linn Co.:
Lacomb; Santiam R., Lebanon; Santiam Rd., Cash Ck.; Marion
Forks; Calapooya R., Albany; S. Fork Crabtree Ck., Lacomb;
Cascade Summit. Polk Co.: Valsetz Lake; Independence. Washing-
ton: Clallam Co.: Crescent Lake, Olympia Nat'l. Park; Hoh Ranger
Station, Olympic Nat'l. Park. Douglas Co.: Lake Wenatchee. Grays
Harbor Co.: Humptulips; Lake Quinault. King Co.: Bothell, Steete
Lake; Duvall; Cedar R., Renton; Lake Sammamish; Carnation; Echo
Lake; Seattle; Cedar Mt. Pacific Co.: Ilwaco. Pierce Co.: Sunrise
Park; Rainier Nat'l. Park; Mt. Rainier, Mowich Lake; Lake Lombard;
Steilacoom Lake; Chamber Ck. Snohomish Co.: Lake Hannah;


Collection records show an emergence period from March to August. In the vicinity of Corvallis, Oregon, peak emergence occurs during April and May. At Paulina Lake, Deschutes Co., Oregon, east of the Cascade Mountains at over 4000 feet, emergence occurred in July. Other mountain lakes also show later emergences than localities at lower elevations.

Biology - Azam and Anderson (1969) studied the biology of this species. The larvae are found in lakes, ponds or the backwaters of streams much like the related species, *S. nevadensis*. As mentioned previously, *S. rotunda* has been collected with *S. californica* and *S.*
hamata. The life cycle may take one or two years. In the study cited above, the life cycle took one year. I have collected large but immature larvae at many locations prior to emergence times and late in the summer after emergence should have occurred, especially at higher elevations or in cold spring areas. This occurred at the following sites: Panther Creek, 17 July 1967, Del Norte Co., California; Headwaters Metolius River, August 1968, Jefferson Co.; 0.2 mi. N. O'Brien, 16 April 1967 and 21 July 1967; 7 mi. S. Williams, 21 July 1967, Josephine Co.; E. Quartz Mt. Summit, 12 July 1967; 18 mi. NE Bly, 24 September 1967, Lake Co., Oregon. The results from laboratory rearing beginning with eggs in June, 1970 and terminating 25 April 1971 showed seven mature and 43 immature larvae. The data substantiate a two-year as well as a one-year life cycle.
DISCUSSION AND CONCLUSIONS

Taxonomy

The adults of the Nearctic sialids are well known and the males may be identified readily. In some cases, the females of closely related species are difficult to separate. This study has shown that the fully developed or mature larvae in the study area could be separated to species by the patterns and color on the dorsum of the head and thorax, or on the dorsum and venter of the abdomen. The lateral crenulations of the labrum are sometimes of taxonomic value. All the mouth parts, and head capsules, were drawn in a dorsal and ventral view. The legs were also drawn in an anterior and a posterior view and the patterns, rows and numbers of setae were evaluated for taxonomic utility. Setal evaluations were done on five specimens for each species. Except for the labrum, nothing of taxonomic value was found. Mature larvae of the closely related species, _S. californica_ and _S. occidens_ cannot be separated. Geographical distribution may assist in separating these species in many cases, but in some areas of the Sierra Nevada Mountains, only rearing the larvae to the adult stage will permit positive identification.

First instar larvae were found to possess setal and color patterns on the head that allow species recognition. Azam and Anderson (1969) stated that the first instar larvae could not be recognized.
They also stated that the lateral abdominal filaments are segmented like those of mature larvae. My observations, using live first instar larvae and a magnification of 400X, show no discrete segments, although the surface of the filament is finely striated around its circumference from the base to near the apex. Other differences between mature and first instar larvae are apparent from the description given for the genus and Figure 17.

The toothed, V-shaped egg bursters shown here are the first described for the sialids and differ greatly from the single ridged forms of other neuropterans (Smith, 1922). The egg bursters were different in each of four species examined, either in the number or shape of the teeth, or both. These data would aid in identifying egg masses that had hatched and lost their color.

The following table summarizes the distribution data regarding overlapping ranges and instances of known sympatry, as previously documented under each species section.

The data on emergence, distribution and microhabitat selection show or suggest ways in which the sialids in the study area limit competition or maintain species isolation. It has been shown that S. nevadensis and S. rotunda are lentic forms and are separated at some locations on this basis from the lotic species of the californica group. Within the californica group, several species have been found together. I have collected the larvae of S. arvalis in streams which for much of
Table 1. Overlapping ranges and known sympatry among the species of *Sialis* in the Pacific Coastal Region of the United States.

<table>
<thead>
<tr>
<th></th>
<th>arvalis</th>
<th>californica</th>
<th>cornuta</th>
<th>occidens</th>
<th>hamata</th>
<th>nevadensis</th>
<th>rotunda</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. arvalis</td>
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<td>0</td>
<td>-</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>S. californica</td>
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<td>0</td>
<td>0</td>
<td>X</td>
<td>X</td>
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<td>X</td>
</tr>
<tr>
<td>S. cornuta</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>X</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>S. occidens</td>
<td>0</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>X</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>S. hamata</td>
<td>-</td>
<td>X</td>
<td>X</td>
<td>-</td>
<td>-</td>
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<td>-</td>
</tr>
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<td>0</td>
<td>X</td>
<td>-</td>
<td>X</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>S. rotunda</td>
<td>0</td>
<td>X</td>
<td>-</td>
<td>-</td>
<td>X</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

X = known sympatry
0 = range overlap and probable sympatry
- = low probability of range overlap and sympatry
the year would be over $20^\circ$C. In the same mountains, I found only *S. californica* in a cold spring area where the temperature would be less than $15^\circ$C for most of the year. This suggests that these two species may be separated in their microhabitats by water temperatures. At two locations where *S. californica* and *S. hamata* have been found together, the latter has always been present in large numbers. This occurs east of the Cascade Mountains along the periphery of the range of *S. californica* and may reflect the competitive advantage of *S. hamata* in this situation. Further collecting in areas of range overlap may clarify the question of microhabitat selection in these two species. Little is known about the microhabitat differences between *S. cornuta* and *S. hamata*.

Geographical separation between species also is evident from the data. Certain species appear widely separated such as: *S. cornuta* and *S. hamata* from *S. arvalis*, and *S. nevadensis* from *S. cornuta*. More interesting, however, are the numerous instances given in the previous table where possible or probable sympatry may occur. Certain geographical areas offer opportunities for investigations of the relationships between a number of species. The Blue Mountain area in northeastern Oregon contains four species: *S. californica*, *S. cornuta*, *S. hamata* and *S. rotunda*. Northeastern California has six species: *S. arvalis*, *S. californica*, *S. hamata*, *S. nevadensis*, *S. occidens* and *S. rotunda*. As these areas of species concentration
were not known until the data were evaluated near the conclusion of this study, more intensive collecting could not be undertaken.

The last way in which species may be separated as indicated by the data is temporal separation. The peak emergence periods show that certain species emerge earlier in the spring than other species. *S. rotunda* emerges earlier than *S. californica* in the vicinity of Corvallis, Oregon. Azam and Anderson (1969) suggested that this difference may be due to a longer pupal stadia for *S. californica*. Ross (1937) noted that emergence peaks for *S. velata* Ross and *S. morhi* Ross have different emergence peaks when found in the same body of water. He also indicated a seasonal succession of the above two species and *S. itasca* Ross in Illinois. Because of the great variation in altitude within the ranges of most western species, the limited and dispersed collecting data do not lend themselves to making a good estimate of the seasonal succession of the western species of *Sialis*. Concentrated collecting in the Blue Mountains and northeastern California would very likely furnish this information.

Ross (1937) also observed that closely related species had not been collected at the same locality at the same time. The only closely related species in the study area, based on the larvae and the adult genitalia, are *S. californica* and *S. occidens*. The collecting data from this study do not refute this statement as they have not been collected together. Again, northeastern California would be an area for study
to find out if temporal isolation occurs between *S. californica* and *S. occidentalis*. The data gathered on distribution in conjunction with morphological data from the wings and male genitalia, may be used to propose an evolutionary scheme for the sialids of the study area as well as the Sialidae of the world.

**Evolution**

The relationships among the sialids of the world as judged from the morphology of the wings are: *Sialis* is widely separated from the remaining genera because the wings are only about three times as broad as long, usually two accessory veins between R₂ and R₃, M₁+₂ simple and M₃+₄ forked. The remaining genera are more closely related (Riek, 1970). *Protosialis, Indosialis, Leptosialis* and *Austrosialis* have the wings almost four times as long as broad, the wings lack accessory veins between R₂ and R₃, and the median vein of the forewing has four branches instead of three. *Nipponsialis* is not considered a valid genus because it is separated from *Sialis* solely on the basis of a single accessory vein between R₂ and R₃. Ross (1937) has shown that variation occurs in the number of accessory veins in the same species.

Within the Holarctic genus *Sialis*, certain relationships based on the morphology of the male genitalia occur. Ross (1931) divided the nearctic sialids into the *californica* group, *aequalis* group, *americana*
group, and the infumata group. The six species of European sialids form two groups of three species each and are related to the californica and infumata groups. The Asian species are not closely related to any of the above but the genitalia drawings are lacking in details and further study may change this view. How these intercontinental distributions might have occurred both within Sialis and between the other genera will be explained in conjunction with the Corydalidae and the idea of continental drift.

From the data gathered on the habitats and distribution of the Sialidae in the study area, a generalized idea of their possible evolution may be surmised. The ancestral Holarctic Sialis became separated into three ancestral populations in Europe, North America and Asia. Those in the Nearctic Region evolved into four groups. The californica and infumata group became transcontinental and the aequalis and americana remained east of the Rocky Mountains. The larvae of the californica group evolved in lotic habitats and the infumata group in lentic habitats. Within the study area the ancestral infumata group became isolated into two populations. The northern populations evolved into S. rotunda and the southern population evolved into S. nevadensis. The ancestral californica group became separated into a Great Basin population with dark colored larvae and a coastal population with light colored larvae. From the former population, S. hamata and S. cornuta evolved. In the latter, S. occidens evolved in the
Sierra Nevada Mountains, *S. arvalis* evolved in the southern coastal mountains and *S. californica* evolved to the north in the coastal mountains. When the isolating mechanisms occurred that produced the speciation given above is not certain. It is possible that these species evolved outside their present ranges. The paleogeography of the area given by Engeln and Coster (1952) suggests that speciation could have occurred in the western part of the continent during its complex geological evolution. Based on the morphology of the male genitalia and the larvae and the microhabitats of the larvae, the phylogeny proposed for the western Sialids seems tenable. Only further study can affix a time when speciation could have occurred. Figure 27 summarizes this evolutionary scheme.
Figure 1. Mature larva of *Sialis rotunda* Banks.
Figures 2-4. Mature larvae of *Sialis* without lateral filaments and cauda.

2. *S. arvalis* Ross
3. *S. californica* Banks
4. *S. hamata* Ross
Figure 5. *Sialis arvalis* Ross, venter of female genitalia.

Figure 6. Egg mass of *S. californica* Banks.

Figure 7. Egg mass of *S. rotunda* Banks.

Figure 8. *S. cornuta* Ross, venter of mature larval abdomen without lateral filaments and cauda.

Figure 9. *S. nevadensis* Davis, mature larvae without lateral filaments and cauda.

10. *Sialis rotunda* Banks
11. *S. hamata* Ross
12. *S. californica* Banks
13. *S. occidens* Ross

Figure 14. Chorion and egg bursters of *S. hamata*.

Figures 15-16. Fully developed embryo of *S. hamata* showing the egg burster in position before hatching.
Figures 17-21. First instar larvae of Sialis.

17. S. rotunda Banks

18-21. Head capsules with setal patterns:

18. S. rotunda Banks
19. S. hamata Ross
20. S. californica Banks
21. S. occidens Ross
Figure 22. Distribution of *Sialis arvalis* Ross, *S. cornutus* Ross, *S. occidens* Ross and *S. rotunda* Banks.

Figure 23. Distribution of *Sialis nevadensis* Davis, *S. hamata* Ross and *S. californica* Banks.
Figures 24-26. Larval habitats of *Sialis*.

24. *S. nevadensis* Davis and *S. californica* Banks
25. *S. rotunda* Banks
26. *S. arvalis* Ross
Figure 27. An evolutionary scheme for the species of *Sialis* known to occur in the Pacific Coastal Region of the United States.
FAMILY CORYDALIDAE

The two subfamilies, as established by Lestage (1927), are distinguished on the basis of wing venation, the type of male genitalia and the larvae. Both subfamilies are found in the study area.

Key to the Corydalidae of the Pacific Coastal Region of the United States

1a Larvae ........................... (p. 66)

1b Adults ........................................... 2

2a(1b) Forewings with white spots in many cells, forewings with M three-branched (Figure 33); mandibles projecting well beyond the labrum; male genitalia with two pairs of claspers (Figure 34); female (Figure 38).
Corydalinae .......................... Corydalus cognatus Hagen

2b Forewings lacking white spots in cells, forewing with M two-branched (Figure 50); mandibles generally small and not projecting much beyond the labrum; male genitalia with a single pair of claspers (Figure 53); female (Figure 56) ........................ Chauliodinae ................................. 3

3a(2b) Posterior branch of Rs forked in both wings (Figure 50) ........................................ 4

3b Posterior branch of Rs in both wings simple (Figure 75) ........................................ 6

4a(3a) Hind wings with posterior branch of M simple (Figure 64); male claspers short (Figure 65); female claspers
bifid with the upper lobe smaller (Figure 67); Napa County, Sierra Nevada Mts. of California, and Cascade Mts. of Oregon (Figure 119) . . . . . .

. . . . . . . . . Orohermes crepusculus (Chandler)

4b Hind wings with posterior branch of M forked (Figure 50); thorax covered with long, wooly hair; male claspers elongate and deeply notched; female claspers bifid with long lobes . . . . . . . . . . . . Dysmicothermes Munroe 5

5a(4b) Forewings with many dense dark spots; male genitalia with upper lobe of claspers blunt apically and wider than lower lobes, broadly notched (Figure 54); lateral bars of aedeagus tapering to a long fine point (Figure 55); female claspers with lobes equal in length (Figure 56); Central California north to British Columbia (Figure 120) . . . . . . . . . . . . D. disjunctus (Walker)

5b Forewings with a few scattered spots and blotches; male genitalia with upper lobe of the clasper about as wide as lower lobe and rounded apically (Figure 51); lateral bars of aedeagus with a short point (Figure 52); female claspers with upper lobe shorter than lower lobe; Sierra Nevada Mts. south to San Bernardino County (Figure 120) . . . . . . . . . . . . D. ingens Chandler

6a(3b) Forewing usually with a crossvein beyond fork of R_{3+4} (Figure 75); antennae of male elongate and moniliform with erect hairs on each segment; female – gonophysis lateralis lacking apical papillae (Figure 79) . . . .

. . . . . . . . . . . . . . . . . . . . . . . . . . Neohermes Banks 7

6b Forewing usually lacking a crossvein beyond fork of R_{3+4} (Figure 88); antennae of male and female filiform.
lacking erect hairs; female* - gonopophysis lateralis with apical papillae (Figure 111).

7a(6a) Male claspers broadly notched apically and decurved at midpoint (Figure 78); female claspers triangular, apex produced into a distinct point (Figure 79); Sierra Nevada Mts., northern California north to central Oregon (Figure 119).

7b Male claspers not notched apically but having an apico-ventral protrusion (Figure 76); female claspers triangular but rounded apically (Figure 77); Trinity County south along coast to Baja, California and east to New Mexico (Figure 119).

8a(6b) Male claspers short and broad, almost twice as long as wide.

8b Male claspers elongate, tapering apically and more than twice as long as wide.

9a Male claspers convex ventrally and dorsally (Figure 98); aedeagus narrowly notched apically; widely expanded laterally and constricted basally (Figure 99); Cascade Mts. of Oregon (Figure 117).

9b Male claspers concave ventrally and dorsally (Figure 102); aedeagus broadly notched apically with lateral sides parallel (Figure 117); Sierra Nevada Mts. of California (Figure 117).

10a(8b) Male claspers with base much wider than apex, tapering both in a lateral and dorso-ventral view (Figures 104, 106);

* Females in most of the species occurring in the western United States cannot be separated to species.
aedeagus broadly notched apically, widened slightly laterally
(Figure 103); Sierra Nevada Mt. foothills from Butte to
Mariposa County, California (Figure 117) . . . . . . P. aridus Maddux

10b Male claspers not much wider basally than apically
(Figures 89, 91, 95) . . . . . . . . . . . . . . . . . . 11

11a(10b) Aedeagus broadly notched apically, expanded laterally
along apical margins and constricted basally
(Figure 90); Tuolumne and Monterey Counties south to
Los Angeles and San Bernardino Counties of
California (Figure 118) . . . . . . P. simplus Chandler

11b Aedeagus broad apically with a small median notch,
slightly expanded on apico-lateral margins with sides
parallel to base (Figure 95); usually dark winged
forms; foothill streams of Sacramento River Basin of
California (Figure 118) . . . . . . P. minimus (Davis)

11c Aedeagus blunt apico-medially with a pointed dorsal pro-
jection on each side, lateral margins almost parallel
to base (Figures 93-94); from Santa Cruz County,
California north to British Columbia, coastal and west of the
Cascade Mountains (Figure 118) . . P. spenceri Munroe

Key to the Mature Larvae (35+mm) of the Corydalidae
of the Pacific Coastal Region of the United States*

1a Lateral abdominal filaments with a ventral gill tuft at
the base . . . . Corydalinae . . . Corydalus cognatus Hagen

*The larvae of P. minimus, P. cascadia and P. simplus are unknown.
1b Abdominal ventral gill tufts absent. Chauliodinae 2

2a(1b) Head and dorsum of thorax concolorous and lacking a distinctive pattern; gena sharply angulate posteriorly (Figures 58, 61, 73) 3

2b Head and dorsum of thorax with a distinctive pattern (Figures 84, 86, 107, 109) 5

3a(2a) Spiracles of segment VIII small, not raised above integument, located above and anterior to base of lateral filaments; lateral filaments robust and longer than width of abdomen; Napa County, Sierra Nevada Mts. of California, and Cascade Mts. of Oregon (Figure 119) Orohermes crepusculus (Chandler)

3b Spiracles of segment VIII large, raised above body surface on short respiratory tubes, located mesally on posterior edge of segment; lateral filaments shorter than width of abdomen Dysmicohermes 4

4a(3b) Abdominal setae pointed, extending above the abdominal spiracles, somewhat appressed (Figure 62); Sierra Nevada Mts. south to San Bernardino County, California (Figure 120) D. ingens Chandler

4b Abdominal setae mostly short and erect, seldom arising above the abdominal spiracles (Figure 59); northern California to British Columbia (Figure 120) D. disjunctus (Walker)

5a(2b) Head dark brown to brownish yellow with a lighter yellow pattern; abdomen light brown to bluish gray, lateral abdominal filaments robust and longer than width of abdomen (Figures 84, 86) Neohermes Banks 6
5b  Head brownish red to brownish orange with dark gray areas; lateral filaments slender and usually shorter than width of abdomen (Figures 107, 109) . . . . . . .

. . . . . . . . . . . . . . . . Protochauliodes Wee le 7

6a(5a) Lighter areas of abdomen distinct, ventral abdominal pattern usually divided into three dark areas on each segment or divided completely by a white area (Figure 87); dorsum of abdomen usually bluish gray, head brown to light brownish yellow; Trinity County of California south along the coast to Baja, Mexico and east to New Mexico (Figure 119) . . . . . . . . . . N. filicornis (Banks)

6b Lighter areas of abdomen shading into darker areas; ventral abdominal pattern on each segment not divided into three distinct areas although anterior segments may be divided by a light area (Figure 85); dorsum of abdomen usually light brown; head brown; Sierra Nevada Mts. and northern California north to the Willamette Valley of Oregon (Figure 119) . . . . . . . . . . N. californicus (Walker)

7a(5b) Head brownish orange and gray; abdomen light grayish brown (Figure 109); Sierra Nevada Mt. foothills from Butte to Mariposa County, California (Figure 117) . . . . . . . . . . P. aridus Maddux

7b Head brownish red, abdomen light brownish red . . . . 8

8a(7b) Lateral abdominal filaments shorter than width of abdomen; from Santa Cruz County, California north to British Columbia, coastal and west of Cascade Mts. (Figure 118) . . . . . . . . . . P. spenceri Munroe

8b Lateral abdominal filaments longer than width of abdomen; Sierra Nevada Mts. of California
Subfamily Corydalinae

Eleven genera have been recognized in the Corydalinae but only _Corydalis_ occurs in the United States and Canada. The larvae and biology of _C. cornutus_ (Linn.) have been studied by several investigators. Barnard (1931) described the larvae of _Chloroniella perin- guiseyi_ Ebs.-Pet. from South Africa. This subfamily is found mainly in the tropics or subtropics.

The Corydalinae may be separated from the Chauliodinae on the basis of the following characters: Rs pectinately branched (Figure 33), with three or more crossveins between Rs and R₁; forewing with M 3-6 branched; labrum not covering mandibles; Male - genitalia with two pairs of anal plates or claspers, with a circular raised area between bases of claspers; lateral expandable scent glands anterior to genital capsule; aedeagus usually a lightly sclerotized bar with two projections, never formed into a single well-sclerotized projection. Female - genitalia with a raised circular area at base of a short upper clasper and separating it from a wide and shortened lower clasper; lateral gonopophysis somewhat triangular, partially sclerotized with an apical papillae. Larvae - ventral hair-like gill tufts at base of carinate lateral filaments; antennae of mature larvae five segmented; first instar larvae with antennae three
segmented and lacking ventral gill tufts.

Genus Corydalus Latreille
(Figures 28, 29, 33-49, 116)

Corydalus Latreille, 1802:290; Weele, 1909:251-252, 1910:9;
Comstock, 1925:288; Essig, 1942:371; Peterson, 1950:360-361;
Townsend, 1935:27; Chandler, 1956:231-232; Gurney and Parfin,
1959:974-976.

Corydalus Latreille, 1802:290; Weele, 1909:251-252, 1910:9;
Comstock, 1925:288; Essig, 1942:371; Peterson, 1950:360-361;
Townsend, 1935:27; Chandler, 1956:231-232; Gurney and Parfin,
1959:974-976.

Corydalus Latreille, 1804:44; Palisot, 1821:Pl. 1, Fig. 1; Olivier,
1825:59; Burmeister, 1839:950; Rambur, 1842:534; Hagen, 1867:
192; MacLachlan, 1869:36; Davis, 1903:452, 470; Banks, 1908:29.

Corydalus is distinct from the other genera in the Corydalinae
on the basis of the following characters: Adults - wings
elongate, brownish gray with white spots in cells; some crossveins
darker, particularly on basal half of forewing; body light brown; head
and pronotum usually patterned. Rs pectinate, M\textsubscript{1+2} forked, M\textsubscript{3+4}
simple, Cu\textsubscript{1} with several branches, Cu\textsubscript{2} simple, usually three cross-
veins between Rs and R\textsubscript{1}. Male - genitalia with elongate claspers
rounded and usually expanded apically; upper claspers longer than
lower; sometimes with elongate mandibles.

Larvae - elongate, somewhat depressed with head, dorsum of
thorax, legs, portions of venter of segments IX and X sclerotized;
non-sclerotized areas with dark decumbent microsetae, larger erect
clavate macrosetae mostly on dorsum of abdomen. Head - large,
depressed and patterned, mandibles dentate, symmetrical and
elongate with three sub apical teeth; antennae five-segmented; six
lateral stemmata; labrum semi-elliptical, slightly longer than wide; clypeus about twice as long as wide, tapered anteriorly; maxilla slightly longer than mandibles, possessing a cardo, stipes, palpifer, four-segmented palups and cone-shaped galea, inner margins with long strong setae; labium with glossae and paraglossae and three-segmented palps. Thorax - pronotum as wide as head, quadrate and patterned; sternellum with a short blunt spine; meso- and meta-thorax about twice as wide as long; legs five-segmented, longer than width of thorax, terminating in paired claws. Abdomen - two-segmented lateral carinate setiferous filaments on segments I-VIII and on dorsum of anal prolegs, ventral gill tufts on I-VII; spiracles cribiform, slightly elevated, located dorsal and anterior to base of filaments; mesothoracic spiracle like abdominals, metathoracic spiracle minute.

First instar larvae - 3.0± mm long, antennae three-segmented; abdominal gill tufts lacking. Egg mass - three-layered, oval, and slightly convex, covered with a white chalky substance; some eggs in upper layer vertical, lower layer and peripheral eggs with long axis parallel to substrate.

Type of Genus - Hemerobius cornutus Linnaeus, 1758:551.

Most of the species of Corydalus are known from the Western Hemisphere but Needham (1909) and Ouchi (1939) have described species from Asia. The species of this genus exhibit a great deal of
polymorphism as Weele (1910) noted. The females are usually larger than the males and have dentate mandibles and short antennae whereas some males have very elongate mandibles and antennae while others resemble the females. The wing venation is highly variable and is of little specific value. The claspers of the male genitalia and the aedeagal bar and its projections vary considerably in those specimens observed. This variation may account for many of the described species and a generic revision is needed as most named species cannot be recognized with certainty.

Biology - The biology of C. cornutus has been of interest to several investigators as it is a conspicuous and abundant species in the eastern United States. The best account of the life history was given by Davis (1903). Parfin (1952) substantiated some of the previous observations of Davis and observed the mating behavior. The adults emerge in early summer, mate, oviposit at night and soon die. The cylindrical eggs are laid on objects over the water in a mass of about 1000 eggs. The eggs have an apical micropylar projection similar to that of the sialids. The larvae emerge from the micropylar end of the egg with the aid of an elongate egg burster (Figures 46-47), and then crawl or fall into the water. Smith (1920) erroneously stated that an egg burster was absent. The life cycle requires at least three years and probably longer under unfavorable conditions. The number of larval instars is unknown. The larvae are usually found in the more
rapid parts of permanent streams but they have also been found in intermittent streams (Stehr and Branson, 1938; Larimore et al., 1959), and around hot springs at 32°C at Los Conchos, Durango, Mexico by J. D. Lattin (1952). They are not usually found under conditions of low dissolved oxygen.

**Corydalis cognatus** Hagen
(Figures 33, 38-42, 44)

*Corydalis cognata* Hagen, 1861:193; Banks, 1892:357, 1907:21; Davis, 1903:476-479.

*Corydalis cornutus* Weele (nec Linneaus), 1910:13.

*Corydalis cognata* Hagen; Chandler, 1956:232; Gurney and Parfin, 1959:974.

**Male** - differs from *C. cornutus* in the following: light grayish brown in color; smaller, wing length rarely over 45 mm; mandibles short, seldom over 10 mm, usually less than 7 mm; genitalia (Figures 34-36), aedeagal bar lightly sclerotized with projections widely separated (Figure 37).

**Female** - Similar to *C. cornutus*, genitalia (Figure 38).

**Larvae** - Similar to *C. cornutus*, properly preserved specimens with head and dorsum of thorax light brown; abdomen grayish yellow. *C. cornutus* usually with head and dorsum of thorax dark brown; abdomen dark gray.

**Eggs** - three-layered with upper two layers with vertical eggs.
Differs from *C. cornutus* where only the top layer has vertical eggs.


Weele (1910) synonomized *C. cognatus* with five other described species which he considered only as forms of *C. cornutus*. This was done because the variation in the male genitalia was thought to be within the range of variation of *C. cornutus*. Chandler (1956) states that the western form of *Corydalus* is *C. cognatus* but gave no reason for this action either then or in his personal notes.

The holotype is a female which had the abdomen crushed during preservation or capture. Hagen (1861) failed to mention the fact that the holotype was a female. Perhaps the crushed abdomen led him to the erroneous conclusion that he was describing a male. Weele (1910) made a similar mistake when he determined from a photograph that the holotype was a small male. The holotype was collected at the Pecos River in east Texas which is a tributary to the Rio Grande. Downstream from the type locality at Big Bend National Park, three males were collected which I examined. These males resembled the other specimens of *Corydalus* which I examined from locations to the west of the Rio Grande River drainage. A comparison between *C. cornutus* and *C. cognatus* as to the ratios of head width-mandible length and pronotum width-wing length is shown in Figures 28 and 29.
Figure 28. A comparison of the head width (mm) and the length (mm) of the mandibles of the males of Corydalus cornutus (Linn.) and C. cognatus Hagen from the United States.
Figure 29. A comparison of the wing length (mm) and the pronotum width (mm) of the males of Corydalus cornutus (Linn.) and C. cognatus Hagen from the United States.
Of the 88 males that I examined which were either from the Rio Grande or west of there, only one specimen had mandibles over 15 mm long. The average mandible length from the lateral base of the mandible diagonally to the apex was less than 7 mm, with a standard deviation of 2.14 and a range of 4-16 mm. For 28 specimens of *C. cornutus* from the eastern United States, the average mandible length was 22.4 mm with a standard deviation of 7.99 and a range of 7-40 mm. The aedeagal bar in *C. cognatus* is usually lightly sclerotized and the papillae are usually widely separated and straight. *C. cornutus* usually has the aedeagal bar heavily sclerotized with narrowly separated and inwardly directed papillae. The variation occurring in the aedeagal bar of these species is given in Figures 48 and 49. The only egg mass of *C. cognatus* examined had two upper vertical rows of eggs instead of one as in *C. cornutus*. Even these data do not clearly show whether *C. cognatus* is a distinct species or only a part of a transcontinental cline. At this time and with this evidence it seems appropriate to retain the name *C. cognatus* and elucidate the morphological and biological differences observed until a more thorough study can be undertaken.

Over 200 females, 100 males, 100 larvae and one egg mass of *C. cognatus* were examined and all male genitalia were cleared. More than 50 adults were reared, 40 by Dr. G. F. Edmunds, and 10 by myself. In addition, about 250 specimens of *C. cornutus* were
examined including about 50 larvae and six egg masses. These were separated on male size and mandible length and distribution.

**Distribution** - Central California east to the Rio Grande R. in Texas and south to the Straits of Tehuantepec in Mexico (Figure 116).


May through September. Emergence peaks in July and August.

**Mexico:** Chiapas: Ixtapa. Jalisco: Plon de Barrancas.

Morelos: 7. 3 mi. SE Yauntepec; Yuantepec; 5 mi. E. Cuernavaca.

Nayart: 20 mi. SE Ixtlan del Rio. **Pueblo:** Iqucar de Matamoros; 3
mi. NW Petialcingo; 12 mi. S. Atlixco.  **San Luis Potosi**: Tamaznachale. **Sinola**: 20 mi. E. Villa Union. **Sonora**: Alamos; 10 mi. S. Alamos. **Vera Cruz**: Fortin de las Flores; Cordoba.

Adults emerge from January to September in Mexico with most records from July.


**Biology** - In addition to the information given for *Corydalus*, the mating behavior of *C. cognatus* was observed and is compared with that of *C. cornuta* as observed by Parfin (1952). A male and two females which were reared from larvae were placed in a cage in the evening. Before the lights were turned out and a red darkroom light
could be turned on, the male became active, fluttering his wings and walking about with his abdomen held off the substrate. At this time, a pair of white eversible lateral glands were easily seen just anterior to the genital capsule. On opening the cage, a very strong odor was detected and was later found to be present in vials where males had been preserved in alcohol. This is the first report of either the eversible lateral scent glands or a strong odor in mating Corydalidae. Further examination of all available specimens has shown that the lateral pre-genital scent glands are found only in the Corydalinae between segments 8 and 9 and not in the Chauliodinae. Internally, a white sac is easily seen in preserved material. The use of this strong odor by the male before mating may be a stimulant to increase the receptivity of the female. Chemical analysis of this odor, which could be obtained from male specimens preserved in alcohol, could serve as a taxonomic character to help solve the dilemma that exists in Corydalus. Further remarks will be made regarding male odors in the discussion of Orohermes crepusculus (Chandler).

The pre-copulatory behavior for both species of Corydalus is similar, consisting of touching their antennae in a head-to-head position, followed by the male sometimes placing his head across the female's wings. Following this, the male of C. cognatus worked his mandibles beneath the costal margin of the female's wing and lifted it upward. This was not always observed in the mating behavior of C.
cornutus as the very long mandibles of the male probably make this difficult. The male of C. cognatus then bent his abdomen up between his wings and over to the female's abdomen and copulation was accomplished. In both species, mating occurred on a vertical surface and lasted for less than a minute. Mating occurred only once during my observations of about an hour, although the male continued to pursue the females. Mating was thought to occur a second time in C. cornutus. No eggs were laid in either case.

**Subfamily Chauliodinae**

Kimmins (1954) has given a detailed description of the distinguishing characters of the Chauliodinae. Of the 12 recognized genera in this subfamily, five are known from the Nearctic region. Three of these occur in the study area in addition to a new genus described in this study. The more obvious characters are: **Adults** - Rs with five branches, rarely more than three crossveins between R₁ and R₂; M in forewing with two branches. **Male** genitalia with a single pair of anal plates or claspers, inner surface usually covered with black spinules, the outer surface with a raised circular punctate area; aedeagus hinged at lower angles of ninth tergite, trough-like or scoop-like, simple or bifid at apex; subgenital plate usually with small membranous protrusions at apex beneath aedeagus. **Female** genitalia with tenth tergite forming a pair of cercoid anal plates of varying
form, each with a circular raised punctate area occupying much of lateral surface.

Larvae - elongate, flattened, 35-65+ mm long; similar to Corydalus in general morphological features; known forms variable; head and thorax patterned or concolorous; abdomen with lateral filaments shorter or longer than width of abdomen; spiracles cribiform, mesothoracic spiracles usually large, metathoracic spiracles small, abdominal spiracles elevated or flush with surface; gill tufts lacking from venter of abdomen. Head - six lateral stemmata, antennae four-segmented; clypeus wider than long, tapered anteriorly; labrum semi-oval sometimes slightly drawn apically; mandibles strong, elongate, asymmetrical, right mandible with four sub-apical teeth, left mandible with three; maxilla elongate, inner margin with long strong setae, possessing a cardo, stipes, palpifer, four-segmented palpus and cone-shaped galea; labrum with glossae, paraglossae and three-segmented palps. Thorax - about as wide a head; pronotum quadrate, meso- and meta-notum together wider than long; legs five-segmented, with a conical coxa, short trachanter, elongate femur and tibia and a shorter tarsi, longer than width of thorax terminating in paired claws. Abdomen - lateral filaments on on segments I-VIII and on dorsum of anal prolegs, finely or coarsely setiferous, two-segmented, the first short and broad, the second long and tapered; spiracles anterior or above base of filaments, those on
segment VIII variable, some smaller and near base of filament, others mesad and on posterior of segment, either on slightly projecting sclerotized cones, tubercles or long tubes; two anal prolegs with paired hooks.

**Eggs** - Single or multi-layered with long axis of egg parallel with substrate, usually with a light, very thin, whitish covering.

**Biology** - Biological information on members of the Chauliodinae has been gathered by several investigators. In South Africa, Barnard (1931) studied *Taenochauliodes ochraceopennis* Ebs.-Pet. and described the stream-side pupation sites, egg masses, mature larvae and pupae. He found that the larvae occurred in mountain streams and inferred that the four other species of Corydalidae occurring in South Africa had similar habitats. In New Zealand, Hamilton (1940) studied *Archichauliodes diversus* Walker, the only Megaloptera in that country. He described the eggs, larvae, pupae, length of adult and pupal stadia, larval habitat, nocturnal feeding habits, numbers of eggs per female and their incubation time. On one occasion, larvae were found in the ocean at the mouth of a stream but further rearing in sea water resulted in their death. Maddux (1954) found the larvae of *Protochauliodes aridus* Maddux living in intermittent streams in California. The egg masses, hatching and feeding of the first instar larvae, the method of larval survival during the dry summer months and the larvae and pupae were observed. Chandler
(1954) noted that Dysmicohermes ingens Chandler crawled from the water to pupate and in 1956 he indicated that Neohermes also occurred in intermittent streams. Chandler's field notes indicate that he observed the egg masses of *N. californicus* (Walker) and *P. minimus* (Davis). He bred the latter species in captivity, noted the length of adult life, mating and the incubation of the eggs. Cuyler (1958) described the larvae of both species of *Chauliodes* and showed that Davis (1903) erred in his work regarding their biology. The general habitat of slow water, swamps and ponds and sometimes intermittent situations are well known for these species as are the pupation sites and egg masses. Neunzig (1966) gave descriptions and the larval habitats of both species of *Nigronia*. Cuyler (1965) had previously described the larvae of *N. fasciatus* Walker and gave the habitat of the larvae. Smith (1970) summarized the unpublished work of Maddux (1952) and Penland (1954) and added further information on the biology, and functional morphology of *N. californicus* and *P. aridus*.

**Genus Dysmicohermes Munroe**
(Figures 50-63, 120)


The two species of this genus may be separated from the other genera by the following characters: **Adults** - large, wing expanse to
120± mm, posterior branch of M forked in hind wings (Figure 50); thorax covered with dense, long, curly hair. **Male** - claspers deeply bifurcate; aedeagus composed of two pairs of pointed projections, lateral pair shorter and finer, an elongate fleshy extensible tube at base of claspers. **Female** - claspers bifid at apex. **Larvae** - resembling *Corydalus* in general appearance, large, robust, 65+ mm; long, dark reddish brown. **Head** - very dark reddish brown, lightly punctate and lacking a pattern, slightly wider posteriorly and bearing a few sparse setae, gena sharply angulate posteriorly; mandibles elongate, asymmetrically toothed, left mandible with four sub-apical teeth, right mandible with three; labrum short, rounded anteriorly; clypeus tapered, light in color with three light stripes, six lateral stemmata; antennae 2/3 length of mandible, segment I short, II longer than III and IV combined, III and IV sub equal in length. **Thorax** - pronotum, colored as head, wider than long, covered with short reddish setae; meso- and metanotum combined, wider than long and clothed with short reddish setae. **Abdomen** - lateral filaments shorter than width of abdomen on most segments; spiracles raised, those of mesothorax, abdominal segments I and VIII equal in size, those on segment VIII more mesad and raised on tubercules, remaining abdominal spiracles smaller; meta-thoracic spiracle minute; abdomen and lateral filaments covered with reddish setae; prolegs with short dorsal filaments and paired apical claws. **Egg** masses unknown.
Type of Genus - Chauliodes disjunctus Walker, 1866:334.

This genus is known only from the Pacific Coast Region of the United States and southern British Columbia. The adults are among the largest corydalids in the Nearctic Region.

Biology - The adults emerge from their stream-side pupal chambers from June to August and fly to nearby trees. Mating occurs during the evening. Adults can sometimes be found around lights but are somewhat reluctant to enter light traps (Chandler, 1954). The larvae have been collected most frequently from small, cold streams in areas where detritus collects (Figure 57). Some of these streams dry up in late summer. The adults have been collected along larger streams and the larvae probably occur in large streams, too. The larvae are active hunters and I have observed them pursuing Baetis nymphs.

Dysmicohermes disjunctus (Walker)  
(Figures 54-60, 120)

Chauliodes disjunctus Walker, 1866:334; McLachlan, 1869:40; Davis, 1903:463.

Neohermes disjunctus; Weele, 1910:54.


Forewings with numerous dark brown spots and a translucent membrane.
Male - claspers broadly cleft (Figure 54).

Female - claspers with lobes of equal length (Figure 56).

Larvae (Figure 58) - 55± mm long; posterior stemmata closer to others (Figure 60); abdominal setae mostly short, erect and blunt, seldom longer than spiracular height (Figure 59).

Eggs - dissected from female, cylindrical, 2.0 mm long, 1.0 mm wide.


During this study, four males, 13 females and over 30 larvae were examined. A single adult was reared from a mature larva.

The holotype is a female in the British Museum and was not examined.

Distribution - Known from central California in the Sierra Nevada Mountains north to southern British Columbia (Figure 120).


The collecting records show that adult emergence occurs in July and August.

**Biology** - The larvae of this species have been collected from small permanent and intermittent mountain streams. I have usually found the larvae where detritus collects around rocks. From my collecting, the size classes of larvae indicate that at least four years are required for the life cycle to be completed in the small streams on Mary's Peak west of Corvallis, Oregon. The adults have been collected along larger streams to tidewater. The spotted owl, *Strix occidentalis* (Xantus), is a predator of *D. disjunctus* as I have identified adult head capsules from their pellets.

*Dysmicothermalmes ingens* Chandler
(Figures 50-53, 61-63, 120)


This species may be separated from *D. disjunctus* on the basis of wing coloration and genitalia. Forewings translucent, faintly
spotted with sparse light brown spots.

**Male** - claspers narrowly cleft (Figure 51).

**Female** - lower lobe of clasper longer than upper lobe (Figure 53).

**Larvae** (Figure 61) - larger than *D. disjunctus*, 65± mm when mature; ventral stemmata posterior to other stemmata (Figure 63); abdominal setae with long tapering points, sub-erect, as long or longer than height of spiracles (Figure 62).

**Type** - Male - Miami Ranger Station, Mariposa County, California, 27 July, 1946, elev. 5000 feet (H. P. Chandler). California Academy of Science, San Francisco, California.

During this study four males, three females and over 30 larvae were examined including three paratypes. One male was reared from a mature larvae.

**Distribution** - This species has been found in the Sierra Nevada and San Bernardino Mountains of California (Figure 120).

**Adults** - California: Mariposa Co.: Miami Ranger Station. Tulare Co.: Sequoia Nat'l. Park.

**Larvae** - California: El Dorado Co.: White Hall; Pyramid Ranger Station. Mariposa Co.: Mosquito Ck., Yosemite Nat'l. Park; Strawberry Ck., Yosemite Nat'l. Park; Miami Ranger Station. Sierra Co.: 3.5 mi. N. Comptonville, Hwy. 49; E. Sierra City, Hwy. 49. Tehama Co.: Hwy. 32, S. jct. Hwy. 36, Adler Cpgd.
Adults have been collected from late June through July.

**Biology** - I have collected the larvae of this species in small cold streams among rocks and debris. At Mosquito Creek in Yosemite National Park, California in a detritus filled pool several large larvae were observed actively pursuing their prey. Two smaller larvae were collected from beneath rocks well impacted into the substrate. These larvae have been maintained in the laboratory for three years and have molted twice. The life cycle for this large insect is probably four years.

**Genus Orohermes** gen. nov.  
(Figures 64-74, 119)

Wing expanse less than 110 mm; posterior branch of M is not forked in the hind wing, posterior branch Rs forked (Figure 64).

**Male** - short broad claspers slightly indented apically; aedeagus weakly fused basally with two rounded posterior projections, ventral plate concave posteriorly, a lateral membranous lobe between aedeagus and ventral plate (Figures 65, 66).

**Female** - claspers with short lobes (Figure 67).

**Larvae** (Figure 73) - gena sharply angulate posteriorly; lateral abdominal filaments longer than width of abdomen; abdominal spiracles smaller posteriorly, not raised on tubercules, those on segment VIII lateral.

*From the Greek ορος, mountain, + Ήρμης, Greek god.*
This genus is proposed for a single species, *D. crepusculus* Chandler. Chandler (1954) recognized the distinctive differences and provisionally placed it in *Dysmicohermes*, the most closely related genus. *Orohermes* is easily separated from *Dysmicohermes* by its smaller size, wing venation and genitalia.


*Orohermes crepusculus* (Chandler)  
(Figures 30, 64-74, 119)


**Larvae** (Figure 73) - 55-65 mm long. **Head** - dark reddish brown, lightly punctate and lacking a distinct pattern, scattered reddish setae laterally; lower posterior facet of eye spot below upper group (Figure 74); antennae 3/4 as long as mandible; gena sharply angulate posteriorly. **Thorax** - dark reddish brown dorsally without a distinct pattern; pronotum slightly wider than long; meso- and metanotum combined, shorter than wide. **Abdomen** - reddish gray brown, clothed with fine reddish setae; lateral filaments robust, longer than width of abdomen, with a dorsal row of fine setae; mesothoracic spiracle larger than abdominal spiracles, abdominal spiracles becoming smaller posteriorly, all located above and anterior to base of filament and flush with surface.
Eggs (Figure 71) - Mass of 3-5 layers, oblong, 30 mm x 25 mm, narrowed anteriorly, all eggs parallel to substrate, grayish yellow when deposited, becoming reddish at hatching, 1000-1700 eggs per mass averaging 1500 for ten masses, each egg 1.0 mm x 0.5 mm, egg burster (Figures 68-70).

Type - Male - Pyramid Ranger Station, El Dorado County, California, 20 August 1952 (J. W. MacSwain). California Academy of Science, San Francisco, California.

During this study, 27 males, 57 females, including three para-types, over 300 larvae and several hundred egg masses were examined. Three mature larvae were reared.

Distribution - This species is found as far south as Napa County, California, throughout the Sierra Nevada Mountains and north through the Cascade Mountains of Oregon. Although collecting records are not available it seems probable that this species will be found as far north as British Columbia (Figure 119).


Adults emerge from late June to early September with July and August the months of most frequent adult collection.


**Biology** - The larvae of this species are usually found in cold permanent streams and rivers, although I have collected them in adjacent intermittent streams. The temperature of these streams probably would not exceed 15°C in most cases as collecting in them even in late summer was uncomfortable. The largest number of larvae were found beneath rocks and among debris in riffles and glides. This species was abundant in trout streams in the vicinity of Breitenbush and Marion Forks, Oregon, and most of the field studies were conducted there.

In the above study areas, which are about 2400 feet in elevation, adult emergence occurs during the last part of July. Mating takes place during early evening. During this time, females also move to oviposition sites and begin laying eggs which sometimes continues during daylight hours. One of the easily observed oviposition sites is on the underside of bridges. With the distinctive egg mass, the presence of this species in a stream can be easily ascertained by observing these locations. The underside of a bridge is also a place where adults may be collected during the day. This species is not attracted to black
light traps at night as I have operated these lights around bridges and failed to collect specimens in the trap while collecting adults nearby with a flashlight.

Mating has not been observed, but I have observed males pursuing a female in flight and also several males that were attracted to an immobile female. In the first instance, a female was dislodged from a bridge in mid-afternoon and made a short downstream flight, which brought three males from the streamside trees. The males pursued her and lit in the nearby trees. The specimens were lost from view because of their protective coloration, which blends in with the mottled colors of the trees. Because of the short duration of the female's flight, it seems reasonable to conclude that the males recognized the female by sight rather than odor because diffusion would not have taken place so rapidly. This does not mean that a sex attractant is not given off by the females, but only that males will pursue large insects with a rather characteristic flight in which the heavy abdomen is vertical, resembling that of stoneflies.

The second observation of a part of the mating behavior of *O. crepusculus* occurred shortly after the sun had set. Insect activity was seen around a large streamside hemlock tree. About ten feet above the ground on a horizontal limb a female was apparently located as some of the flying males had landed and could be seen against the sky fluttering their wings in the same manner as that previously
described for the male of *C. cognatus* during its mating behavior. During this short period of time, which lasted no more than 15 minutes, more than a dozen males were collected around this tree with a net. While holding the males in the net, a pungent odor was detected. As they were placed in individual containers the everted membranous tubes on the genital capsule were easily seen. This scent may serve as a sex stimulant for the female, as previously suggested for *C. cognatus*, and it may also attract males to the place where the female is located. When several males are attracted to one female, mating fights may occur as observed by Parfin (1954) in *C. cornutus*. Competition between the males would give certain genotypes a mating advantage, as the stronger individuals may more readily secure a mate. Another possible use of this odor is defense, as during the brief period of time when these observations were made, a bat flew down on the flying males and failed to seize a male or return for another try. Odor might have played a repellant role in this instance. The mandibles are strong and sharp as I have been bitten on several occasions and blood was drawn from my fingers.

The time between mating and oviposition is not known. As mentioned before, the distinctive egg masses are deposited on bridges and on the downstream surface of rocks projecting above the water surface or on trees overhanging the water. If a rock is selected, it is usually large and slanted downstream. The female
begins laying the eggs, from what will be the posterior end of the egg mass. She moves her abdomen from side to side, completing each row before moving forward to the next. After the bottom layer is completed, the second is started anterior to the beginning of the first layer. Each succeeding layer is somewhat smaller (Figure 71).

Most of the eggs in each mass hatch at the same time. The egg masses brought into the laboratory hatched in the evening. On two occasions, eggs were seen hatching during the day in the field. Hatching is initiated when the mature embryo pushes the head against the upper surface of the micropylar end of the egg. This causes the egg to stretch and bulge. Beneath the bulge and between the mandibles, the egg burster may be seen (Figure 69). The egg burster punctures the stretched egg initiating a longitudinal tear through which the larva emerges. Within ten minutes after emerging from the egg, the larva undergoes a post-embryonic molt, shedding the egg burster and a thin membrane which is left attached to the micropylar end of the egg. The larva then becomes more active and crawls or falls into the water.

Embryonic development under field conditions was ascertained by marking egg masses and observing when they hatched. A total of 53 egg masses were marked in the Marion Forks and Breitenbush area. Data were recorded from only 34 as the markings became illegible or the egg mass was removed. Egg masses were marked on 14, 20, 25 July and on 6 and 12 August 1968. Those marked on the
first day were assumed to be less than a week old as adults are
seldom collected earlier than the first week of July. On each subse-
quent visit, the egg masses which had hatched or had failed to hatch
were noted. The sites were also visited on 5 and 20 September and
26 October. The data in the following table show that the average time
for embryonic development was 43 days with a range of 26 to 63 days.
These data show that embryonic development varies considerably under
field conditions depending upon whether the egg mass is in the shade,
exposed to the sun or near cold water. A newly deposited egg mass
was brought into the laboratory and hatched in 25 days at room tem-
perature (20°C). On 26 October, 1968, a single mass was observed
hatching with the larvae slowly carwling down the rock surface into
the water. This oviposition site was one that was always in deep
shade and the egg mass was only about a foot above the water surface.
It is very probable that these eggs exceeded 63 days in maturing as
no females were collected after 12 August 1968. This egg mass had
survived the frequent frosts that occurred by that time of year because
the rock was kept above freezing by conductance of heat from the
water. Air temperatures near the moving water surface would also
be raised.

An experiment was undertaken to determine the effects of
freezing on the eggs of O. crepusculus. A single egg mass was
collected in August, 1968, and brought into the laboratory and stored
Table 2. Embryonic development of the egg masses of *Orohermes crepusculus* in the headwater region of the North Santiam River, Linn County, Oregon.

<table>
<thead>
<tr>
<th>Date of egg mass</th>
<th>Days to hatch</th>
<th>No. of egg masses</th>
</tr>
</thead>
<tbody>
<tr>
<td>14 July, 1968</td>
<td>29</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>37</td>
<td>2</td>
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<td></td>
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<tr>
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<td>31</td>
<td>3</td>
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<tr>
<td></td>
<td>39</td>
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<tr>
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</tr>
<tr>
<td></td>
<td>62</td>
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<tr>
<td>25 July, 1968</td>
<td>26</td>
<td>2</td>
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<td></td>
<td>42</td>
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<tr>
<td></td>
<td>57</td>
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</tr>
<tr>
<td>6 August, 1968</td>
<td>30</td>
<td>1</td>
</tr>
<tr>
<td>12 August, 1968</td>
<td><strong>39</strong></td>
<td><strong>2</strong></td>
</tr>
<tr>
<td>Totals</td>
<td><strong>1437</strong></td>
<td><strong>34</strong></td>
</tr>
</tbody>
</table>

at 7°C. Twenty or more eggs were separated from the mass and placed in each of 16 petri dishes and again stored at 7°C. The following day the eggs were placed in a -14°C freezing compartment with the covers tilted to one side to assure rapid temperature change. At intervals of 3, 6, 9, 12, 15, 30, 45, and 60 minutes one dish was removed. Thereafter, a dish was removed every hour for the next seven hours with the last dish remaining for 24 hours. After removal, the dishes were covered and placed on a laboratory bench with the two control dishes of eggs. The eggs exposed for three
minutes and the controls, which were placed on the laboratory bench when the eggs were placed at -14°C, hatched the following evening. Eighty-four percent of the control eggs hatched and 91 percent of those exposed for three minutes did likewise. The remainder of the test eggs failed to hatch. Failure to hatch in the controls, which included the remainder of the egg mass, can be attributed to damage in collecting and handling. These data suggest that the eggs of *O. crepusculus* could withstand freezing for only a short period of time when the embryos are well developed.

Other factors affecting embryonic development observed during this study were parasites and predators. The only predator observed feeding on egg masses was a slug, *Arion circumscriptus* Johnston. It was seen on two occasions crawling over egg masses and feeding, as damaged and missing eggs were evident. Two insects were collected with egg masses brought into the laboratory. A small predaceous bug, *Empicoris culiciformis* (DeGeer), and psocids or bark lice were found on eggs collected at Marion Forks, Oregon, but it is not known whether they feed on the eggs. Egg parasites were not found although sialid eggs were heavily parasitized by *Trichogramma semblidis* (Aurivillius) within inches of egg masses of *O. crepusculus*.

Two genera of fungi caused considerable egg mortality on metal bridge girders which were shaded and frequently wet from condensation. *Cladosporium* sp. was the most common and conspicuous fungus
and caused the egg masses to turn black when infected. *Alternaria* sp. was also identified from the same egg masses. On a shaded metal bridge on the headwaters of the Clackamas River, Clackamas County, Oregon, all of the estimated 75 egg masses were black on the north side of the bridge. This same kind of infestation could be seen on the metal bridge girders at Marion Forks, Linn County, Oregon.

The following observations and the rearing experiments with *N. californicus* which are presented later, show that the life cycle of this cold water species may be five years. At Shellrock Creek, tributary of Oak Grove Fork of Clackamas River, Clackamas County, Oregon, at an elevation of 2100 feet on 9 August, 1968, a collection of 64 larvae of *O. crepusculus* was made. All were preserved by oral injection and immersion in KAAD. At this time, some larvae had molted as indicated by their light head capsules. The head capsules of the larvae were measured and their width-frequency is given in Figure 30.

To interpret these data in terms of year classes and the length of the life cycle of *O. crepusculus* the following information is of value. Several hundred first instars that hatched from eggs in the laboratory were cultured in a single container at 13°C. After 16 months, the lone survivor had a head capsule width of 2.7 mm. Cannibalism probably accounted for much of the mortality. This may represent a maximum growth rate for this species as I have collected the larvae
Figure 30. Estimated year classes of *Orohermes crepusculus* (Chandler) from larval head capsule widths (mm). Collected at Shellrock Creek, tributary to the Oak Grove Fork, Clackamas River, 9 August, 1968.
in streams which are seldom above 20°C for any extended period of time. The growth rate of *N. californicus* is almost the same at 13°C as at 21°C (Table 3), as indicated by the number of molts, while a decrease in temperature to 8°C decreases the larval growth rate by about 50 percent. Temperatures of 8°C or less persist for much of the year in streams where *O. crepusculus* larvae are found because they inhabit mountain streams which are the result of snow melt.

Rearing of some larvae to adults and the relationship between their respective head widths also aid in interpreting the data on larval head capsule width frequencies.

Rearing mature larvae to the adult form shows a decrease in width of the posterior of the head between the larvae and adult. The head capsules of three males and the larvae from which they were reared are as follows: Larvae - 5.2, 5.8 and 6.0 mm; adults - 4.9, 5.1 and 5.6 mm, respectively. Ten adult females had a mean head capsule width of 6.0 mm with a range of 5.3-6.5 mm while five males had a mean head capsule width of 5.0 mm with a range of 4.5-5.6 mm. Females were not successfully reared but it is assumed that the larvae would have wider head capsules as in the case with *Neohermes californicus* (Table 6).

The head capsule width-frequency data can therefore be divided into year classes in the following manner: Those larvae with head capsule widths less than 3.1 mm are at least one year old, those
between 3.1 and 4.3 mm are two years old; and those larvae from 4.6 to 7.8 mm are three or four years old. The wide range in head capsules in this last group is due to sexual dimorphism as was indicated for the adults above. A three-year-old female larva could have a wider head capsule than some four-year-old male larvae. In view of the increase by about 1/3 in head capsule width of _N. californicus_ between molts of the later instars, it seems reasonable to assume that most of the larvae of _O. crespusculus_ with head capsules over 6.0 mm had head capsules over 4.3 mm before their last molt and were three years old. The four-year-old larvae found in the stream in August when this sample was taken did not pupate until the following summer, making them five years old on emergence. When this sample was collected, eggs from year class 5 had been laid. While this species is adapted to a cold stream existence, the above data suggest a five year life cycle. If the growth rate of the larvae reared for 16 months at 13°C represents a maximum growth rate for the species, the five year estimate might have to be increased.

Genus _Neohermes_ Banks
(Figures 31, 75-87, 112, 113, 119)

Male with distinctive setose moniliform antennae about 3/4 as long as as forewings; female antennae subserrate about half as long as forewing. Forewing with R_3 + R_4 fused for about half their length usually with a crossvein beyond the fork; anterior branch 2A united with 1A for a short distance. Anterior branch M in hindwing forked (Figure 75), wing membrane grayish, forewing marked with black spots, a large spot basally. Male - claspers cylindrical, apex often decurved with an apicomesal patch of short black setae; ninth sternum forming a broad scoop; aedeagus flat, bilobed apically with a central ridge. Female - claspers triangular, gonopophysis may have an apical papillae. Larvae - western species 35-55 mm long at maturity, head and dorsum of thorax punctate, yellow to dark brown with a lighter pattern; abdomen light brown to dark gray with a darker medial stripe. Head - Antennae 3/4 length of mandible, segment I short, segment II longest, equal in length to III and VI together, III and IX sub-equal in length; posterior of gena gradually sloping to occiput. Thorax - dorsum lighter anteriorly with sparse fine setae. Abdomen - filaments longer than width of abdomen, spiracles slightly raised above base of filament, those on segment VIII mesad on short broad conical projections on posterior of segment. First instar larvae - 2 mm long; head and body white. Head - mandibles reddish brown apically; labrum elliptical; antennae three-segmented. Abdomen - with 12 dorsal setae on each segment; lateral
filaments short, rounded apically with two sub-equal seta; spiracles present in same position as mature larvae. **Eggs** in a single layered mass of 2000-3000, eggs about 0.9 mm long and 0.4 mm wide, all with long axis parallel to substrate (Figure 83); egg burster a raised toothed ridge (Figure 82).

**Type of Genus** - *Chauliodes filicornis* Banks, 1903:238.

This North American genus was recently revised by Flint (1965), who recognized five species on the basis of the male genitalia. Two species occur in the Pacific Coastal Region. **Neohermes** is closely related to **Protochauliodes**. The males of **Neohermes** are easily recognized by their long, hairy antennae. The females of the two genera are sometimes difficult to separate because the crossvein between R₃ and R₄ in the forewing may be present or absent in either genus. The females of the western species of **Neohermes** lack apical papillae on the lateral gonopophysis while those of **Protochauliodes** possess one. The larvae of the western species of **Neohermes** differ from those of **Protochauliodes** by the longer abdominal filaments and body color. Separation of the two species of western **Neohermes** larvae is made on the basis of color, pattern and geographic distribution. Dissections, drawings and observations of the head, legs, spiracles and abdominal appendages show little morphological difference.

**Biology** - The larvae of the western species of **Neohermes**
usually occur in rocky intermittent streams but on occasion I have collected them in warm permanent streams (Figures 112 and 113). In these habitats, the larvae coexist with various species of Protochauliodes. Pupation occurs when the stream dries up or recedes or after the larvae leave the water. The exarate pupae use their mandibles to tunnel to the surface from their pupal cells. The adults emerge at dusk and mate on the rocks and streamside vegetation during the evening. Eggs are laid beneath large flat rocks in the dry stream bed or over the water if the stream is permanent. Hatching occurs in about two weeks and the larvae crawl into the cracks and crevices of the dry stream bed or into the water, if present. The life cycle varies and can probably take from two to five years depending on the habitat.

**Neohermes filicornis** (Banks)  
(Figures 76, 77, 86, 87, 115, 119)

**Chauliodes filicornis** Banks, 1903:238.

**Neohermes filicornis**; Banks, 1908:29; Weele, 1910:52-54; Van Dyke, 1944:110; Gurney and Parfin, 1959:974; Flint, 1965:256-257.

**Males** - genital claspers apicoventrally produced (Figure 76).

**Females** - genital claspers triangular with apical point barely developed (Figure 77).

**Larvae** (Figure 86) - 35-55 mm long. **Head** - yellow to dark
brown with a lighter yellow pattern. **Thorax** - pronotum, lighter than head, mesonotum and metanotum darker than pronotum, all patterned yellow and gray or brown. **Abdomen** - dark to light bluish-gray dorsally, lateral filaments and lateral abdominal margins lighter; ventral pattern variable, sometimes with three dark areas on each segment, sometimes only two anteriorly or similar to **N. californicus**. Lighter areas on lateral margins of abdomen distinctly separated from dark areas and not shading into them (Figure 87).


During this study, 174 males, 93 females, 6 pupae, about 200 larvae and several egg masses were examined. Forty-six specimens were reared from mature larvae.

**Distribution** - This species is found from Trinity and Humbolt Counties in northern California south along the coast to Baja, Mexico, and east into Arizona, New Mexico, and Mexico (Figure 119).

Miller Cpgd.; 17 mi. N. Clifton. Maricopa Co.: Middle Ck.,
Wickenburg. Santa Cruz Co.: Santa Rita Mts.; Madera Cyn.; Pena
Blanca, Oro Blanco Mts. Yavapai Co.: Indian Ck. Cpgd., Prescott
Nat'l. For.; E. Prescott. California: Humboldt Co.: 3 mi. NW
Garberville; Glendale. Kern Co.: Poso. Lake Co.: Anderson
Spgs.; 4 mi. NW Glenbrook. Los Angeles Co.: W. Br. San Gabriel
R.; 2-1/2 mi. S. Valyermo; Mt. Lowe; Avalon, Santa Catalina Island; Los Angeles; Glendale, Temescal Cyn.; Santa Monica Mts.;
Tan Bark Flats; Cold Brook, San Gabriel Mts.; Buckhorn Flats, San
Gabriel Mts.; My. Lyell; Topango Cyn.; Boquet Cyn.; Temescal Cyn.; Santa Monica Mts.; Pearblossom. Marin Co.: Upper Monte
Vista Ave., Mill Valley; Novato; Fairfax. Orange Co.: Orange,
Trabuco Ck. Riverside Co.: P. L. Boyd Desert Res. nr. gaging
Station; P. L. Boyd Desert Res., Deep Cyn.; Riverside; Fern Valley,
2 mi. E. Idyllwild; Idyllwild. San Benito Co.: Pinnacles Nat'l. Mon.;
Chalone Cpgd. San Bernardino Co.: Stream nr. Toll Road Camp,
San Bernardino Mts.; Big Bear Lake; Camp-O-Ongo nr. Running
Spgs.; Camp Baldy. San Diego Co.: Hauser Ck. nr. Compo; Del
Mar; Mt. Palomar State Park; Alpine. San Luis Obispo Co.: Atascadero; Cal. Poly. Cyn., San Luis Obispo. Santa Barbara Co.: Los Prietos Cpgd., nr. Chachuma Lake; Santa Cruz Island; 3 mi. N.
Refugio Beach. Santa Clara Co.: San Antonio R.S. Santa Cruz Co.: Madera Cyn. Solano Co.: Green Valley. Sonoma Co.: 6 mi. E.
Collecting records show that adults emerge from May to October with the emergence peaks from June to August depending on the location.

Larvae - Arizona: Cococino Co.: Williams. California:
Ck. below Lake Cachuma at Hwy. 154. Santa Clara Co.: Morgan Hill.
San Marcus.

**Biology** - *N. filicornis* is found in rocky areas of warm intermittent or permanent streams. From the collecting data this species apparently exists with *C. cognatus* in Arizona and New Mexico. The microhabitat differences between these species is not known. The observations of the biology of the closely related *N. californicus* discussed next is applicable in a large part to *N. filicornis*.

**Neohermes californicus** (Walker)
(Figures 31, 75, 78-85, 114, 119)

Chauliodes californicus Walker, 1853:199; Hagen, 1861:190; MacLachlan, 1867:259; Banks, 1892:357, 1907:21; Davis, 1903:463.

**Male** - genital claspers forked apically and decurved near middle (Figure 78).

**Female** - genital claspers drawn to a slender point apically
(Figure 77).

**Larvae** - Similar to *N. filicornis* with the following differences:
Head - dark brown with yellow markings, reddish brown in more immature larvae. Thorax - pronotum lighter than head or meso- and metanotum, all patterned yellow and brown. Abdomen - light brown, lateral filaments same color as dorsum of abdomen, ventral pattern not separated into three distinct areas, light areas of abdomen shading into darker areas (Figure 85).

Type - Female - California (from M. Hastwegs' collection).

British Museum (Natural History), London, England.

During this study, 76 males, 68 females, 14 pupae, over 200 larvae and at least 50 egg masses were examined. Of the adults and pupae examined, 69 were reared from larger larvae.

Distribution - From the Sierra Nevada Mountains and Napa County of California north to the Willamette Valley of Oregon (Figure 119).

Flat. Tulare Co.: Three Rivers. **Nevada**: Washoe Co.: Verdi.

**Oregon**: Lake Co.: Bullard Ck., 2 mi. E. Lakeview. Linn Co.: E. Crabtree.

The collection data show that adults emerge from May to October with July the peak month of emergence.


**Biology** - The larval habitat of *N. californicus* is rocky intermittent or permanent warm streams. In intermittent streams, I have collected it with *P. aridus* in Bidwell Park, Chico, California and with *P. spenceri* near Crabtree, Oregon.

The number of larval instars for any species of Corydalidae had not been determined prior to this study. As this is written, I have five larvae which hatched from eggs and are now in their 11th instar. By comparing their head capsule measurements (Table 3)
Table 3. Larval head capsule widths (mm) and duration of instars (days) of *Neoliermes californicus* (Walker) reared from eggs at 21 °C.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Instars</th>
<th>Days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>0.3</td>
<td>0.37</td>
</tr>
<tr>
<td>2</td>
<td>0.3</td>
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</tr>
<tr>
<td>3</td>
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<td>0.4</td>
</tr>
<tr>
<td>4</td>
<td>0.3</td>
<td>0.4</td>
</tr>
<tr>
<td>5</td>
<td>0.3</td>
<td>0.4</td>
</tr>
<tr>
<td>X</td>
<td>0.3</td>
<td>0.39</td>
</tr>
</tbody>
</table>
with those of larvae that pupated, it appears that *N. californicus* has 12 larval instars. Among all the larvae collected and reared during this study, one specimen of this species was found to have thoracic protruberances resembling wing buds (Figure 80).

To gain a better understanding of the length of the life cycle of this species, a rearing experiment to determine the effects of temperature on the rate of larval development was undertaken. Six early instar larvae were placed in plastic rearing trays at 6°C and 13°C, while 12 were placed at 21±°C. All were supplied with an excess of food during most of the experiment. Mortality was high with only six of the initial larvae developing to the last instar. Death resulted from fungal infections, injury and a failure to molt properly. Five larvae survived at 21±°C. While pupating, two died as pupae, two as larvae and one emerged as an adult. The other larva was at 6°C and died 28 months after the experiment started. It was probably a small mature larvae but it was not removed from the water and allowed to pupate.

These data (Table 4) show that temperature has a marked effect on the growth of the larvae of *N. californicus*. At 7°C, the larvae molted 18 times with an average stadium of 4.3 months, while at 13°C 16 molts had an average stadium of 1.9 months. Larvae at 21±°C molted 41 times with an average stadium of 1.6 months. The difference between the higher temperatures may not be significant as a
Table 4. Head capsule widths, wet weights and duration of instars of *Neohermes californicus* (Walker).

Reared at 7, 13, and 21°C.

<table>
<thead>
<tr>
<th>Species no.</th>
<th>Molts 0</th>
<th>Molts 1</th>
<th>Molts 2</th>
<th>Molts 3</th>
<th>Molts 4</th>
<th>Molts 5</th>
<th>Molts 6</th>
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<td></td>
<td>7°C</td>
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<td></td>
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<tr>
<td>1</td>
<td>a 1.2</td>
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<td></td>
<td>b 2.5</td>
<td>7</td>
<td>5</td>
<td>2.5</td>
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<td>a 1.2</td>
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Total molts = 18

Total time between molts = 78 months

\( \bar{x} \) time between molts = 4.3 months

*Died after 28 months

(Continued on next page)
Table 4. (Continued)

<table>
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Total molts = 16  
Total time between molts = 31 months  
\(\bar{x}\) time between molts = 1.9 months

\[21^\circ\text{C}\]

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</table>

Total molts = 41  
Total time between molts = 65.4 months  
\(\bar{x}\) time between molts = 1.6 months  
*A = adults; DL = died as a larva; DP = died as a pupa.
large number of first instar larvae, obtained from an egg mass, was placed in a single container and the sole survivor was mature in about 12 months, the same length of time as those at \(21 \pm 0^\circ C\). The data also show that weights tend to approximately double with each additional instar.

The data on effects of temperature on rate of larval development allow estimates to be made for the life cycle under field conditions at various locations. The life cycle may be completed in two years in permanent warm water streams. However, the life cycle is extended in intermittent streams where the water flows only during the winter months. In these situations, the larvae burrow into the stream bed and form a small chamber. This period of quiescence may last for more than six months. Some streams in the vicinity of Chico, California dry up in April and fall rains may not cause stream flow again until November. In these streams, the period for maximum growth is thus reduced. Low water temperatures in the winter also retard development.

Field collections were made in a small intermittent stream W. Quartz Mountain Summit, Hwy. 66, Lake County, Oregon, at an elevation of 5200 feet on 7 April, 1968 when the water temperature was \(6^\circ C\). Figure 31 gives the frequency distribution of the head capsule widths of the 43 larvae collected. This stream was dry by July. The stream probably begins to flow in late October and ends in June.
Figure 31. Estimated year classes of Neohermes californicus (Walker) from larval head capsule widths (mm). Collected in an intermittent stream W. Quartz Mt. Summit, Hwy. 66, 5200 ft. elevation, Lake County, Oregon, 7 April, 1968.
the assumed growing period is eight months but for much of that
time water temperature would be less than 6° C.

The larvae with head capsule widths from 4-6 mm were final
instars as Tables 5 and 6 show and would be ready to pupate before
July. Some of those larvae with head capsule widths between 3-4 mm
could become last instars before the stream dried up but would not
pupate until the following year because sufficient growth would not
have accrued to permit reproductive tissues to develop. The smallest
specimens collected with head widths of 1.9-2.2 mm would be about
the 8th instar and would be two years old and those with head capsule
widths from 2.2-3.0 mm would be 9th or 10th instars and three years
old. The larvae that hatched from eggs the previous summer were too
small to be collected by the method used. Thus it is estimated that
the fastest development at this site would entail at least a three-year
larval stage, and that four or five years would be required for most
of the larvae.

The mating behavior of *N. californicus* was observed on several
occasions in the laboratory. After their cages were placed in a room
illuminated only by red light, 15-20 minutes passed before the insects
began to walk and flutter about their cage. Both males and females
moved about, especially if touched by another. Males were very
responsive when touched by another male and they quickly moved
away, but no attempt was made to fight as Parfin (1954) observed in
Table 5. Larval head capsule widths (mm) of *Neohermes californicus* (Walker). Collected W. Quartz Mountain Summit, Hwy. 66, 5200 feet elevation, 7 April, 1968 and placed in soil to pupate 17 July, 1968, after being fed and kept at 13°C.

<table>
<thead>
<tr>
<th>Larval head capsule width (mm)</th>
<th>No. and sex of adults</th>
<th>Larvae</th>
<th>Surviving</th>
<th>Not surviving</th>
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<tbody>
<tr>
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<td>5.8</td>
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% Survival = 57%.
Table 6. The association of larval-adult head capsule widths (mm) of *Neohermes californicus* (Walker). Reared from larvae collected W. Quartz Mountain Summit, Hwy. 66, 5200 feet elevation, Lake County, Oregon, and allowed to pupate 17 July, 1968.

<table>
<thead>
<tr>
<th>Larval head capsule width (mm)</th>
<th>Adult head capsule width (across eyes) (mm)</th>
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<tbody>
<tr>
<td><strong>Males</strong></td>
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<td>4.0</td>
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<td>5.0</td>
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<tr>
<td>5.1</td>
<td>5.1</td>
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<tr>
<td>$\bar{X} = 4.5$</td>
<td></td>
</tr>
<tr>
<td><strong>Females</strong></td>
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<tr>
<td>5.0</td>
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<tr>
<td>5.0</td>
<td>4.5</td>
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<td>5.3</td>
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<tr>
<td>5.4</td>
<td>4.6</td>
</tr>
<tr>
<td>$\bar{X} = 5.2$</td>
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</tr>
</tbody>
</table>

$\bar{X} = 4.5$ for males and $\bar{X} = 4.6$ for females.
C. cornutus. When a female was ready to mate, she straightened her legs, contacting the surface only with the tarsi while raising the thorax and abdomen off the substrate and spread her wings slightly so that the costal margins were pressed against the substrate for support. The posterior half of the abdomen was curved dorsad. When a male found her, he crawled beneath her without any pre-copulatory touching as in Corydalus, until his head was under her thorax. He then raised his abdomen, uniting their genitalia, and they then assumed a tail to tail position. The male released his grip and swung free with his legs dorsad and supported only by the genital connection. Needham and Betten (1901) show this position in two photographs of Nigronia (Chauliodes) serricornis (Say). Copulation lasts for several hours. Females have been observed to only mate once but males will mate again although the abdomen decreases in size with each mating. Males were usually dead within 2-3 days. Oviposition occurred a day or two after mating and the females died a day or two following that. Eggs were sometimes laid in small patches in the cage, probably because the ovipositing females were disturbed by the other specimens in the cage. The eggs hatched in 7-10 days in the laboratory.

No egg parasites were found but fungi frequently attack larvae in the field and laboratory. Under field conditions, the pupae are very susceptible to fungal attacks if the soil remains wet or becomes wet after pupation has occurred. At Ruch, Oregon, 6 of 12 pupae collected
from wet pupal chambers were dead from fungus. Injured areas on
the larvae turn black and death occurs within a few days.

Smith (1970) also has studied *N. californicus* near Chico,
California. His observations of large larvae in a plastic tray show
that they will seek out and feed on small pieces of meat or dead insect
larvae. This scavenging feeding behavior is of value to larvae living
in intermittent streams as I have found many dead terrestrial inverte-
brates in these streams when other food organisms were apparently
scarce. This is very noticeable when the streams begin to flow in the
fall. Davis (1903) also observed that *C. cornutus* would eat meat.

In the laboratory, Smith (1970) found that pre-pupal larvae
would crawl from the water 7-20 days before pupation with an average
of about 13 days. The pupal stadium took 9-12 days with an average of
11 days for 11 pupae at about 25°C. The quick rearward avoidance
action of the larva was observed as was the defensive biting and
vomiting of a dark, foul-smelling liquid. The ecdysis of the pre-
pupae and pupae took about five minutes. Newly emerged adults
voided a white smelly meconium and also did this if handled later.

The assumption of a one year life cycle for *N. californicus* by Smith
(1970) in the intermittent habitats near Chico is erroneous in view of my
larval rearings and field observations. This conclusion was reached
because of insufficient collecting, as I have collected samples of
larvae in the Chico area with size ranges similar to those obtained W.
Quartz Mountain Summit, Hwy. 66, Lake County, Oregon. The further assumption that the life cycle of most or all of the California corydalids is similar to that of _P. aridis_ and _N. californicus_ is speculation and in error, as at least five species, not including _N. californicus_ and _P. aridis_ have different life cycles in the nearby Sierra Nevada Mountains. The specimens of _N. californicus_ that live in Big Chico Creek, a permanent stream in Chico, would also have a different life cycle (Maddux, personal communication). The selection of intermittent streams by an insect with a larval stage of several years' duration is unique among aquatic insects. Some of the physiological adaptations will be discussed later.

**Genus Protochauliodes Weele**
(Figures 32, 88-113, 117, 118)


Wings (Figure 88) dark brown to light translucent gray with many small dark spots, usually along veins; forewing with large dark basal transverse spot; hindwings with most spots apical. Posterior branch of R simple, M in hindwing three-branched; crossvein between R₃ and R₄ lacking in forewing with anterior branch 2A joined to 1A for short distance beyond anal cell, 1A appearing three-branched. Head - orange to dark reddish brown, lighter anterior to insertion of antennae,
patterned posteriorly with raised smooth areas; antennae long, filiform to sub-serrate. Thorax - dark reddish brown to black.

Abdomen - color as thorax. Male - genitalia with claspers or anal plates from rounded and elongate to ovoid and truncate, tending to bifurcate apically; raised, circular punctate area near base of claspers, inner surface covered with short black setae; aedeagus flattened, with central ridge from base to apex which is generally notched or bi-lobed. Female - genitalia with short claspers with raised basal circular punctate area. Larvae - 35-55 mm; dorsum of head and thorax patterned. Head and thorax similar to Neohermes. Abdomen - lateral filaments slender, usually equal to or shorter than width of abdomen on anterior segments. Eggs - like Neohermes in size of eggs and type of egg mass.

Type of Genus - Chauliodes cenerascens Blanchard, 1851: Pl. 2, Figure 10.

Gurney and Parfin (1959) suggested that some species and genera of Corydalidae occurring in western North America were in an "unsettled state." As this study progressed, it became apparent that the western species of Protochauliodes required revision before larval-adult associations could be made. Protochauliodes has a disjunct world distribution, occurring in Australia, Chile, and the western United States and Canada. Related genera occur in Madagascar, South Africa, New Zealand, and Australia.
Protochauliodes is closely related to Neohermes. The males of the genera are easily separated by their antennae. Neohermes has noticeably setose moniliform antennae while Protochauliodes has filiform or sub-serrate antennae. The absence of a crossvein between R₃ and R₄ in the forewing is usually reliable for separating the females of Protochauliodes from those of Neohermes. However, on occasion this crossvein may be present or absent in either genus. Sometimes this crossvein can be found in only one forewing of a specimen. The males of the North American Protochauliodes have an apical papilla on the gonopophysis lateralis while the two species of Neohermes found in the study area do not. The larvae are also similar, but those of Protochauliodes usually have short, fine lateral filaments while the lateral filaments of Neohermes are longer than the width of the abdomen.

Biology - Most of the biological work for this genus was done by Maddux (1952) and Penland (1953) in two unpublished theses. Smith (1970) published some of the information they obtained on P. aridus. The 1954 field notes of H. P. Chandler show that he observed the egg mass and mating of P. minumus.

The larvae of some species of this genus are known to live in intermittent streams and their life cycles and behavior is similar to that of Neohermes. The larval microhabitats differ from Neohermes and keep the larvae of Protochauliodes and Neohermes separated.
when in the same stream. These differences will be discussed under each species where the microhabitat distribution is known.

Protochauliodes minimus (Davis)  
(Figures 95-97, 118)

Chauliodes minimus Davis, 1903:463; Banks, 1907:22.


Male - Alar expanse 60 mm, wing membrane grayish. Head, thorax, and abdomen - blackish. Genitalia (Figure 95) - claspers rounded, about twice as long as wide, slightly restricted medially, expanded apically, rounded, slightly indented with an apico-ventral protrusion; aedeagus flattened in lateral view, in dorsal view notched apically with apico-lateral expansions, broadly ridged medially (Figure 97).

Female - Alar expanse 74 mm, wings smoky brown, anterior part of forewing with light spots. Head, thorax and abdomen - dark reddish brown. Genitalia - similar to other species of genus in North America.

Larvae - unknown.
Type - Male - "San Rafael, California, 26 May, O. Sacken."

Number 2031, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. I examined all the other types.

The holotype is an atypical specimen and Davis (1903) and subsequent investigators failed to figure the male genitalia. Dissection and clearing of the male genitalia has resulted in synonymizing the species given above. Munroe (1953) and Usinger (1956) suggested that N. nigrinis was a synonym of P. infuscatus, probably on the basis of the dark wing color mentioned in their descriptions, but neither figured the male genitalia. During this study, 43 males and eight females were examined. Only one other specimen had grayish wings like the holotype. The remainder had wings that ranged in color from light brown to dark smoky brown, appearing almost black when folded over the abdomen. The aedeagi were similar but some variation occurred in the apico-lateral expansion where the expansion ranges from a small triangular expansion to an elongate expansion. P. minimus has also been confused with P. spenceri and P. simplus because the claspers of the males of these closely related species are similar. Figure 96 shows a variation in the shape of a clasper that occurred in a male of P. minimus. The males of the three closely related species mentioned above can be readily separated by their aedeagi. The females may be separated from the other females by Protochauliodes and Neohermes by the brown wings.
**Distribution** - Found in the foothill streams surrounding the Sacramento River Basin in the northern half of California (Figure 118).


Adults emerge from April to June with peak emergences in May.

**Biology -** Larvae have not been collected so the microhabitat is not known. As previously mentioned, the 1954 field notes of H. P. Chandler show he observed this species. Specimens collected at Bidwell Park, Chico, California, 12 May 1954, were placed in a cage where they mated and oviposited. Eggs were laid on the 15th and the adults were dead three days later. The egg mass was single-layered and the eggs hatched in 21 days.

The adults of *P. minimus* are commonly collected during the afternoon in open wooded areas near streams. This behavior is unique among the corydalids in the study area where adults of most of the other species are crepuscular. However, collecting data indicate other dark species of *Protochauliodes* found in South America and *Nigronia* found in the eastern United States exhibit diurnal behavior. The dark coloration of these insects might give them the advantage of
protective coloration in the shaded woodlands where flight occurs.

Protochauliodes simplus Chandler
(Figures 89, 90, 118)


Similar in size and shape to other species of the genus in North America, body dark reddish brown, wings grayish.

Male - claspers similar to those of P. minimus and P. spenceri (Figure 89); aedeagus widely notched apically, convexly expanded laterally to near mid-point and constricted basally (Figure 90).

Female - Similar to other females in the genus with grayish wing membranes but with more intensely colored markings.

Larvae - unknown.

Type - Male - Tanbark Flat, San Dimas Experimental Forest, Los Angeles County, California, 13 July 1950 (J. D. Paschke). California Academy of Science, San Francisco, California.

During this study, 28 males and four females were examined, including six paratypes and four topotypes.

Distribution - Known from the mountains surrounding the San Joaquin River basin in the southern half of California (Figure 118).

Adults - California: Los Angeles Co.; Tanbark Flat, San

The adults have been collected from April to August with July the month of most frequent collection.

Biology - The microhabitat of larvae is unknown but I have visited the type locality and the only stream in the vicinity was a small intermittent one. I have also collected three males of this species with a black light along large permanent streams.

Protochauliodes spenceri Munroe (Figures 32, 91-94, 107, 108, 112, 118)

Protochauliodes disjunctus Munroe, 1951:33-35; (male only), nec. Walker, 1866).


Similar in size and shape to other members of the genus in North America, body dark reddish brown, wings grayish.

Male - Claspers similar to P. minimus and P. simplus (Figure
91); aedeagus flattened in lateral view, viewed dorsally, lateral margins slightly expanded apically, apex with a pair of dorsad pointed projections, central ridge slightly wider apically (Figures 93-94).

Female - Similar to other females in genus with grayish wings.

Larvae (Figure 107) - 35-55 mm long; reddish gray-brown with head and dorsum of thorax darker reddish brown patterned in yellow.

Head - clypeus and labrum lighter than frons; frons dark reddish brown, sometimes with a single light spot or with three light spots triangularly arranged or without spots; latero-posterior portion patterned yellow, stemmata as in Figure 108. Thorax - pronotum subquadrate, about as wide as head, grayer than head as are meso- and metanotum, all segments clothed with short, fine, recumbent reddish setae. Abdomen - clothed with fine reddish setae; lateral filaments slender equal to or shorter than width of abdomen on anterior segments; venter lighter than dorsum, intersegmental areas lighter than venter, segment VIII partially divided by light area, segment IX completely so; spiracles located above and anterior to base of filament, those of meso-thorax and segment I largest; those of segments II-VII smaller, segment VIII with spiracles medio-posterior, raised on short broad conical projection, meta-thoracic spiracle minute.

Eggs - yellowish gray becoming reddish when about to hatch.

Type - Male - Duncan, British Columbia, 1 August, 1918 (W. Downes). Canadian National Collection, Ottawa, Ontario.
This species has been frequently confused with P. minimus not only because the claspers of the males are similar but the wings of preserved specimens sometimes have a brownish cast to the membranes. The aedeagus is the only way to positively separate the males of P. spenceri from those of P. minimus and P. simplus. The females cannot be separated reliably on a morphological basis at the present time.

During this study, 54 males, 39 females and over 75 larvae were examined and eight mature larvae were reared to adults.

Distribution - From the San Francisco Bay region north to southern British Columbia (Figure 118).


Adults have been collected from June to October with most specimens collected in July and early August.

Biology - I have collected the larvae of *P. spenceri* among the leaves and debris in the current of small intermittent streams having a soft substrate (Figure 112). Some of these streams are mere trickles or seepage areas and in some cases run for less than six months of the year. An intermittent stream 8 mi. NW of Corvallis, Oregon near Berry Creek started to flow during the first week of November 1969 and had little surface water by the middle of April 1970. Mature larvae dig pupal chambers beneath rocks in the stream bed as it dries up. Other larvae dig deep into the stream bed and make a cell in which they pass the dry months. Adults have been collected along permanent streams and it is assumed that larvae occur there also. Adults emerged from pupal cells in the laboratory in the evening and are
active only during the night. Eggs are laid on objects overhanging the larval habitat; when the larvae hatch, they crawl into the crevices in the dry stream bed and form small cells or they fall into the water.

From the rearing data for *N. californicus*, an estimate for the length of the life cycle of *P. spenceri* in two intermittent streams can be made. It is estimated to be five years from the larval head capsule width frequencies. Head capsule width frequencies from larvae collected at Berry Creek, 9 mi. NW Corvallis and 3.5 mi. E. Crabtree, Oregon, during November and December, 1969, are given in Figure 32. At the latter location, the larvae of *N. californicus* were also collected, but only in areas where leaves and detritus were largely absent. It is assumed that larvae of *P. spenceri* could also mature in two years in a permanent stream much as those of *Neohermes*.

*Protochauliodes aridus* Maddux (Figures 104-106, 109, 110, 117)


Similar in size and shape to other members of the genus in North America, body dark reddish brown, wings grayish.

Male - Claspers twice as wide at base as at apex (Figure 104); aedeagus flattened in lateral view, in dorsal view, widely notched
Figure 32. Estimated year classes of Protocauhuliodes spenceri Munroe from larval head capsule widths (mm). Collected in intermittent streams at Berry Creek, 9 mi. NW of Corvallis, and 3.5 mi. E of Crabtree, Oregon during November and December, 1969.
apically, lateral expansions wider basally, gradually narrowing apically (Figure 105).

**Female** - Similar to other females in genus with grayish wings.

**Larvae** (Figure 109) - 35-50 mm long, body brownish yellow.

**Head** - patterned orange and dark gray; mandibles dark brown apically, lighter basally, stemmata, as in Figure 110. **Thorax** - patterned dorsally in same colors as head. **Abdomen** - clothed with fine setae, lateral margins lighter than dorsum or venter, venter patterned like *N. californicus*; spiracles as in *P. spenceri*.

**Eggs** - single layered in masses of 2000-3000.

**Type** - Male - Neal Road, 7 mi. SE Chico, Butte Co., California. Reared from larvae, 15 May, 1951 (D. Maddux). California Academy of Science, San Francisco, California. During this study, 14 males, 3 females, 3 pupae and 14 larvae were examined, including 3 males reared by Maddux. Seven of these adults were reared by me.

**Distribution** - Western foothills of Sierra Nevada Mountains from Butte to Mariposa County, California (Figure 117).

**Adults** - California: Butte Co.: Chico; Oroville; Bidwell Park, Chico; Humlin Slough; 1/2 mi. below Salmon Hole, Bidwell Park, Chico; Neal Rd. nr. dump, S. Chico. Calaveras Co.: Arnold. Mariposa Co.: Miami Ranger Station. Tuolumne Co.: Twain Haste.

**Larvae** - California: Butte Co.: Bidwell Park, Chico; 4 mi. N.
Chico, Neal Rd. nr. dump, S. Chico.

Adults have been collected from May to August. In the Chico area peak emergences occur in late May and early June.

**Biology** - The larvae of *P. aridus* are found in intermittent streams with a hard rocky substrate in areas where the current flows gently among the rocks. I have collected the larvae of *N. californicus* in the same streams where the rocks were larger, looser in the substrate and in the deeper and faster parts of the stream. Maddux (1952) found the pupal stage to be about 11 days but this was prolonged to 40 days when the pupae were kept at 4°C. Adults were maintained for 7-10 days in the laboratory and virgin females oviposited. An egg mass found in the field was reported by Maddux (1952) to be 250 mm by 500 mm, but this should be 25 mm by 50 mm. This mass contained about 3000 eggs and was laid on the underside of a large rock in a dry stream bed. Eggs measured 1 mm by 0.3 mm. Newly hatched larvae crawled into the crevices of the stream bed. Penland (1953) found that egg masses hatched in the field in 7-10 days and the larvae burrowed into the substrate 4-12 inches and built small cells in which they await the fall rains. He also reared newly hatched larvae by keeping them in damp soil and feeding them termites, showing that estivation is not obligatory. The life cycle of this species closely parallels that of *N. californicus* and *P. spenceri*.

I observed the precopulatory behavior of a female during this
study. On two occasions, larvae were reared to adults but only females survived or males were not available when the females emerged. *P. aridus* females differed in precopulatory behavior from females of *N. californicus* by bending their abdomens at almost a right angle to their thorax and wriggling the upthrust abdomen. In *N. californicus*, only the posterior half of the abdomen is curved upward and held motionless.

**Protochauliodes montivagus** Chandler
(Figures 102, 103, 117)


Similar in size and shape to other members of genus in North America, body dark reddish brown, wings grayish with spots more intense than other species.

**Male** - Claspers short, stubby, as wide apically as basally, slightly constricted medially, indented apically (Figure 102). Aedeagus flattened in lateral view, in dorsal view broadly notched apically, lateral margins almost parallel (Figure 103).

**Female** - Similar to other females in genus with grayish wings.

**Larvae** - Similar to *P. spenceri* but distinguished by the lateral filaments being longer than the width of the abdomen on all segments.

The larva of this species was not reared and is described from
a poorly preserved specimen collected in a small stream 3 mi. S. Child's Meadows, Hwy. 39, 19 June 1967, Tehama County, California (T. Yamamoto). This is within the known range of this species and the larvae of the other coryalid species known to occur there can be identified. During this study, ten males and four females were examined, including two paratypes.

**Type** - Male - St. Charles Hill, Sierra County, California, 7 July 1921 (E. H. Nast). California Academy of Science, San Francisco, California.

**Distribution** - Known from the Sierra Nevada Mountains of California above 4000 feet elevation.


Adults have been collected from July to September.


**Biology** - The larvae mentioned above were collected in a small permanent stream.

Protochauliodes cascadius sp. n. (Figures 98-101, 117)

**Male** - wings and body similar to *P. spenceri*, alar expanse 67
mm; genitalia short, stubby, less than twice as long as broad, convex
dorsally and ventrally, indented apically (Figure 98); aedeagus
flattened in lateral view, in dorsal view, narrowly notched apically,
markedly expanded laterally to about mid-point and sharply con-
stricted basally (Figure 99).

Female - Similar to other females of genus in North America;
alar expanse 81 mm.

Larvae - unknown.

Type - Male - ca. 8 mi. W. Mill City, along Little Santiam
R., Marion Co., Oregon, 26 July 1963 (S. Jewett). California
Academy of Science, San Francisco, California.

Allotype - Female - same as holotype.

Three paratypes from Oregon as follows: Male - Silver Ck.
Falls State Park, Marion Co.; 22 May, 1957 (S. Jewett). United
States National Museum, Washington D.C. Male - 40 mi. E. Eugene,
30 July, 1965 (Ken Goeden). Oregon State University Entomological
Collection, Corvallis, Oregon. Male - 4 mi. S. McKenzie Bridge,
Horse Ck., Lane Co. (J. Bedea). E. D. Evans collection.

Distribution - Cascade Mountains of Oregon (Figure 117).

Adults - Date and localities as above.

Biology - The adults have been collected along permanent
streams. The microhabitat of the larvae is unknown.
DISCUSSION AND CONCLUSIONS

This study of the corydalids has shown that the larvae of different species have different microhabitats. The adults were found to differ in mating and oviposition. Morphological studies of the adults and larvae have resolved many taxonomic uncertainties, and have also shown relationships that indicate a possible evolutionary sequence.

Ecological Segregation of Species

The Corydalinae as a group are tropical and sub-tropical in distribution. *C. cognatus*, the only representative in the study area, is found in rocky riffles of warm permanent streams and rivers. The Chauliodinae, however, are a group with a temperate climate world distribution and the larvae select a variety of habitats. Those found in the study area were found in colder or smaller streams or in streams with a highly variable flow.

The species of Chauliodinae found in the study are exhibit a cold-warm water dichotomy. Among the known larvae, *O. crepusculus*, *P. montivagus*, *D. ingens* and *D. disjunctus* are found in cold water habitats. As *P. cascadius* has been collected only in mountainous areas it is assumed to also be a cold water species (water temperatures seldom exceeding 20°C). *O. crepusculus* is most
frequently found in headwater streams and rivers in areas where detritus collects in the current around rocks. *Dysmicothermes*, while sometimes collected with *O. crepusculus*, is found most frequently in small creeks among rocks and detritus. The larvae of *P. montivagus* were collected in a small cold stream in an open woodland. This single collection is not a sufficient basis for further discussion of the species.

The warm water species are segregated on the basis of substrate and duration of stream flow. Near Crabtree, Oregon, *P. spenceri* and *N. californicus* exist in two small connected intermittent roadside streams. In the tributary that flows 3-4 weeks longer, the substrate was firm gravel with larger rocks. Only larvae of *N. californicus* were found there. In the other stream, where the substrate contained more clay and was softer and had more leaves trapped among the rocks, larvae of *P. spenceri* were found almost exclusively. I have also collected *P. spenceri* in a stream in Novato, California, with *N. filicornis*. The substrate in this stream was also clay and I presume a similar segregating mechanism was in effect.

I have collected *N. californicus* and *P. aridus* in the same streams in the vicinity of Chico, California. In these streams, *P. aridus* was found in areas where the water was shallow and moved slowly among the rocks. *N. californicus* was found in deeper and
faster water. In some streams which were probably the first to dry up in the spring, I only found *P. aridus*.

As the larvae of *P. minimus* and *P. simplus* have not been collected, I can only conjecture as to how the various species of larvae are separated. At Tanbark Flat, Los Angeles County, California, where the type series of *P. simplus* was collected, I found only the larvae of *N. filicornis* in the only small stream in the vicinity. On several occasions I have collected adults of *P. simplus* along permanent streams. The larvae of this species may be found in areas of soft substrate and gravel much like the related *P. spenceri* and thus be separated from *N. filicornis* and *N. californicus* which occur in areas of harder substrate and rocks. The adults of *P. minimus* have usually been collected near permanent foothill streams surrounding the Sacramento River basin. If the larvae are assumed to live in these streams, which seems likely, this would separate the larvae of *P. minimus* from those of *Neohermes, P. aridus* and *P. spenceri* which are usually found in intermittent situations. From my collecting experience and field observations, it seems that temperature, substrate, current, stream size and duration of stream flow are the isolating mechanisms among the corydalid larvae. More intensive collecting for larvae in streams by which adults of *P. montivagus, P. simplus, P. minimus* and *P. cascadia* have been found should further clarify how the larvae of related species
are separated.

**Relationships of the Corydalidae**

The relationships proposed for the corydalids in the study area and for the world genera of the Chauliodinae are based on wing venation, similarity of male genitalia and distribution, supplemented by characters of the larvae and adult mating behavior where possible.

Wing venation is of primary importance in determining the main phylogentic sequences at or above the generic level. Taxa with wing venation more closely resembling the hypothetical primitive wing of Mackerras (1970) are considered to be more primitive. The two subfamilies have been shown to be distinct groups on the basis of male genitalia and wing venation. Reik (1970) suggests they are different enough to be families. On the basis of wing venation and male genitalia, the Corydalinae have the most primitive genera. In *Neoneuromus* Weele, the most primitive genus, the media has six branches reaching the wing margin in both pair of wings. *Protohermes* Weele has this character in the hind wings. The most primitive genus in the Chauliodinae, *Dysmicohermes*, has the media of the hind wing with four branches and the fore wing with two branches. Weele (1910) concluded that the Corydalinae were the most primitive on the basis of the complex male genitalia and then stated that *Neuromus* and *Chloronia* were the most primitive genera because the male genitalia
were the least complicated.

Changes in wing venation result from addition of new secondary veins for further stiffening of the wings or veins are lost due to atrophy or fusion. Additional veins commonly occur in the Corydalinae, especially in larger specimens. Weeke (1910) found the veins so variable that he concluded they were of little value, at least in Corydalis. The addition of longitudinal veins in the wings of the Chauliodinae must be rare as it has not been noted in the literature nor have I observed it. In the Chauliodinae, the presence or absence of the primary wing veins and the fashion in which they branch or fuse is the basis for the present proposed phylogeny. Changes in the larger veins in the anterior portion of the wings are considered to be more important than in an evolutionary sense, than those in the posterior portion of the wings because changes in this aerodynamically important region would probably have more effect on the ability of the insect to fly. Venation changes in the anal veins of the forewing are also important as they strengthen the jugum. The veins of the radius and media serve as the main phylogentic markers and are sometimes generically distinct as in the four genera in the study area. The anal veins of the forewing usually place a genus in a generic group. Anachauliodes Kimmins is the only genus with the 1A of the forewing three or four-branched.

The most primitive genera of the Chauliodinae have the
posterior branch of the Rs forked in both wings and the anterior
branch of the media in the hind wing with two branches. The genera
with these characters are known only from the study area. Dysmico-
hermes, the most primitive genus, has the media of the hind wing
four-branched. Orohermes has the media of the hind wing three-
branched. The remaining Chauliodinae have the posterior branch of
the Rs simple and the media either two- or three-branched in the
hind wing. The two most primitive genera of this remaining group
are also found in the study area. Protochauliodes and Neohermes
have the media in the hind wing three-branched while the remaining
nine genera have the media of the hind wing two-branched. Neo-
hermes is a transcontinental North American genus while Proto-
chauliodes is found in Chile, Australia and the study area. The
occurrence of the four most primitive genera in one area suggests
that evolution may have proceeded slowly in western North America.

The remaining Chauliodinae are separated into genera or groups
of genera on the basis of the anal veins. Taenochauliodes Ebsen-
Petersen of South Africa has the anterior branch of 2A in the forewing
partly fused with 1A, as in Protochauliodes and Neohermes, and
represents the most evolved form in the subfamily. In the remaining
genera, 2A is connected to 1A by a crossvein. Anachauliodes
Kimmins has 1A with three or four branches in the forewing and is
distinct from the other Chauliodinae in this respect. Platychauliodes
Ebsen-Petersen from South Africa and Madagascar and Ctenochauliodes Weele from Asia have 2A sessile in the forewings. Archichauliodes Weele from New Zealand, Australia and Chile, Chauliodes Latrielle and Nigronia Banks from the eastern United States, and Parachauliodes Weele and Neochauliodes Weele of Asia, all have 2A stalked from the anal cell in the forewing. The suggested relationships of the world Chauliodinae based chiefly on wing venation are shown in Figure 121.

Two other evolutionary schemes have been proposed for the Chauliodinae and are described below. Weele (1910) thought Archichauliodes was the most primitive genus and was closely related to Protochauliodes and Neohermes. Chauliodes and Parachauliodes were also closely related to Protochauliodes. Parachauliodes was thought to be the ancestral form of Neochauliodes. Ctenochauliodes was derived from the latter and Nigronia was the most evolved genus. The basis for this phylogenetic scheme was not given. Munroe (1951), using the anal veins of the forewing as the basis for a phylogenetic scheme, thought that Protochauliodes and Neohermes were the primitive taxa and were ancestral and that Archichauliodes, Chauliodes, Parachauliodes, Neochauliodes and Nigronia, in this sequence, represented the phylogenetic progression in the group. Because the second branch of 2A arises separately from the anal cell in the Protochauliode and Neohermes as well as
in the Corydalinae he suggested that Protochauliodes may be the ancestral form of the Corydalidae. Munroe (1954) supported his previous phylogenetic scheme while describing Dysmicothermes, the most primitive genus in the Chauliodinae, which also has the second branch of 2A arising separately from the anal cell. My studies substantiate the relationships proposed in these two previous studies in the sequence of genera from Archichauliodes to Nigronia and also the close relationship between Protochauliodes and Neohermes. The relationships between the other genera are not supported by this study. The conclusions reached by Weele (1910) apparently resulted from a lack of wing venation analysis. Munroe (1951) did not consider venation patterns in the anterior portions of the forewing or the venation of the hind wings. The phylogenetic scheme proposed here has incorporated a more complete analysis of wing venation.

The larvae of Corydalidae have evolved along two main lines. In the Corydalinae of the tropics and subtropics, ventral abdominal gill tufts have evolved on the first seven segments and there is little modification of the spiracles which are large and located above the base of the lateral filaments.

The larvae of the Chauliodinae which form the second evolutionary line, are better known than the Corydalinae. The larvae have the posterior abdominal spiracles highly modified in some species and are situated on long tubes in Chauliodes. The larvae of
the primitive genus *Dysmicothermes*, of the Chauliodinae, resemble the larvae of *Corydalus* in having the gena sharply angulate posteriorly, the spiracles of the abdomen and meso-thorax large and approximately equal in size and the lateral filaments short. *Orohermes crepusculus* has a multi-layered egg mass as does *Corydalus*. These characters, in addition to those given in the discussion on wing venation, further substantiate the proposed phylogeny of the Corydalidae.

The larvae of the Chauliodinae have lost or did not evolve ventral gill tufts. This may have resulted because the larvae of this group live in temperate climates where high stream temperatures and low oxygen tensions would not exist for extended periods of the year. Gill tufts would be a disadvantage to those species living in intermittent situations as water loss through these surfaces may be critical during extended dry conditions.

Modification of larval spiracles is related to the habitat. With the exception of the cold stream form, *O. crepusculus*, all the known larvae of the Chauliodinae have the spiracles on the posterior margin of the eighth abdominal segment. It is assumed these spiracles are functional. All observed species possessing this type of spiracle have been noted with the posterior part of the abdomen out of the water during period of oxygen stress. *O. crepusculus* and *C. cognatus* held their heads out of the water under the same conditions. These
spiracles may be slightly elevated above the surface of the abdomen on a short broad conical projection such as those found in *Proto-
chauliodes* and *Neohermes* or on short tubular projections as in *Dysmicohaeremes*, *Nigronia* and *Archichauliodes* or on elongate flexible tubes like those found in *Chauliodes*. This last genus is usually found in swamps, marshes, lakes or the backwaters of streams. The other genera mentioned are stream forms. Functional dorsal spiracles permit the larvae to utilize atmospheric oxygen during periods of low oxygen tensions in the water. Smith (1970) concluded that this may have represented a primitive type of respiratory behavior antecedent to the more complex spiracular modifications now evident. The lack of modification and atrophy of the posterior spiracles of *O. crepusculus* is probably the result of living in cool, permanent streams where low oxygen tension would seldom develop.

The genitalia of the males offer additional clues to some of the phylogeny of the Corydalidae. The female genitalia of both sub-families are similar and do not show as much variation as the male genitalia. The more primitive genera of the Corydalinae have a comparatively complex genitalia with two pairs of claspers, the lower of which is segmented, a circular raised area between their bases, a transverse aedeagal bar and a pair of lateral pre-genital scent glands between segments VIII and XI. The males of Chauliodinae have a more simplified type of genitalia, having but a single short pair of
claspers with a basal raised area. This single pair of claspers has resulted from a fusion of the dorsal and ventral pair. This is most discernible in **Dysmicohermes** where the claspers are only fused basally. The aedeagi of the Chauliodinae is more evolved and in most cases is a single fused solid structure. This has probably resulted from the fusion of highly developed aedeagal papillae of the transverse aedeagal bar. This fusion is not complete in **Dysmicohermes** and only partially complete basally in **O. crepusculus**. These two genera also have scent glands but they are extensible tubes located at the base of the claspers.

The mating behavior is different between the two subfamilies of the Corydalidae. The observations of **Corydalus** suggest that the Corydalinae have evolved a mating behavior where the female plays a rather inactive pre-copulatory role and the male is active and produces a strong scent. Mating also occurs in a side to side position which may be an adaptation to the large size of these insects. In the Chauliodinae, the female plays an active pre-copulatory role and copulation is effected by the male crawling beneath the female and then assuming an end to end position. This may not be the case with **Dysmicohermes** and **O. crepusculus** as these large insects have scent glands in the males and they may exhibit a mating behavior similar to the Corydalinae. On the basis of wing venation, larvae, structure of the egg masses and the genitalia, **Dysmicohermes** and
O. crepusculus form a primitive and distinct group of the Chauliodinae and probably could be placed in a separate tribe.

Relationships of the Corydalidae in the Pacific Coastal Region

According to Riek (1970), the Megaloptera were a recognizable group in the Permian Period 230 million years ago. The ancestral forms of the present species in the study area are assumed to have been present before the breakup of Pangaea as proposed by Wegener (1924). Engeln and Caster (1952) show that the west coast of the United States was repeatedly divided into isolated areas, ultimately to be rejoined in its present form. During the late Cenozoic Era, when the mountains of the western United States were evolving, this area was divided into a northern coastal area from Washington to Alaska, a central area in the Sierra Nevada and Siskiyou Mountains of California and a southern area in Baja, Mexico. These divisions could have resulted in isolating ancestral populations that resulted in speciation. Based on distribution and the male genitalia, the ancestral Neohermes in the area would have been divided into a central and a southern population giving rise to N. californicus in the northern region and N. filicornis in the southern region. The ancestral forms of the three closely related valley species of Protochaulides, P. spenceri, P. simplus and P. minimus, would have divided into three
groups with *P. spenceri* arising in the northern region, *P. simplus* in the southern region and *P. minimus* in the central region with *P. aridus*. The sialids of the coastal *californica* group probably evolved in a similar fashion, with *S. californica* and *S. rotunda* in the northern region, *S. occidens* and *S. nevadensis* in the central region and *S. arvalis* in the southern region. The ancestral mountain forms of *Dysmicohoeremse*, *P. montivagus* and *P. cascadius* would have been separated into a northern group and a central group. *D. ingens*, *P. montivagus* evolved with *S. occidens* and *S. nevadensis* in the central group and *D. disjunctus*, *P. cascadia* with *S. californica* and *S. rotunda* in the northern group. *Orohermes crepusculus* does not fall into this pattern but it may be reasonable to assume that it existed in the central region where it still exists. The location of *C. cognatus* during this period is uncertain. This proposed phylogeny is shown in Figure 122.

**World Distribution of the Chauliodinae**

The disjunct world distribution of *Archichauliodes* (Chile, New Zealand and Australia) and *Protochauliodes* (Chile, Australia and the western United States), and the close relationships between genera in Asia and North America, Asia and South Africa and North America and South America as shown in the phylogenetic scheme (Figure 121) can best be explained in view of the theory of continental
drift. Wegener (1924) proposed the idea of Pangaea ("all lands") which has since been widely discussed and recently reviewed by Dietz and Holden (1970) and Dott and Batten (1971). There seems to be little doubt that the continents were once joined to each other and have since moved apart. This original land mass is usually referred to as Pangaea. Only Antarctica remains in the same approximate geographical location while the other continents have moved northward. The following explanation of how the ancestral forms of the Chauliodinae became separated should only be considered a working hypothesis for further research.

Riek (1970) shows that two families of Megaloptera were evolved by late Permian. Carpenter (1943) figures a wing of the earliest unquestionable corydalid which is from Oligocene Baltic Amber. It is assumed that the ancestral stocks of the Corydalidae and Sialidae were well developed before Pangaea began to separate into Laurasia and Gondwana 200 million years ago. At this time, the ancestral Protochauliodes may have been divided into two populations, one on the western margin of Laurasia and another on the western coast of Gondwana which was continuous with what would later become Australia. The ancestral form of the related genera Archichauliodes and Chauliodes may have also been separated during this time.

By the end of the Triassic period 180 million years ago, Gondwana had become separated into three large land masses, South
America-Africa, Antarctica-Australia, and India. South America, however, remained close to Antarctica-Australia. The climate during the 130 million years of the Cretaceous was warm and equable throughout the world (Engeln and Caster, 1952). This would have allowed further dispersal to occur into developing habitats. The ancestral forms of the closely related Ctenochauliodes and Platychauliodes may have also been separated in the Triassic, the former on the continent of India and the latter in Africa and Madagascar.

At the end of the Jurassic, 135 million years ago, North America began to move westward and separate from Europe and Asia, isolating the ancestral Nigronia from the related ancestral forms of Neochauliodes and Parachauliodes of Eurasia. The ancestral Orohermes, Neohermes, and Dysmicohermes of North America also may have been separated from Eurasian stock. Sixty million years later, at the close of the Cretaceous, South America was widely separated from Africa but still very near Antarctica-Australia. Madagascar was separated from eastern Africa and India had not reached Asia at this time. Protochauliodes and Archichauliodes were on the continents of South America and Antarctica-Australia. Taenochauliodes was divided into a population in Africa and another in Madagascar. In the 65 million years since the Cretaceous, India continued to move north and collided with Asia, Australia separated from Antarctica and moved northward while North America continued
to move westward and separated from Greenland and Europe. Also, during this time, an isthmus joined North and South America.

Munroe (1951) stated that the North American genera, *Chauliodes* and *Nigronia*, both arrived in eastern North America via the Bering Strait. His phylogenetic scheme indicates *Chauliodes* and *Archichauliodes* to be more closely related. The latter has a South American, New Zealand and Australian distribution. The nearest relatives to *Nigronia*, *Neochauliodes* and *Parachauliodes* are in Asia. The phylogenetic and distributional scheme proposed in this study is more consistent with the morphological data and continental drift in the case of *Chauliodes* and *Archichauliodes*. *Nigronia* may have arrived via the Bering Strait but this seems doubtful because of the limiting factors given below and the absence of other close Asian-North American relationships in the order as a whole. The sialids I have examined from eastern Asia and Europe and the figures of the male genitalia given by Nakahara (1915) and Klingstedt (1931) show that the relationship between the species of *Sialis* in Asia and North America are not as close as those between Europe and North America. This evidence in addition to the biological limitations given below, tends to cast some doubt on the dispersal ideas of Munroe (1951) regarding *Nigronia* and *Chauliodes*.

Following the same sequence of events as for the Chauliodinae, a working hypothesis for the present world distribution may be
proposed for the Sialidae. The ancestral Sialis became isolated on Laurasia and was eventually divided into a North American and European population. Riek (1970) states that the other four known genera are closely related. On the basis of having similar wing venation, Indosialis, Austrosialis and Protosialis are more closely related, while Leptosialis is a more evolved form. The ancestral forms of these genera were present on Gondwana and as the breakup of this super continent continued these forms probably evolved into the four genera as we know them.

Biological factors which have been discussed previously that would largely negate distribution of Megaloptera across oceans since the present continents became separate land masses are: (1) The short-lived adult forms are large insects and weak flyers and could not be dispersed easily by flight or by winds to suitable habitats. (2) Cold temperatures impede egg development until freezing temperatures could kill them. (3) Eggs that could be removed from oviposition sites by animals and carried to a suitable habitat must not be wet or fungus will kill the embryo. (4) Larvae are unable to live in salt water for extended periods. (5) Many corydalids and all the known sialid larvae are restricted to permanent fresh water habitats.

The conclusions reached as to the distribution of those genera mentioned above and the mechanism for explaining this distribution have in part been reached previously by other investigators. Based
on the evidence of their systematic studies, Illies (1965 - Plecoptera-Oripopterygidae), and Brundin (1967 - Diptera-Chironomidae) have assumed that the austral disjunct distributions of the groups investigated could best be explained by continental drift. Future investigations of other groups of animals may also find their distribution and evolution best explained in light of the theory of continental drift.
Figures 33-42. Corydalus wings, male genitalia and egg burster.

33. Wings of _C. cognatus_ Hagen
34-37. Male genitalia of _C. cornutus_ (Linn.)
   34. lateral view
   35. dorsal view
   36. ventral view
   37. aedeagus-dorsal view
38. Lateral view of female genitalia of _C. cognatus_
39-42. Male genitalia of _C. cognatus_
   39. lateral view
   40. dorsal view
   41. ventral view
   42. aedeagus-dorsal view
Figures 43-49. Corydalus egg bursters, aedeagi and habitat.

43. Dorsal view of mature embryo of \textit{C. cornutus} (Linn.) with egg burster in place.

44. Larval habitat of \textit{C. cognatus} Hagen.

45. Lateral view of mature embryo of \textit{C. cornutus} with egg burster in place.

46-47. Egg bursters of \textit{C. cornutus}.

48-49. Variations of aedeagi of \textit{Corydalus}. 
Figures 50-57. Wings, genitalia and habitat of Dysmicohermes.

50. Wings of *D. ingens* Chandler.

51-52. Male genitalia of *D. ingens*
   51. lateral view
   52. ventral view

53. Lateral view of the female genitalia of *D. ingens*.

54-55. Male genitalia of *D. disjunctus* (Walker).
   54. lateral view with fleshy protrusion
   55. ventral view

56. Lateral view of the female genitalia of *D. disjunctus*.

57. Larval habitat of *Dysmicohermes*. 
Figures 58-60. Larva of *Dysmicohermes disjunctus* (Walker).

58. Dorsal
59. Vestiture and spiracle
60. Stemmata
Figures 61-63. Larva of *Dysmicothermes ingens* Chandler.

61. Dorsal
62. Vestiture and spiracle
63. Stemmata
Figures 64-72. *Orohermes crepusculus* (Chandler).

64. Wings.
   65. lateral view
   66. ventral view with lateral protrusions
67. Female genitalia, lateral view.
68. Mature embryo with egg burster in position.
69-70. Egg burster.
71. Egg mass.
72. Habitat.
Figures 73-74. Larva of *Orohermes crepusculus* (Chandler).

73. Dorsal view
74. Stemmata
Figures 75-83. *Neohermes*.

75. Wings of *N. californicus* (Walker).
76-77. *N. filicornis* (Banks).
  76. Male genital clasper
  77. Lateral view of female genitalia
78-83. *N. californicus*.
  78. Male genital clasper
  79. Lateral view of female genitalia
  80. Larvae with wing pads
  81-82. Egg bursters
  83. Egg mass
Figures 84-85. Larva of *Neohermes californicus* (Walker).

84. Dorsal
85. Ventral
Figures 86-87. Larva of *Neohermes filicornis* (Banks).

86. Dorsal
87. Ventral
Figures 88-97. Wings of Protochauliodes and male genitalia.

88. Wings of Protochauliodes.
89-90. P. simplus Chandler.
  89. Lateral view of genitalia
  90. Aedeagus-dorsal view
91-94. P. spenceri Munroe.
  91. Lateral view of genitalia
  92. Clasper variant
  93. Aedeagus-dorsal view
  94. Aedeagus-lateral view
95-97. P. minimus (Davis).
  95. Lateral view of genitalia
  96. Clasper variant
  97. Aedeagus-dorsal view
Figures 98-106. Male genitalia of *Protochauliodes*.

98-101. *P. cascadus* n. sp.
98. Lateral view of genitalia
99. Aedeagus-dorsal view
100. Clasper-dorsal view
101. Clasper-ventral view

102-103. *P. montivagus* Chandler.
102. Lateral view of genitalia
103. Aedeagus-dorsal view

104-106. *P. aridus* Maddux.
104. Lateral view of genitalia
105. Aedeagus-dorsal view
106. Clasper-dorsal view
Figures 107-111. Larvae and female of *Protochauliodes*.

   107. larva
   108. stemmata

   109. larva
   110. stemmata

111. Lateral view of female genitalia of *Protochauliodes*. 
Figures 112-115. Habitats of Protochauliodes and Neohermes.

112. Habitat of \textit{P. spenceri} Munroe and \textit{N. californicus} (Walker).
113. Habitat of \textit{P. aridus} Maddux and \textit{N. californicus}.
114. Habitat of \textit{N. californicus}.
115. Permanent stream habitat of \textit{N. filicornis} (Banks).
Figure 116. Distribution of *Corydalus cognatus* Hagen.
Figure 117. Distribution of *Protochauliodes aridus* Maddux, *P. montivagus* Chandler and *P. cascadius* n. sp.

Figure 118. Distribution of *Protochauliodes minimus* (Davis), *P. simplus* Chandler and *P. spenceri* Munroe.
Figure 119. Distribution of Neohermes filicornis (Banks), N. californicus (Walker) and Orohermes crepusculus (Chandler).

Figure 120. Distribution of Dysmicohermes ingens Chandler and D. disjunctus (Walker).
Ancestral Corydalinae

Tropical; 20 or more veins reaching wing margins posterior to R1, M 3-6 branched forewing; male genitalia with two pairs claspers and pre-genital lateral scent glands; larvae with ventral abdominal gill tufts.

M in hindwing 2 branched

Forewing with anterior branch 2A connected by a crossvein

1A forewing 3 or 4 branched

Anachauliodes Asia

Taenochauliodes S. Africa

2A sessile in forewing

Platychauliodes S. Africa & Madagascar

Ctenochauliodes Asia

Ancestral Corydalidae

Posterior branch Rs simple in both wings

Forewing with anterior branch 2A partly fused with 1A

Ancestral Chaulioidinae

Temperate; 20 or fewer veins reaching wing margins posterior to R1, M forewing 2 branched; male genitalia with one pair claspers; larvae without ventral abdominal gill tufts.

Posterior branch Rs forked in both wings

Hindwing with M 3 branched

Hindwing with M 4 branched

Dysmicothermes W. U. S.

Orohermes W. U. S.

Ctenochauliodes Asia

Crossvein between R3 & R4 in forewing

Dysmicothermes W. U. S.

Neohermes U. S.

Neohermes U. S.

Crossvein lacking between R3 & R4 in forewing

Protochauliodes W. U. S., Chile, Australia

Figure 121. The relationships of the world Chaulioidinae based chiefly on wing venation, and supplemented by male genital characters, larvae and distribution.
Figure 122. Relationships of the Corydalidae of the Pacific Coastal Region of the United States. Based on wing venation, male genital characters, larval habitats and distribution.
Figure 123. Hypothesized distribution of the Megaloptera of the Pacific Coastal Region of the United States during the middle Cenozoic Era. Paleogeographic area diagrammatically presented after Caster (1950, in Engln and Caster, 1952).
Figure 124. Travel routes along which collections and observations of the Megaloptera were made from 1967-1970.
PHYSIOLOGY

Temperature tolerance and oxygen consumption were evaluated for the larvae of those species which were readily obtainable to aid in understanding how the larvae are limited in their distribution. The release sites for carbon dioxide were investigated for several species of larvae to ascertain if the corydalids were similar to those reported for the sialids (Thorpe, 1933).

Temperature

Field observations of larval habitats showed that some species were apparently isolated from closely related or competing species on the basis of water temperatures. Larvae to be tested for heat tolerance were acclimated for over a week at 12 and 21°C and tested at temperatures of 35, 33, 30.5, 28.5, and 27°C. From the times at which mortality occurred (see Appendix), an estimated time at which percent of the larvae would have died was calculated by log-probit analysis and are compared in Table 7.

These limited data suggest the following: Of the four species of corydalid larvae used, Orohermes crepusculus was more sensitive than the other three species. This correlates with my field observations that this is a cold water species. The second species, in terms of heat tolerance, is Protochauliodes spenceri. The difference between P. spenceri and Corydalus cognatus is not clear as in three
Table 7. Estimated lethal times for 50% mortality (LT50) for the larvae of some Corydalidae and Sialidae occurring in California, acclimated at 21 and 12°C and exposed to water temperatures of 35, 33, 30.5, 28.5, and 27°C.

<table>
<thead>
<tr>
<th>Species</th>
<th>Acclimated at 12°C</th>
<th>Acclimated at 21°C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Test temp. (°C)</td>
<td>35</td>
</tr>
<tr>
<td>Corydalus cognatus</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3.5</td>
<td>--</td>
</tr>
<tr>
<td>Neohermes californicus</td>
<td></td>
<td>8.5</td>
</tr>
<tr>
<td>Pseudochauliodes spenceri</td>
<td></td>
<td>2.5</td>
</tr>
<tr>
<td>Orohermes crepusculus</td>
<td></td>
<td>1.5</td>
</tr>
<tr>
<td>Sialis rotunda</td>
<td></td>
<td>3.2</td>
</tr>
<tr>
<td>S. nevadensis</td>
<td></td>
<td>1.8</td>
</tr>
<tr>
<td>S. californica</td>
<td></td>
<td>2.5</td>
</tr>
<tr>
<td>S. occidentis</td>
<td></td>
<td>1.8</td>
</tr>
<tr>
<td>S. hamata</td>
<td></td>
<td>1.8</td>
</tr>
</tbody>
</table>

0 = no death
X = 1 death
out of six cases *P. spenceri* exceeded *C. cognatus* in the estimated time for 50 percent mortality. These occurred where the acclimation temperature was 12°C and the test temperatures were 30.5 and 27°C. The other instance was at a test temperature of 27°C with an acclimation temperature of 21°C. In none of these did all the specimens die and all the estimated 50 percent mortality times are over 48 hours. The larvae that died in these instances may have been stressed by other factors, as those of *C. cognatus* had been collected eight months previously in Three Rivers, California and this species is not as easily maintained under the same conditions as the other species. *P. spenceri* prefers cool intermittent or permanent streams while *C. cognatus* is found in warm rivers.

The next most heat tolerant species tested was *C. cognatus*. This species was used in only the first experiment because of the difficulty of obtaining specimens. When compared with the most heat tolerant species in this experiment, *N. californicus*, *C. cognatus* died sooner in all cases except at a test temperature of 35°C and a 21°C acclimation temperature. This species is found in larger warm streams and in one case, in a hot spring where the temperature was 32°C. Except for the one case mentioned above, *N. californicus* lived as long or longer than the other species as indicated from the estimated 50 percent mortality times. In three out of 12 cases, no differences occurred between *N. californicus* and *P. spenceri*. At
acclimation temperatures of 12°C and test temperatures of 30.5 and 27°C, no specimens of either species died. At a test temperature of 28.5°C and an acclimation temperature of 21°C only a single specimen died in each species. As these two species are found in the same intermittent streams in part of their ranges, a similarity of heat tolerance at the lower test temperatures is not surprising. At the higher test temperatures of 35 and 33°C, marked differences are apparent with *N. californicus* being more than twice as tolerant as *P. spenceri* in three out of four cases. This tolerance for higher temperatures in *N. californicus* is reflected in its occurrence in warm intermittent Sierra Nevada Mountain foothill streams.

From this limited data on the heat tolerance of four species of corydalid larvae, some ideas about habitats and distribution may be surmised. First, *O. crepusculus* is not tolerant of high water temperatures for any length of time as a 50 percent mortality occurred first at each test temperature except one and all specimens died during the tests except one at a test temperature of 27°C and an acclimation temperature of 12°C. Secondly, temperature probably plays a role in limiting larval distribution, especially higher temperatures such as those used in these experiments. Lastly, these experiments indicate that this may be a fruitful approach in understanding the distribution and abundance of the corydalids.

The heat tolerance data gathered on five species of *Sialis* are
ambiguous and do not correlate with habitats nor give evidence of species separation. Specimens were of *S. nevadensis* and *S. hamata* were available for only one test. The five larvae of *S. nevadensis* acclimated at 21°C and tested at 27°C were all dead at 13.5 hours but none died at the same test temperature when acclimated at 12°C. The reason for this is unknown. Other than suggesting a great deal of variability in each species to heat tolerance these data indicate a need for further experiments with larger samples which might only show that water temperatures have little to do with the distribution and abundance of sialid larvae.

**Oxygen Consumption**

As temperature tolerance failed to give insight into the distribution and abundance of the species of sialid larvae tested, an experiment was undertaken to ascertain if oxygen consumption could be a factor. Oxygen consumption was considered because it is assumed that the soft substrates in which the larvae are usually found would be places of low oxygen tensions for varying times during the larval instars. It was hypothesized that the larvae usually found in lentic situations would be best suited for this habitat if they consumed lower amounts of oxygen.

Two experiments using a Gilsen respirometer were completed. Six specimens of *S. rotunda* and *S. californicus* were used in the first
experiment and six specimens of *S. occidens* and *S. californicus* in the second experiment. These species were selected because they are closely related morphologically. Three hourly readings of oxygen consumption for each specimen in three runs of three hours, making nine hourly readings, at each temperature were taken. The means for each specimen are given in Tables 8 and 9. These means were compared using a paired t-test and the values for all combinations of species means are given in Table 10 at a probability of .05 with five degrees of freedom. During these experiments larvae were allowed to acclimate at the test temperature for three hours before readings were taken. The highest temperature (26.7°C) was run first followed by 18.3°C and then 10°C, while keeping the same larvae in each chamber.

From the limited data given, the hypothesis that species with lentic larvae would use less oxygen than those with lotic larvae appears to be false. *S. rotunda*, a lentic species, uses more oxygen/g wet wt/hr than *S. californicus*, a lotic and sympatric species. This is most evident when the total means for µl oxygen/g wet wt/hr are considered. Using the average from both experiments for *S. californicus* and comparing it with those of *S. rotunda* as in Table 10, the following differences occur at each temperature: 26.7°C - 143 µl/g wet wt/hr; 18.3°C - 50 µl/g wet wt/hr; 10°C - 39 µl/g wet wt/hr. These differences were also statistically significant in four out of six
Table 8. Mean hourly oxygen consumption values per g wet weight for three experiments of three hours each for *Sialis rotunda* Banks and *S. californica* Banks at 27, 18, and 10°C.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Run</th>
<th><em>S. rotunda</em> µl oxygen/g wet wt/hr</th>
<th><em>S. californica</em> µl oxygen/g wet wt/hr</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>S. rotunda</td>
<td>S. californica</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>27</td>
<td>1</td>
<td>198 233 743 264 196 131</td>
<td>1 173 111 210 347 428</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>178 191 429 271 667 144</td>
<td>132 166 132 166 281 294</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>644 649 603 733 1150 241</td>
<td>165 260 210 215 672 416</td>
</tr>
<tr>
<td></td>
<td>X</td>
<td>340 324 592 422 671 172</td>
<td>97 200 151 197 432 380</td>
</tr>
<tr>
<td>18</td>
<td>1</td>
<td>646 779 294 1157 419 126</td>
<td>40 260 63 345 409 304</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>684 512 127 581 413 567</td>
<td>125 288 84 310 373 241</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>576 135 121 271 283 379</td>
<td>82 231 84 388 179 140</td>
</tr>
<tr>
<td></td>
<td>X</td>
<td>634 474 181 669 371 358</td>
<td>82 259 75 348 319 228</td>
</tr>
<tr>
<td>10</td>
<td>1</td>
<td>198 246 50 157 333 262</td>
<td>75 52 42 172 58 84</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>173 339 50 111 345 278</td>
<td>75 69 54 105 84 55</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>250 530 50 89 333 229</td>
<td>50 45 27 176 255 43</td>
</tr>
<tr>
<td></td>
<td>X</td>
<td>207 372 50 119 337 256</td>
<td>67 55 41 151 132 61</td>
</tr>
</tbody>
</table>
Table 9. Mean hourly oxygen consumption values per g wet weight for three experiments of three hours each for *Sialis occidentes* Ross and *S. californica* Banks at 27, 18, and 10°C.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Run</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
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<tbody>
<tr>
<td>27</td>
<td>1</td>
<td>514</td>
<td>227</td>
<td>373</td>
<td>750</td>
<td>638</td>
<td>401</td>
<td>392</td>
<td>342</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>475</td>
<td>178</td>
<td>401</td>
<td>586</td>
<td>354</td>
<td>413</td>
<td>361</td>
<td>257</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>487</td>
<td>227</td>
<td>421</td>
<td>820</td>
<td>354</td>
<td>449</td>
<td>675</td>
<td>265</td>
</tr>
<tr>
<td>X</td>
<td></td>
<td>492</td>
<td>210</td>
<td>398</td>
<td>718</td>
<td>448</td>
<td>420</td>
<td>474</td>
<td>287</td>
</tr>
<tr>
<td>18</td>
<td>1</td>
<td>151</td>
<td>283</td>
<td>252</td>
<td>395</td>
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<td>287</td>
<td>557</td>
<td>150</td>
</tr>
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<td></td>
<td>2</td>
<td>295</td>
<td>268</td>
<td>269</td>
<td>243</td>
<td>294</td>
<td>275</td>
<td>339</td>
<td>150</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>413</td>
<td>251</td>
<td>297</td>
<td>191</td>
<td>354</td>
<td>257</td>
<td>355</td>
<td>165</td>
</tr>
<tr>
<td>X</td>
<td></td>
<td>285</td>
<td>266</td>
<td>272</td>
<td>276</td>
<td>308</td>
<td>273</td>
<td>416</td>
<td>155</td>
</tr>
<tr>
<td>10</td>
<td>1</td>
<td>168</td>
<td>105</td>
<td>168</td>
<td>91</td>
<td>200</td>
<td>100</td>
<td>100</td>
<td>57</td>
</tr>
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<td></td>
<td>2</td>
<td>156</td>
<td>88</td>
<td>185</td>
<td>54</td>
<td>187</td>
<td>113</td>
<td>122</td>
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<tr>
<td></td>
<td>3</td>
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<td>105</td>
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<td>75</td>
<td>164</td>
<td>131</td>
<td>115</td>
<td>65</td>
</tr>
<tr>
<td>X</td>
<td></td>
<td>156</td>
<td>97</td>
<td>174</td>
<td>72</td>
<td>184</td>
<td>115</td>
<td>111</td>
<td>60</td>
</tr>
</tbody>
</table>
### Table 10

Values calculated by comparing $\mu l \text{O}_2/gm$ wet wt. utilized during nine hours by *S. rotunda*, *S. occidentes* and *S. californica* during two experiments at 26.7, 18.30 and 10°C with five degrees of freedom. Underlined numbers are statistically significant at .05.

<table>
<thead>
<tr>
<th>Test</th>
<th>$26.7^\circ C$</th>
<th>$18.3^\circ C$</th>
<th>$10^\circ C$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>S. occidentes</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>.72 19.5 -- 6.81</td>
<td>2.40 13.4 -- 1.45</td>
<td>2.72 7.3 -- 4.9</td>
</tr>
<tr>
<td></td>
<td><em>S. californica</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>1.49 -- 19.5 5.6</td>
<td>4.9 -- 13.4 .80</td>
<td>5.38 -- 7.3 1.75</td>
</tr>
<tr>
<td></td>
<td><em>S. californica</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>7.56 5.6 6.81 --</td>
<td>7.86 .80 1.45 --</td>
<td>.42 1.75 4.9 --</td>
</tr>
<tr>
<td></td>
<td><em>S. rotunda</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>-- 1.49 .72 7.56</td>
<td>-- 4.9 2.40 7.86</td>
<td>-- 5.38 2.74 .42</td>
</tr>
</tbody>
</table>
Table 11. Total mean oxygen consumption in µl/g wet wt/hr of *Sialis californicus*, *S. occidens* and *S. rotunda* from two experiments at temperatures of 26.7, 18.3 and 10°C.

<table>
<thead>
<tr>
<th>Species</th>
<th>Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>26.7</td>
</tr>
<tr>
<td><em>S. rotunda</em></td>
<td>447</td>
</tr>
<tr>
<td><em>S. californicus</em> I</td>
<td>367</td>
</tr>
<tr>
<td></td>
<td>304</td>
</tr>
<tr>
<td><em>S. californicus</em> II</td>
<td>241</td>
</tr>
<tr>
<td><em>S. occidens</em></td>
<td>418</td>
</tr>
</tbody>
</table>

cases. When *S. rotunda* is compared with *S. occidens*, a species found in lakes and streams of the Sierra Nevada Mountains, little difference in oxygen consumption occurs at 26.7°C. However, *S. occidens* consumes 167 µl/g wet wt/hr more than *S. rotunda* at 18.3°C and 93 µl/g wet wt/hr at 10°C. This higher degree of metabolism at lower temperatures may indicate a more active larvae giving this species some competitive advantage in cold water.

The comparison between those specimens of *S. californicus* used in each experiment shows that a significant statistical difference occurred only at 26.7°C. Because of the small numbers of larvae used, this variability was not unexpected although at 18.3 and 10°C there was no significant difference which is apparent from comparing the total means in Table 10. The same kind of situation exists between *S. californicus* and *S. occidens* as between *S. californicus* and *S.*
rotunda. The differences between the total means of *S. occidens* and *S. californicus* are: 114 μl/g wet wt/hr at 18°F; 217 μl/g wet wt/hr at 18.3°F; and 132 μl/g wet wt/hr at 10°F. In five out of six comparisons, these differences are statistically significant. Perhaps in habitats where sympatry might occur, this relatively low level of activity as judged by its metabolic rate might be disadvantageous, but the extensive range of *S. californicus* in the Pacific Coastal region indicates a rather successful adaptation to a wide range of common situations.

**Carbon Dioxide Diffusion**

Thorpe (1933) has shown that carbon dioxide is lost from the ventral surface of the abdomen and thorax of *S. lutaria* Linn. The release sites of carbon dioxide have not been reported for the corydalid larvae and the following observations were made on five species of corydalid larvae and *S. occidens*. Brom-thymol blue pH indicator was made in an aqueous solution. This indicator is blue at a pH greater than 7 and yellow when the pH is less than 7. If carbon dioxide is dissolved in water, carbonic acid results lowering the pH. The larvae were held with the fingers in a petri dish of indicator. The color change of the indicator was observed with a dissecting microscope by passing light through the solution from beneath. The color change from blue to yellow was visible within a minute indicating a
decrease in pH at active carbon dioxide release sites.

The ventral gill tufts of *C. cognatus* were rhythmically moving during the observations and were the most active sites of carbon dioxide loss. The ventral surface of the abdomen and the less sclerotized areas of the thorax also gave indications of carbon dioxide loss. *N. californicus, O. crepusculus, D. ingens, P. spenceri* and *S. occidens* also lost carbon dioxide from the ventral surfaces of the abdomen and thorax. The intersegmental areas of the abdomen were the most active release sites. The head, legs, and the dorsum of the thorax and abdomen, including the lateral filaments, were areas where carbon dioxide loss was not evident.

**Oxygen Uptake**

Using a flagellate, *Polytoma* sp., as a biological indicator, Thorpe (1933) demonstrated that an oxygen deficit occurs around the lateral filaments of the larvae of *S. lutaria* Linn. In addition, he found larvae lived well for several days and remained active after the lateral abdominal filaments were amputated. All the lateral filaments were functional, the anterior being more so. The venter of the abdomen and second and third thoracic segments around the base of the legs were also sites where an oxygen deficit occurred. Shaw (1955) has shown that the lateral abdominal filaments of *S. lutaria* have a cuticle about 5 µ thick while the abdomen has cuticle 7 µ thick,
suggesting that cuticle thickness may not be a factor in oxygen uptake.

Smith (1970) has assumed the megalopteran larvae have very thin cuticle in the lateral abdominal filaments and states that gaseous exchange undoubtedly takes place across the entire integument but the principle sites of transfer are the lateral filaments. This conclusion is based on the unpublished work of Penland (1953), who boiled water until the oxygen was removed and placed larvae of P. aridus in the water when it cooled. He reported that bubbles formed on lateral abdominal filaments. I repeated this experiment using larvae of P. aridus and N. californicus and no bubbles were observed anywhere on the body even when the larvae were left in the water for half an hour. Why Penland (1954) observed gas bubbles is not certain, but it seems that if oxygen was released into water without oxygen it would dissolve immediately and not be seen as bubbles.

Smith (1970) has stated that the gill tufts of Corydalus probably evolved to meet the oxygen requirements of a large larvae. It was previously hypothesized in this study that the gill tufts evolved to meet oxygen requirements of larvae evolving in warm tropical and subtropical streams. Size is probably not the critical factor for gill tuft evolution as small larvae of the Corydalinae have gill tufts. The evolution of thin elongate lateral filaments would also be a way of efficiently increasing a respiratory surface as in the Chauliodinae and Sialidae. The relationships of the lateral filament surface area to
the remainder of the body are given in Table 12. These were calculated by assuming the body and lateral filaments to be cones. The head and dorsum of the thorax were shown by Thorpe (1933) to be sites of little gaseous exchange so the head length was not included in the body length measurements.

The difference between species in the ratios of body/filament surface area may be unimportant as oxygen uptake efficiency may not be directly correlated with surface area but to the physical nature of the gill. My observations of first instar larvae of _S. rotunda_ have shown that the lateral abdominal filaments have what appear to be fine striae surrounding them. It is uncertain whether this is a plastron or not at this time but all the lateral abdominal filaments of the megalopteran larvae have a spiracle at the base of the filaments which make this hypothesis tenable as spiracles are necessary for their functioning.

Oxygen can also be secured from the atmosphere by some corydalid larvae through the modified spiracles on the dorsum of the eighth abdominal segment. Smith (1970) has observed mature larvae of _N. californicus_ back up to the surface and expose the spiracles. I have observed this same behavior in many sizes and species of *Protochauliodes, Neohermes, Dymphicohermes, Nigronia* and *Chauliodes*. The latter does not expose any part of the body as the spiracles are on long respiratory tubes which break the surface film.
Table 12. Ratios of the body-lateral abdominal filaments surface area of the larvae of some species of *Sialis*, *Dysmicohermes*, *Orohermes*, *Neohermes* and *Protochauliodes* found in the Pacific Coastal Region of the United States.

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<th>Body/lateral abdominal filaments ratio</th>
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*(small specimens)*
Larvae of *C. cognatus* and *O. crepusculus* do not exhibit this type of behavior and do not have spiracles on the meso-posterior of the eighth abdominal segment. *C. cognatus* also moves its ventral gill tufts in a rhythmic fashion when under stress from low oxygen. The abdominal and meso-thoracic spiracles are probably functional when the larvae leave the water to pupate or when buried in the soil.

**Discussion and Conclusions**

While the small amount of data presented on the corydalids are not conclusive, they suggest that temperature does play a role in the distribution and abundance of the larvae. Further research with larger numbers of larvae should more accurately determine the role of temperature in species segregation. The species of *Sialis* used in these temperature experiments are apparently not segregated on the basis of the water temperature of the larval habitat. The data also show that the sialids are more tolerant of temperatures near the upper lethal limits (33 and 30.5°C) than the corydalids. At 35°C both groups are of a similar magnitude of intolerance. The higher temperature tolerance of the sialid larvae is assumed to be an adaptation to their lentic habitats which are usually warmer.

The loss of carbon dioxide in the larvae of the Megaloptera is through the venter of the abdomen and the second and third segments of the thorax. The movement of oxygen into the tracheal system is
not as certain, however. While it is known that oxygen deficits occur around the lateral filaments, this does not conclusively demonstrate that oxygen passes directly through the filament wall into the tracheae. Until further observations with a scanning electron microscope are made, the hypothesis of a plastron is still valid. This seems reasonable in the case of Corydalus, Chlorienella and Dysmicothermes where the lateral abdominal filaments are short, densely setose, and appearing thick like the dorsum of the abdomen. In these cases, the plastron may be nearer the spiracular opening or on the venter.

The lateral abdominal filaments of the Megaloptera are also sensory. Smith (1970) observed N. californicus in containers of water, an unnatural situation, and found that the filaments of alternate segments were held down and the others held up at a slight angle. In streams the filaments of the corydalid larvae are appressed to the substrate and extended from the body at right angles to the body when at rest. The lateral filaments which are usually about as long as, or longer than, the width of the abdomen increases the sensory area of the larvae by a factor of three or more. This is very important for predaceous larvae with poorly developed eyes that live beneath rocks or in the substrate. It aids them in locating prey or other predators, including cannibalistic members of its own species. I have frequently collected larvae which are missing a part of one or
more of their lateral abdominal filaments.

Observations made during feeding also show that the lateral filaments are tactively sensitive. The "tubifex" worms used as food were quickly seized and eaten if contact was made with the lateral filaments. A slight pinch of the filaments with forceps also resulted in a quick biting, thrashing, response by the larvae. These observations also apply to the sialids except that the filaments are all angled upward when held at right angles to the abdomen. When crawling, the gills of *Sialis* lay back along the abdomen but are quickly extended when the larvae stops, even in the soft substrate where it is usually found. These observations show that one important function of the lateral filaments of the abdomen of the Megalopteran larvae is the reception of stimuli.

A number of physiological studies have been carried out using *S. lutaria*. Beadle and Shaw (1950) studied the retention of salt and the regulation of non-protein nitrogen in the blood. Staddon (1955) investigated the excretion and storage of ammonia and Shaw (1955) examined ionic regulation and balance. No similar studies have been published on the Corydalidae. The larvae of this family offer good opportunities for future physiological research because of their varied biologies, large size, toughness, ease of rearing, rather common occurrence and lack of basic knowledge about the physiology of these insects.


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Percent mortality (hrs) occurring in the larvae of some Corydalidae and Sialidae from California acclimated at 12 and 21°C and exposed to water temperatures of 35, 33, 30.5, 28.5 and 27°C.

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### Percent mortality (continued)

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