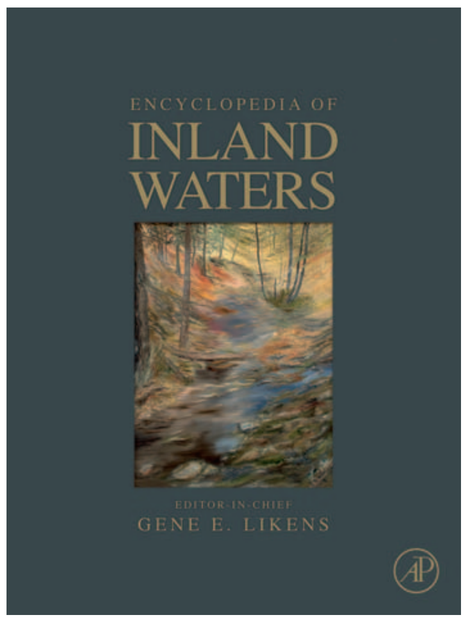

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Megaloptera (Alderflies, Dobsonflies)

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Phylogenetic Relationships

The Order Megaloptera, along with the Raphidioptera and Neuroptera, comprise the superorder Neuropterida. Megalopterans represent an old holometabolous lineage of aquatic insect, with the earliest probable ancestor dating back to the late Permian. The oldest fossil evidence of the group dates to the Tertiary of the old world and Australia. No fossil evidence of the order has been discovered in North America, but several specimens have been identified from Eocene-age Baltic and Dominican amber. There are roughly 275 species identified within the order, grouped into approximately 29 genera and two families (Sialidae and Corydalidae). The Sialidae is represented by just six genera, whereas approximately 23 genera are currently recognized within the Corydalidae. Of the genera, *Sialis*, *Corydalus*, *Protohermes*, and *Archichauliodes* appear the most speciose, having approximately 50, 40, 30, and 20 species identified, respectively. Most genera exhibit a restricted global distribution, occurring primarily within a single biogeographic region (Table 1). The major exceptions to this are the genera *Sialis*, which occurs in the Nearctic, Neotropic, and Palearctic; *Corydalus*, found throughout the Nearctic and Neotropic; and *Protochauliodes*, occurring in the Australian, Nearctic, and Neotropic.

General Identifying Characteristics

The Megaloptera are of a moderate to large size, both as adults and larvae. Larvae might range from 10 to 90 mm whereas adults can be slightly larger and have very long wingspans (up to 180 mm). Larvae are generally flattened dorsoventrally, with chewing mouthparts designed for their predatory lifestyles. The head and thorax are sclerotized whereas the abdomen is unsclerotized. All members have three pairs of jointed walking legs attached to the thorax and no wing pads. Corydalids tend to have dark grey abdomens, devoid of color, and a thorax and head which are tan, brown, or black in color and often have distinct patterns of alternating color. The sialids tend to have lighter-colored abdomens and a yellow, tan, brown, or black head and thorax. The megalopterans possess lateral abdominal filaments (segments 1–8 in Corydalidae and 1–7 in Sialidae). The corydalids have a pair of anal prolegs, each possessing a pair of claws whereas the sialids have a single, caudal filament (Figure 1(a) and 1(b)). Within the Corydalidae, larvae may posses either gill tufts at the base of each lateral abdominal filament (Subfamily Corydalinae) or short respiratory tubules on the dorsum of abdominal segment 8 (Subfamily Chauliodinae). Adults have a folded anal area of the hindwing and the wings are held tent-like over the abdomen when not in flight (Figure 2(a) and 2(b)). In many corydalids, the wings have gray, white, or black blotches, though they might also simply have dark streaking throughout. Males in the Corydalidae (especially *Corydalus* and *Acanthacorydalus*) often possess elongate mandibles used in courtship.

Ecology

Habitats

Larval megalopterans are found in all types of freshwater aquatic habitats, including wetlands, large or small streams and rivers, lakes, and ponds. They have even been documented from habitats as unique as within pitcher plants (*Sarracenia purpurea* L.). The Sialidae tend to be associated more with slower moving waters like pools in streams, wetlands, ponds, and lakes whereas the Corydalidae are more frequently associated with flowing waters like streams and rivers. There are, of course, exceptions. For example, the *Chauliodes* species found in North America tend to occur in ponds rather than streams or rivers. Representatives of the order seem to be missing from extreme habitats, like thermal springs, desert systems, or glacial brooks.

The sialids are most numerous in habitats with organic deposits, such as in stream pools with leaf deposits or wetlands with macrophyte debris. Presumably, these habitats provide abundant food resources and refuge from potential predators. Members of the family also tend to exhibit some tolerance for depressed oxygen levels, as might be found in organic-matter rich substrates with low water velocity or exchange rates. The larvae are mostly nocturnal, remaining within interstitial or organic matter microhabitats throughout the day, but move around more to forage at night. Adults, on the other hand, are generally more active during the day.

The corydalids are generally associated with flowing water, and, like sialids, also are found within the substrate. Species in the family are most common within leaf packs, under stones, or within crevices or

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Table 1 Estimated number of Megaloptera species from world ecoregions

Sialidae	*Ecoregion and (no. species)*	*Corydalidae*	*Ecoregion and (no. species)*
Austrosialis	B(2)	*Acanthacorydalis*	C(7)
Indosialis	C(1)	*Anachauliodes*	C(1)
Leptosialis	A(1)	*Archichauliodes*	B(21)
Nipponosialis	F(2)	*Chauliodes*	D(2)
Sialis	D(24); E(~20); F(4)	*Chloronia*	E(14)
Stenosialis	B(2)	*Chloroniella*	A(1)
		Corydalus	D(3); E(27)
		Ctenochauliodes	C(6)
		Dysmicohermes	D(2)
		Madachauliodes	A(1)
		Neochauliodes	C(18)
		Neohermes	D(5)
		Neoneuromos	C(8); F(1)
		Neoromus	C(4)
		Nigronia	D(2)
		Notochauliodes	E(1)
		Orohermes	D(1)
		Parachauliodes	C(6)
		Platychauliodes	A(6)
		Platyneuromus	E(3)
		Protochauliodes	B(7); D(4); E(4)
		Protohermes	C(42)
		Taeniochauliodes	A(1)

A, Afrotropical; B, Australian; C, Indomalayan; D, Nearctic; E, Neotropical; F, Palearctic.
Compiled from New and Theischinger (1993), Contreras-Ramos (1997), and Nearctica (1998).

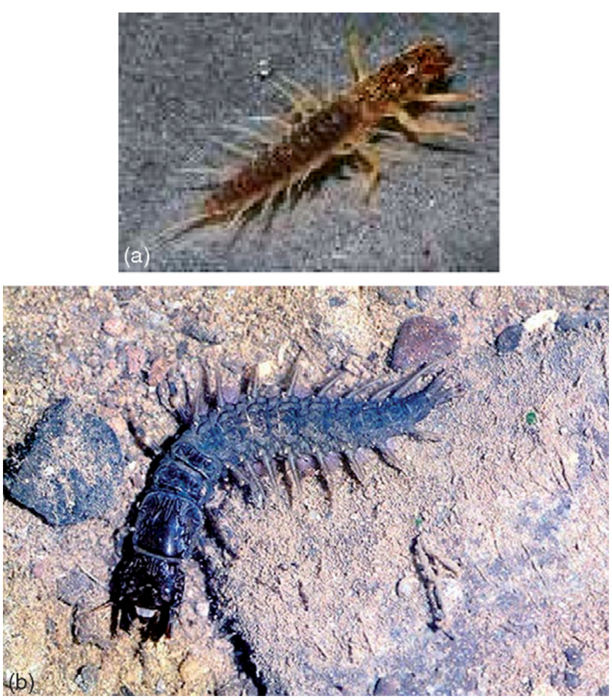

Figure 1 (a) Larval Sialidae and (b) larval Corydalidae.

under the bark of tree debris. Like sialids, they tend to remain under cover during the day, but may move in search of food at night. They may remain in a fixed position under a stone or log for extended periods.

Figure 2 (a) Adult Sialidae and (b) adult Corydalidae.

Both laboratory and field studies have documented some corydalids (e.g., *Protohermes* and *Nigronia*) remaining in the same position for up to 2 weeks or more, presumably as an ambush predator capturing whatever prey came within reach. Larvae are able to swim, though not well. Sialids tend to use lateral undulations and the legs to propel themselves, even if weakly, forward. Both sialids and corydalids perform repeated abdominal flicks to move backward through the water.

Trophic Relationships

All megalopteran larvae are macrophagous predators, consuming their prey whole. They tend to be gape limited, eating whatever they can capture and fit into their mouths. Diets are dominated by smaller invertebrates, especially midges, blackflies, caddisflies, ostracods, mayflies, small crustaceans, and even each other. There is some literature suggesting that captive corydalids will consume carrion.

Foraging by most megalopterans is by active pursuit, although some corydalids have been shown to remain in the same location for extended periods of time. An ambush posture is held by some corydalids, snagging prey as it either drifts past or crawls underneath the body. Due to their large size, and relatively long larval period, corydalids are important predators in many systems. Megalopterans are also important prey for a range of invertebrate and vertebrate predators. Larger invertebrate predators, like dytiscid beetles (*see* **Coleoptera (Beetles) in Aquatic Ecosystems**) or odonates (*see* **Odonata (Dragonflies and Damselflies)**) will prey on small sialids or corydalids. Several fish species are known to consume megalopteran larvae.

In streams of eastern North America, many species spend up to 3 years in the larval stage, prior to leaving the stream for pupation. This long larval period, in addition to a large body size and a predatory foraging habit, make corydalids an attractive host to a variety of ectosymbiotic organisms. The long larval period and large surface area provide ample opportunity for colonization, and the predatory life style (coupled with a large body size) restricts its number of predators. Several stalked ciliates, fungi, protozoans, and insect larvae, most notably larval Diptera, are documented epizooites on the epidermis of fishflies and dobsonflies. Certainly, some of these epizooite occurrences (e.g., stalked ciliates) are chance events since the symbionts are not restricted to the dermis of corydalids, being found attached to stone, wood, plant, or even other organism surfaces. However, several Diptera (*see* **Diptera (Biting Flies)** and **Ephemeroptera (Mayflies)**) ectosymbionts are obligately associated with their corydalid host. *Nigronia serricornis*, for example, is the sole host for some midge taxa [e.g., Chironomidae: Nanocladius (Plecopteracoluthus)].

There are no records of the incidence or identity of megalopteran parasites. As with other aquatic insect groups, it is likely that associations with water mites, merminthid nematodes, or other parasitic organisms will eventually be documented.

Life History

Larval Development

Megalopterans have larval periods ranging from 1 to 5 years. The sialids tend to have shorter duration larval periods relative to the corydalids. Larval durations tend to be longer in higher latitude or higher altitude locations relative to equatorial latitudes or low altitudes. *Sialis* larval pass through ten instars prior to pupation whereas *Corydalus* has been documented to have 10–12 instars, depending on latitude. As with many aquatic insects, water temperature can have a significant effect on larval growth rate, development rate, and larval duration. Colder temperatures generally translate into slower growth and development in relation to warmer temperatures.

Pupae and Adults

Mature larvae (prepupae) leave the aquatic habitat to pupate. Larvae may travel up to 10 m or more (generally less) away from the water and construct a chamber under a rock, log, or even human debris like a discarded tire or old board. Larvae dig a shallow chamber, generally no deeper than 10 cm of the soil surface. Species from ephemeral habitats are known to synchronize their life cycles with seasonal drying patterns and pupate under rocks or within moist streambed sediments. During the pupal state, the legs, antennae, and wings are not attached to the body (i.e., exarate) (Figure 3(a) and 3(b)). After a final larval molt, they will spend about a 3-week period (~10–40 days for Corydalidae and 10–30 days for Sialidae) in the chamber prior to emerging as an adult. Adults require up to 60 min drying time before taking flight.

Adults are generally poor fliers and do not disperse far from the larval habitat. In flight, corydalids exhibit a slow wingbeat and the abdomen is often carried in a vertical position, giving the image that the posterior body is just too heavy to be lifted off the ground. They tend to be night active, although sialids are more day-active than corydalids. Adults are not long-lived and usually do not feed. There is some

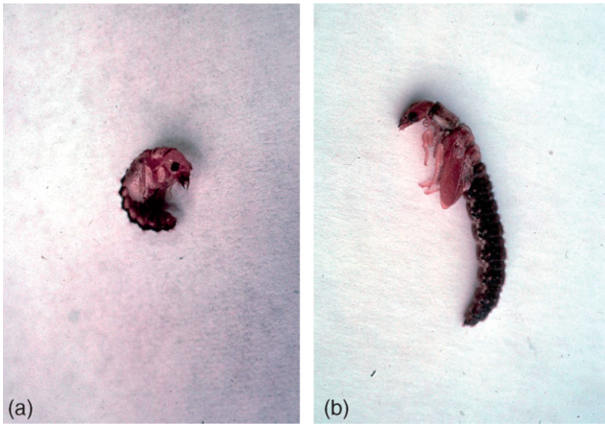

Figure 3 (a) Sialidae pupae and (b) Corydalidae pupae.

indication that adults will drink water or nectar. The mouthparts remain intact in adults. Adult life spans are probably around a week for most species and adult corydalids can be captured in good numbers around lights at night in areas with high density of appropriate habitats. Sialids can be collected by sweeping a net through the vegetation near aquatic habitats.

Oviposition and Fecundity

Mating occurs on vegetation or on the ground, and egg laying is terrestrial. Species tend to lay eggs on the undersurfaces of branches, leaves, or other structures overhanging the larval habitat (e.g., docks, bridges). Upon hatching, the larvae drop into the aquatic habitat below. Thus, selection of an appropriate oviposition location would seem critical to ensure newly hatched larvae reach good larval habitat. Several studies have assessed oviposition site selection by egg-laying females. In general, females have not been shown to exhibit strong preferences for specific tree species within riparian corridors, but there has been a general observation for height preferences above the water surface. Egg masses tend to be located above the high-water mark, but not at the most extreme heights available.

All sialids and corydalids lay egg masses with neat rows of eggs. The sialids tend to deposit a single row of eggs whereas corydalids often lay masses with two or more egg layers (Figure 4(a) and 4(b)). Some species are known to lay a single egg mass and others lay several egg masses per oviposition event. Egg masses of Sialidae range in size from 200 to 900 eggs whereas corydalid egg masses tend to be larger, holding up to 3000 eggs per mass, though generally 1200 is an average. Although there is evidence of differing numbers of eggs laid per egg mass per female, no evidence indicates the eggs from different masses are of different sizes. As with most aquatic insects, fecundity is related to female body size; larger females lay more eggs. Eggs tend to hatch within 5–20 days. Upon hatching, the larvae drop into the aquatic habitat below. First-instar *Corydalus* retain a gas bubble in their gut after hatching. This bubble has been suggested as providing needed buoyancy to allow larvae hatched over pools to remain afloat until reaching riffle habitat. Some predation on eggs has been documented, primarily from hemipteran predators, parasitic wasps, or leaf-mining or leaf-harvesting insects. Both sexes die after reproducing.

Figure 4 (a) Sialidae egg masses and (b) Corydalidae egg masses.

Water-Quality Indicators

The use of aquatic insects in water-quality monitoring has gained wide acceptance in North America, Europe, and Australia. The Sialidae are generally considered tolerant of moderate levels of organic enrichment whereas the corydalids are generally moderately tolerant-to-sensitive to organic enrichment. Species level identifications can be critical to accurate estimation of water-quality conditions using aquatic insects. For example, in eastern North America, *Nigronia fasciatus* is less tolerant to elevated water temperatures or organic enrichment than the conspecific *N. serricornis*, and both are less tolerant than the larger *Corydalus cornutus*. Less work has investigated water-quality limits for the diverse sialids in North America or for the megalopteran throughout the rest of the world.

Larvae rely primarily on dissolved oxygen for respiratory needs. Since the lateral abdominal filaments of megalopterans and gill tufts of dobsonflies are hemolymph filled, they increase available surface area for oxygen diffusion. Some fishflies are also able to breathe atmospheric oxygen through short respiratory tubules located near abdominal segment 8. Even with these potential oxygen-enhancing organs, corydalids, in general, do not do well under poor water-quality conditions.

See also: Coleoptera (Beetles) in Aquatic Ecosystems; Diptera (Biting Flies); Ephemeroptera (Mayflies); Odonata (Dragonflies and Damselflies).

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