

6 Introduction

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WEB-SPINNING OR LEAF-ROLLING SAWFLIES



The family Pamphiliidae is confined to the Holarctic region. There are 2 extant subfamilies, Cephalciinae and Pamphiliinae, containing 8 living genera represented by 327 species, and 5 extinct genera, 3 of which are classified in the fossil subfamily Juralydinae.

As in the Megalodontesidae these are large sawflies with wide, flattened bodies. Their antennae are long and thin, tapering to points.

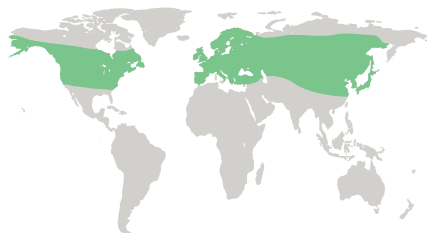
Eggs are laid in slits in the plant tissue. The gregarious larvae often feed in groups clustered in silken webs or silk tents on coniferous and other plants, with other species feeding within leaf rolls. Many species are gregarious in early larval instars, living in silk tubes, then solitary in later instars,

ABOVE | *Acantholyda erythrocephala*, the distinctive Pine False Webworm, or Red-headed Pine Sawfly; sawflies have often acquired different names in the pest control literature versus the recording community.

RIGHT | Pine Tree Web-spinner (*Acantholyda posticalis*). Although considered a forestry pest in parts of its range, in other areas, such as Britain, this is a declining species.

although some species are gregarious under silken webbing throughout their development. Many Pamphiliinae live within leaf rolls in later instars.

Pupation is in the soil and the winter is spent as a prepupa. Larvae of most species feed on trees, either conifers or angiosperms, while species that feed on herbaceous plants are restricted to Rosaceae.



DISTRIBUTION

Widely distributed across the temperate areas of Asia, Europe, and North America

GENERA

Acantholyda, *Caenolyda*, *Cephalcia*, *Kelidoptera*, *Neurotoma*, *Onycholyda*, *Pamphilius*, *Pseudocephaleia*

HABITATS

Woodland

SIZE

$\frac{9}{16}$ – $\frac{11}{16}$ in (8–18 mm) body length

ACTIVITY

Diurnal

REPRODUCTION

Males approach females and mating lasts several minutes. Females can be aggressive, resisting further mating



attempts and at least in some species exhibiting aggressive egg-guarding behavior

DIET

Phytophagous. Larvae feed on trees or herbaceous plants. Adults do not feed

The subfamily Cephalciinae are pine feeders while Pamphiliinae feed on angiosperms. Adults do not feed, in contrast to Megalodontesidae.

Some species are considered to be pests of the forestry industry, such as *Cephalcia lariciphila*, which can defoliate stands of larch (*Larix*), and the Pine False Webworm (*Acantholyda erythrocephala*), which attacks pines.

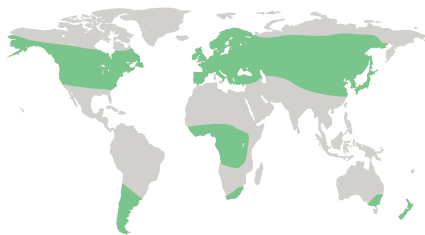
HORNTAILS AND WOODWASPS



This family is most common in the temperate northern hemisphere, but *Afrotremex* is an African genus and *Sirex noctilio* has spread to Africa, Australia, and South America. It comprises 2 extant subfamilies, Tremicinae (horntails) and Siricinae (woodwasps), containing 10 genera and 108 species. An additional nine genera and three subfamilies are only known by fossils, an ancient group of wasps that was more diverse during the Paleogene and Mesozoic eras.

Woodwasps develop within conifers and horntails feed on broad-leafed deciduous tree species. Horntails are so named for the hard spine-like projection at the end of the abdomen, which facilitates penetration of plant tissue in the process of egg-laying. They need toughened cuticle to oviposit into and emerge from wood, and have zinc-enriched ovipositor tips and mandibles to aid this. The Pigeon Horntail (*Tremex columba*) is a massive North American wasp reaching up to $1^{15}/_{16}$ in (50 mm) in body length.

Woodwasps carry symbiotic fungi in specialized “pouches,” mycangia, on the abdomen. Adult woodwasp females lay eggs and fungal spores into stressed trees, providing rotten wood for larval feeding. *Xeris* species lack mycangia, taking advantage of wood pre-infested by woodwasps.



DISTRIBUTION

Species richness is centered in the northern hemisphere, but *Afrotremex* is present in the African tropics and *Sirex noctilio* has been introduced to several countries in the southern hemisphere

GENERA

Afrotremex, *Eriotremex*, *Sirex*, *Siricosoma*, *Siotremex*, *Teredon*, *Tremex*, *Urocerus*, *Xeris*, *Xoanon*

HABITATS

Temperate and tropical forests

SIZE

$3/8$ – $1^{15}/_{16}$ in (10–50 mm) body length

ACTIVITY

Diurnal. Some species are reported to have mating swarms at the tops of trees or hills (“hilltopping”)

REPRODUCTION

Females lay several eggs directly into the wood of dead or stressed trees,



ABOVE | Female of the European Giant Woodwasp (*Urocerus gigas*), a fearsome-looking but harmless species that is a mimic of stinging wasps.

OPPOSITE | Pigeon Horntail (*Tremex columba*), a North American woodwasp, larvae of which eat the wood of deciduous trees with females dying soon after they have finished ovipositing.

RIGHT | Male of the European (and widely introduced) Sirex Woodwasp (*Sirex noctilio*). A notorious pest of conifers, a large body of research has built up around *Sirex noctilio* and its parasitoids.



with ovipositor valves working like saws to slice through wood fibers. The larvae are long-lived, for two to three years. They usually pupate just below the bark surface

DIET
Larvae are wood-borers, phytophagous or mycophagous, feeding on dead wood being broken down by commensal fungi

Sirex noctilio has become a major forestry pest and has been accidentally introduced to several countries in the southern hemisphere. Several other species are invasive, mainly in the Americas, where they are frequently intercepted in wood imports. *Sirex noctilio* is successfully controlled by a combination of parasitoid wasps (*Ibalia leucospoides* and species of Rhyssinae, Ichneumonidae) and parasitic nematodes (*Deladenus siricidicola*).

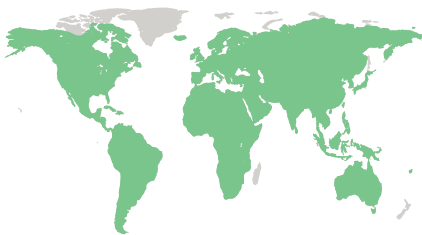
ARGID SAWFLIES



Argids are nearly worldwide in distribution, but most prevalent in tropical regions. They are absent only from Antarctica, Madagascar, and New Zealand. They comprise 2 subfamilies, Arginae and Sterictiphorinae, containing 59 living genera, with over 900 species. One fossil genus has been described (two extant genera also have fossil species). The Zenarginae was recently raised to family status, and the other four subfamilies absorbed into the two current subfamilies based on phylogenetic analyses.

Argid sawflies are frequently brightly colored and conspicuous. A characteristic feature of Argidae (and a very few other sawflies) is that the antenna is reduced to three segments. Males of Sterictiphorinae have bifurcate (resembling tuning forks) antennae, whereas Arginae all have simple antennae.

This abundant family represents an important herbivory component in tropical ecosystems. Larvae may be gregarious, and a few exposed feeders are different colors on each side of their body, as camouflage for feeding on the edges of



DISTRIBUTION

Worldwide, with species richness centered in tropical and subtropical regions, although the huge genus *Arge* is well represented in temperate regions

GENERA

59 extant genera classified in 2 subfamilies: Arginae and Sterictiphorinae

HABITATS

Wide range, from arid desert environments to tropical forests. Most abundant in tropical areas

SIZE

$\frac{1}{8}$ – $\frac{1}{2}$ in (3–12 mm) body length

ACTIVITY

Diurnal. Many argids are rather slow-moving, “bumbling” along

LEFT | An argid sawfly, *Arge ochropus*, with a typical bright color pattern for an argid, although the distantly related *Athalia* sawflies can look similar. Adult argids are often rather slow-moving.

RIGHT | The Poison Ivy Sawfly (*Arge humeralis*) with black-and-red warning colors. Note the antennal flagellum, reduced to one long segment.

BELOW | Larvae of the Large Rose Sawfly (*Arge pagana*), conspicuous and distasteful to many predators, although some specialized wasps are parasitoids of argid larvae.



REPRODUCTION

Females use the saw-like ovipositor to cut slits into host plant to lay eggs. Maternal care may occur with egg guarding. Larvae may be gregarious; Sterictiphorinae pupate in dense cocoon masses

DIET

Phytophagous, larvae feed externally on angiosperms. Some are leaf-miners with *Aproceros* and *Sterictiphora* leaving a distinct zig-zag pattern

leaves. Adults are flower visitors feeding on pollen and nectar, and consequently play a role in pollination services.

The family contains several pest species and a couple of beneficial species used as biocontrol agents. The Sumatran species *Cibdela janthina* has been successfully used to control the invasive Giant Bramble (*Rubus alceifolius*, Rosaceae) on the island of Réunion and is now also present in Mauritius. *Aproceros leucopoda* is a pest of elms (*Ulmus*), having invaded Europe from East Asia, and can completely defoliate the trees. The rose sawflies *Arge ochropus*, *Arge rosae*, and *Arge xanthogaster* are serious pests of both ornamental and wild roses, the gregarious larvae feeding on both flowers and leaves. Larvae of *Arge pullata*, a widespread species that can defoliate birch, are toxic to livestock, which frequently eat the larvae as they move to the ground to pupate.

FERN SAWFLIES

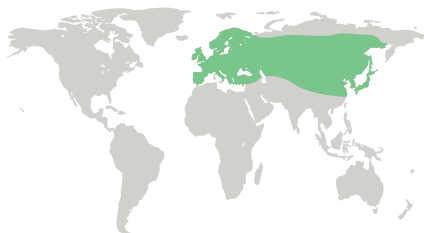
Blasticotomidae are restricted to Eurasia, occurring in temperate areas. This small family of sawflies comprises 2 living genera represented by only 12 species, and has 1 fossil genus.

As in Argidae and Zenargidae, most of the antenna is one enlarged flagellar segment, but this is followed by a tiny fourth antennal segment in Blasticotomidae.

BELOW | Female of a Fern Sawfly (*Blasticotoma filiceti*). Adults can be hard to find but the presence of larvae is often indicated by froth around a hole in a fern rachis, with ants attending.

The young larva chews out a cavity in the rachis of the fern foodplant, where it feeds on sap leaking into the hollow cell. The larva chews a hole at each end of the cavity it develops in, the bottom one for defecation and the other for breathing. The excrement is sugar-rich and attracts ants, their presence likely providing indirect protection for the larvae from parasitoids and predators. Pupation is within the stem, without a cocoon.

The most widespread species, *Blasticotoma filiceti*, is thelytokous (reproduces parthenogenetically); occasional introductions outside its native range, and in gardens, mean it can easily spread, as only one female needs to be transported.



DISTRIBUTION

Species are confined to temperate areas of Asia, with one species in Europe, and are rarely found in numbers

GENERA

Blasticotoma, *Runaria*

HABITATS

Boreal forests and wetlands, where ferns occur

SIZE

$1/4$ – $3/8$ in (7–9 mm) body length

ACTIVITY

Diurnal

REPRODUCTION

Females lay eggs directly into the stem of a fern

DIET

Phytophagous. Larvae are stem-borers of ferns and can sometimes be detected by accumulations of froth outside their feeding hole

TENTHREDINOIDEA: CIMBICIDAE

GIANT SAWFLIES

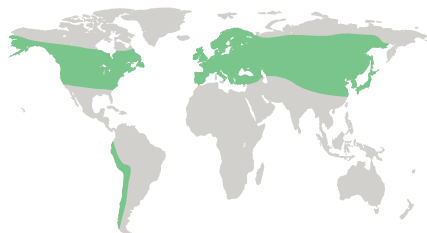
The family Cimbicidae is mostly a northern hemisphere family with one subfamily occurring in South America. It comprises 16 living genera represented by 182 species, and 5 extinct genera, in 4 subfamilies: Abiinae, Cimbicinae, Corynidiinae, and Pachylostictinae.

Giant sawflies are a family of mostly large, fast-flying sawflies with characteristic clubbed antennae. Male fighting is known in some species and they can be highly territorial, using their massive mandibles and enlarged hind legs as weapons. This might be an evolutionary driver behind the very large body size of many species, as might mimicry, as some species mimic bumblebees (*Bombus*) or vespid wasps.

Cimbicinae feed mainly on trees, other subfamilies mainly on shrubs and herbs, although the biology of Pachylostictinae is very poorly known. Although the larvae are large and striking, cimbicids are usually found at low density. Larvae feed externally on foliage and pupate in cocoons constructed on the foodplant or in the soil.



RIGHT | Female of the European honeysuckle-feeding *Abia fasciata*. Larvae feed on a range of plants in the family Caprifoliaceae.



DISTRIBUTION

Species richness is centered in the northern hemisphere with Pachylostictinae restricted to South America

GENERA

16 genera

HABITATS

Wide range, from grassland to forests

SIZE

$\frac{1}{4}$ – $1\frac{3}{16}$ in (6–30 mm) body length

ACTIVITY

Diurnal. Adults often buzz when caught and have a strong defensive bite. Males aggregate at the top of hills

REPRODUCTION

Eggs are laid in incisions on foodplants

DIET

Phytophagous. Larvae are plant-feeders, all on angiosperms

CONIFER SAWFLIES

The family Diprionidae is restricted to the northern hemisphere, with species richness centered in the boreal regions of Asia, Europe, and North America, but some species extend south to the Oriental region and to North Africa.

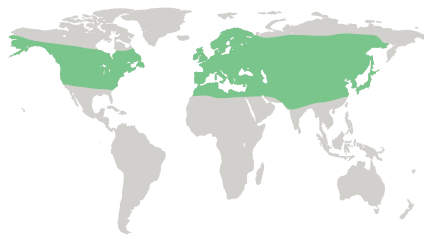
Conifer sawflies comprise 11 living genera represented by 136 species, and 2 extinct genera in 2 subfamilies. Some species have gregarious larvae and

can be serious forestry pests, such as the White Pine Sawfly (*Neodiprion pinetum*), which attacks the Eastern White Pine (*Pinus strobus*). Population explosions under favorable conditions can result in complete defoliation of forest trees resulting in the death of the tree, an impact attributing a major economic pest status to these species. *Neodiprion sertifer* is a notorious pest in North America, introduced from Europe, where massive defoliation of pines occurred before some control was achieved using parasitoid wasps.

Males of many species have extravagantly pectinate antennae, and these are attracted to pheromones produced by females. Larvae of solitary species are cryptically colored while gregarious larvae can be conspicuous and display synchronized movements when threatened. The very well-studied *Neodiprion sertifer* overwinters as an egg, unusual for Diprionidae; most species overwinter as prepupae in cocoons either in the ground or on the food tree.



LEFT | Female of the pine-feeding *Diprion similis*. In hot, dry years, there can be increased defoliation of pines as *Diprion* species can then manage two generations in a year.



DISTRIBUTION

Species richness is centered in Eurasia and North America

GENERA

Augomonotenus, *Diprion*, *Gilpinia*, *Macrodiprion*, *Microdiprion*, *Monotenus*, *Neodiprion*, *Nesodiprion*, *Prionomein*, *Rhipidoctenus*, *Zadiprion*

HABITATS

Temperate conifer forests

SIZE

$\frac{3}{16}$ – $\frac{9}{16}$ in (5–14 mm) body length

ACTIVITY

Diurnal. Slow-flying, with males ranging much further than females

REPRODUCTION

Eggs are laid in slits on conifer needles

DIET

Phytophagous. Larvae feed on conifers, Diprioninae on Pinaceae and Monotენinae on Cupressaceae

FERN-TIP SAWFLY WASPS

BELOW | Female *Heptamelus dahlbomi*; males are unknown. Classified as tenthredinid sawflies until recently, this is a difficult family to recognize.



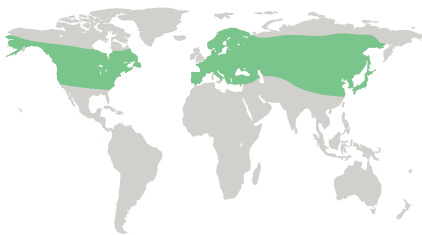
The family Heptamelidae, only recently split from Tenthredinidae, is restricted in its native range to Eurasia. It comprises 2 living genera represented by 38 species, with no known extinct genera.

The larvae of *Heptamelus* are stem-borers whereas those of *Pseudoheptamelus* feed mostly externally. Eggs of both genera are laid at tips of the fern rachis, entirely within the plant tissue.

Larvae of *Heptamelus* feed by boring downwards toward the base of the stem. Larvae of

Pseudoheptamelus prefer to feed externally

on freshly dead fern. The foodplants are known for very few species; European heptamelids seem to prefer Lady Fern (*Athyrium filix-femina*). The ovipositing females of *Pseudoheptamelus runari* make additional cuts with their ovipositors above the egg, which might help kill the fern frond, to the advantage of the larva. As with most other fern-feeding sawflies, larvae do not pupate in the soil nor form cocoons, but burrow into lower, dead sections of fern stem, or nearby dead wood to pupate.



DISTRIBUTION

Species are most diverse in the Eastern Palearctic and Oriental regions, with a few species in Europe. *Heptamelus dahlbomi* has been accidentally introduced to North America

GENERA

Heptamelus, *Pseudoheptamelus*

HABITATS

Forests, wetlands (including dune slacks), gardens

SIZE

$\frac{3}{16}$ – $\frac{1}{4}$ in (4–6 mm) body length

ACTIVITY

Diurnal

REPRODUCTION

One widespread species, *Heptamelus dahlbomi*, is thelytokous

DIET

Phytophagous on ferns

TENTHREDINOIDEA: PERGIDAE

SPITFIRE SAWFLIES

The family Pergidae, with 60 living genera represented by 442 species, is the third-largest sawfly wasp family after the argids and torpedo sawflies (Tenthredinidae), being most species-rich in South America, followed by Australia. The family also occurs in eastern North America (the genus *Acordulecera*) and the Indonesian region (New Britain, Papua New Guinea, and Sulawesi). One species has been introduced to New Zealand.

RIGHT | Larval Australian pergid sawfly (*Trichorhachus* species) feeding on Common Smokebush (*Conospermum stoechadis*), and well disguised on its white fluffy foodplant.

BELOW | Adult Australian pergid sawfly (*Perga* species). *Perga* adults have extremely short antennae and the larvae are highly gregarious.



DISTRIBUTION

Species richness is centered in the southern hemisphere; it is the best-represented sawfly family in Australia and is well represented in South America

GENERA

60 genera contained in 12 subfamilies: Acordulecerinae, Conocoxinae, Loboceratinae, Parasyzygoniinae, Perginae, Pergulinae, Perreyiinae,

Philomastiginae, Pterygophorinae, Pteryperginae, Styracotechyinae, Syzygoniinae

HABITATS

Wide range, from grassland to forests

SIZE

$\frac{1}{8}$ – $\frac{3}{8}$ in (3–10 mm) body length

ACTIVITY

Most are diurnal, but some species are crepuscular or nocturnal



Males home in on receptive females by detecting pheromones released by the females. Pergids exhibit several unusual traits. Unusually within sawflies, some species exhibit maternal care, aggressively looking after their eggs and young larvae by making a buzzing sound. Sawfly adults are frequently carnivorous, so this is not an empty threat, and some pergids are known to be highly toxic. Another unusual feature, found in *Perreyia flavipes*, is thanatosis—that is to say, they “play dead.”

REPRODUCTION

Fertilized females usually lay their eggs by inserting them directly into the host plant tissue, but sometimes lay eggs on or in the soil

DIET

Extremely varied, most are phytophagous (plant-feeders) although some specialize on aquatic ferns, and others on fungi

Larvae feed mostly on leaves (commonly eucalypts in Australia) or are borers attacking new shoots or mining within the leaves themselves. Others only feed on decomposing plant matter. Several species are of economic significance, as the gregarious larvae can completely devour all the leaves on the host plant, which can be crops such as guavas or potatoes in South America, or forest trees. The South American *Perreyia flavipes* has gregarious and highly toxic larvae that are sometimes known as “pig killers,” responsible for many livestock deaths in Brazil. Others are beneficial, helping to control invasive plant species such as the Brazilian Peppertree (*Schinus terebinthifolia*) and the Peruvian Peppertree (*Schinus molle*).

TENTHREDINOIDEA: TENTHREDINIDAE

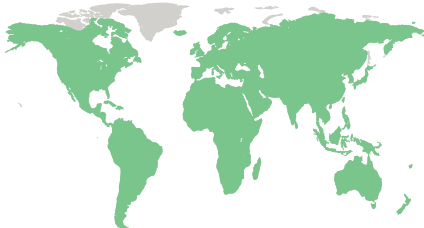
TORPEDO SAWFLIES



ABOVE | *Rhogaster viridis*; as with many other bright green insects, the green pigment fades after death.

OPPOSITE | *Tenthredo* species, either *T. arcuata* or a close relative; another mimic of stinging wasps. *Tenthredo* species are active, relatively large, and eat other insects.

The Tenthredinidae are by far the largest family of sawflies, with 400 genera. Torpedo sawflies occur worldwide but are a particularly conspicuous part of the northern temperate fauna. The number of subfamilies recognized in Tenthredinidae has been unsettled but we follow recent phylogenetic studies that agree on six subfamilies: Allantinae, Athaliinae, Blennocampinae, Nematinae, Selandriinae, and Tenthredininae.



DISTRIBUTION

Species richness is centered in the temperate areas of North America and Eurasia, but members of most subfamilies range far south into Africa and South America, and Selandriinae is more diverse in the tropics

GENERA

400 genera in 6 subfamilies: Allantinae, Athaliinae, Blennocampinae, Nematinae, Selandriinae, Tenthredininae

HABITATS

Wide range, from more arid environments to tropical forests, but most species-rich in temperate areas

SIZE

$\frac{3}{16}$ – $\frac{3}{4}$ in (5–20 mm) body length

ACTIVITY

Diurnal, although some species appear in light traps and might be partly crepuscular



REPRODUCTION

Females use their saw-like ovipositor to cut slits into plants for egg-laying

DIET

Phytophagous, mainly on angiosperms but with significant numbers of species feeding on ferns and monocots, and a few on conifers

In line with the majority of recent phylogenetic studies, we recognize Athaliinae as a separate subfamily, as it has usually been found to be the sister to the rest of Tenthredinidae, or could even be a separate family within Tenthredinoidea. The former subfamily Heterarthrinae has recently been split, with its genera reassigned to Blennocampinae.



While many of the smaller species tend to be monochromatic and difficult to identify on external features, larger species of Tenthredininae can be very colorful, with some vivid green and orange species. Athaliinae species have distinctive black- and yellow-striped legs and a mainly orange abdomen.

In sub-Arctic and Arctic areas, species in the Tenthredinidae family are particularly important components of the plant-feeding insect community. Tenthredinids are very important hosts for several groups of Ichneumonidae and a few other groups of parasitoids.

Quite a few species bring attention to themselves as agricultural and ornamental plant pests, such as the Pear Slug (*Caliroa cerasi*), which feeds on ornamentals such as roses and deciduous fruit trees, or the Solomon's Seal Sawfly (*Phymatocera aterrima*), which defoliates *Polygonatum* ornamentals. The European Turnip Sawfly (*Athalia rosae*) has caused

ABOVE | Mating pair of the Turnip Sawfly (*Athalia rosae*). Very recently, the Athaliidae have been recognized as a family, separate from Tenthredinidae.

BELOW | The strange-looking “slugworm” larva of *Caliroa cerasi* are covered in mucous and feed on the leaves of various trees and shrubs.

RIGHT | Female *Strongylogaster multifasciata* ovipositing in a frond of bracken; the larvae feed externally on the foliage.



extensive damage to crops in Northern Europe but has become much less common. However, *Athalia rosae* and sometimes other *Athalia* have regular population explosions, when they can arrive in swarms in coastal areas.

Larvae of most species feed externally on leaves, but some are gall-formers, stem-borers, or leaf-miners. Larvae of Allantinae and Athaliinae are external feeders, the former on a variety of trees and shrubs (with a preference for Rosaceae), the latter on herbaceous plants and particularly Brassicaceae. Blennocampinae is a diverse subfamily containing leaf-miners (fenusines, heterarthrines), leaf skeletonizers (caliroines), borers in roots and twigs, and many external feeders. While angiosperms are preferred by most, with many larvae on trees, a few species eat monocots. The more than 1,000 species of Nematinae feed mainly on angiosperm trees, but with radiations onto various other plants.

Gall-forming and leaf-rolling are particularly prevalent in species feeding on *Salix*, and many of the nematines that feed on willows will only feed on one

or very few species. With willows being species-rich in the far north, this has resulted in huge numbers of nematine species, particularly in the genera *Euura* and *Pristiphora*. Selandriinae are largely fern feeders, including *Strongylogaster*, which has been used to try and control Bracken (*Pteridium aquilinum*). Some species eat monocots, including the tribe Dolerini, often common in grassland. Adults of many tenthredinids feed on nectar and pollen, and larger tenthredinids, such as the genus *Tenthredo*, which are predators of other insects, often hunt on flowers.

Most temperate species only have a single generation every year and adults are most conspicuous in spring and early summer, but some (e.g., *Athalia*) produce multiple generations in a year. Larvae of solitary species tend to be cryptic, but gregarious species can have strikingly conspicuous larvae. The larvae pupate in the ground or in a protected situation such as in their galls, stems, leaf-mines, etc., and survive adverse cold season conditions in this phase of their life cycle.



CYPRESS PINE SAWFLIES

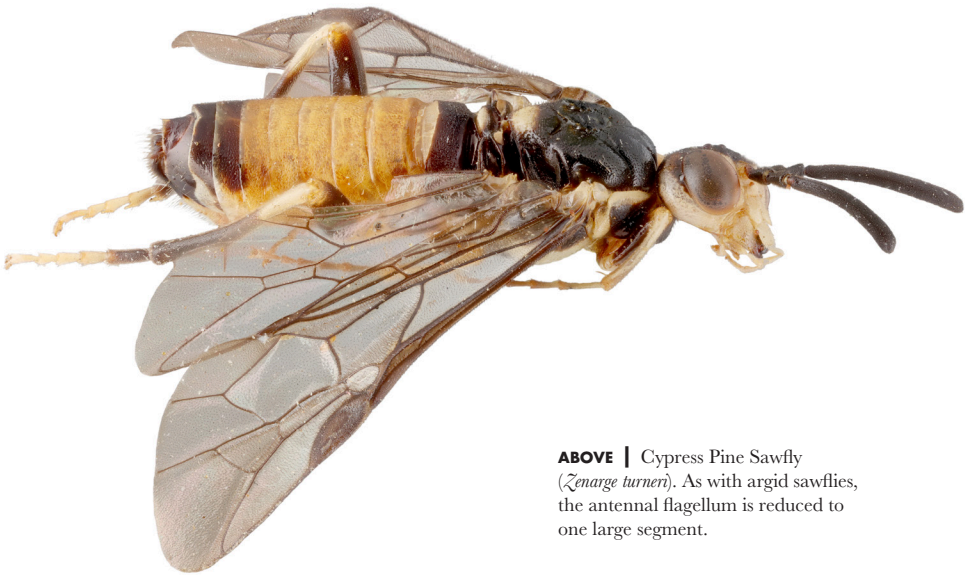
The family Zenargidae was only recognized as distinct in 2021. The single included species, *Zenarge turneri*, is endemic to Eastern Australia and had previously been classified in the family Argidae.

Large areas of *Callitris* and *Cupressus* have been defoliated by *Z. turneri*, with younger trees preferred.

Emergence of adults requires a certain amount of winter rainfall and moderate temperatures at other times. As a consequence, *Zenarge* can spend

up to six years as a prepupa in the cocoon, waiting for the right conditions.

Larvae of *Z. turneri* feed on gymnosperms, including cypress pine, native to Australia, as well as introduced conifers, which contrasts with the closely related families Argidae and Pergidae, mostly angiosperm feeders.



ABOVE | Cypress Pine Sawfly (*Zenarge turneri*). As with argid sawflies, the antennal flagellum is reduced to one large segment.



DISTRIBUTION
Eastern Australia

GENUS
Zenarge

HABITATS
Coastal areas and highlands of eastern Australia, where *Callitris* (cypress pine) and introduced *Cupressus* (cypress) occur

SIZE
 $\frac{5}{16}$ – $\frac{3}{8}$ in (8–10 mm) body length

ACTIVITY
Adults are diurnal and emerge at various times of the year, but particularly the fall. Little is known about their behavior

REPRODUCTION
Eggs are laid singly on shoots of gymnosperms and larvae are not gregarious

DIET
Phytophagous

XIPHYDROIDEA: XIPHYDRIIDAE

LONG-NECKED WOODWASPS

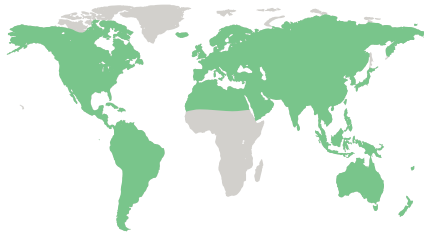
The family Xiphydriidae is represented worldwide on most continents, except for sub-Saharan Africa. It comprises 27 living genera represented by 153 species contained in 2 subfamilies, Derecyrtinae and Xiphydriinae, and 2 extinct genera.

Long-necked woodwasps are rarely collected but some species can be found to be reasonably common when their feeding habits are known.

BELOW | Female Alder Woodwasp (*Xiphydria camelus*). The natural history of this species and its parasitoids was documented in a groundbreaking 1961 film by Gerald Thompson.

Females inject fungal spores during the process of egg-laying. The larvae require the presence of these symbiotic fungi that subsequently grow in the tunnel they bore in the host trees for their development. Females oviposit in wood using their conspicuously exerted ovipositors.

Several eggs are laid in one drill hole and the larvae then bore fairly shallow tunnels in the wood. As in siricid woodwasps, larvae have a stiff structure at the rear end that might be used by the larva as a prop while rasping at hard substrate. Larvae are wood-borers in dead or decaying branches of deciduous trees in the families Aceraceae, Betulaceae, Salicaceae, and Ulmaceae. Feeding is essentially on the fungal hyphae breaking down the wood.



DISTRIBUTION

Xiphydriinae are worldwide in distribution with the exception of sub-Saharan Africa

GENERA

27 genera

HABITATS

Forests and woodland

SIZE

$1/2$ – $3/4$ in (12–20 mm) body length

ACTIVITY

Diurnal. As with some siricids and cimbicids, males have been found in swarms at the tops of hills, where presumably females find them

REPRODUCTION

Females drill holes in wood with their ovipositor and lay eggs in the hole

DIET

Phytophagous/mycophagous

XYELOIDEA: XYELIDAE

WEIRD-ANTENNAE SAWFLIES

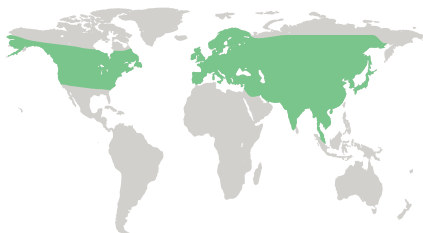
The family Xyelidae is restricted to the northern hemisphere, mostly occurring in temperate areas. It comprises 5 living genera represented by 63 species, classed in 2 subfamilies: Macroxyelinae and Xyelinae. There are also 53 extinct genera.

This is an ancient radiation of sawflies, with species richness best represented in the fossil record (120 species). Some of the oldest Hymenoptera fossils dating back to the Triassic (245–208 MYA) belong to this family.

Although they attack tree species of economic importance, most species are not major pests. One species, *Megaxyela major*, is regarded as a pest of Pecan plantations in the USA.

OPPOSITE | A North American *Xyela* species. *Xyela* are relatively diverse in North America but species are difficult to identify.

BELOW | Female *Xyela* species. The long ovipositor is used to lay eggs between the scales of pine cones.



DISTRIBUTION
Species richness is centered in the boreal temperate regions, but some species extend to the Oriental region

GENERA
Macroxyelinae: *Macroxyela*,
Megaxyela, *Xyelecia*; Xyelinae:
Pleroneura, *Xyela*

HABITATS
Temperate forests

SIZE
 $1/16$ – $9/16$ in (2–15 mm) body length

ACTIVITY
Diurnal. Adults can sometimes be swept in numbers, especially around pines

REPRODUCTION
Females lay eggs in pinecones or pine leaf buds



DIET

Phytophagous. Larvae of species in the subfamily Macroxyelinae feed on leaves of deciduous trees, commonly species in the walnut family (Juglandaceae), or on elms. Those in the subfamily Xyelinae feed on pollen (or within the developing buds) of conifers, commonly firs, pines, or spruces

The large maxillary palps present in species of Xyelinae have evolved to facilitate extracting pollen from flowers.

Reproductive strategies differ markedly between genera. Females of *Xyela* oviposit in staminate (pollen-producing) pinecones. *Xylecia* and *Pleroneura* oviposit in buds and young shoots of pines. *Macroxyela* stick their eggs to the leaf surface after folding the leaf using their long hind legs. Larvae of xyelids burrow into the ground to pupate within a silk cocoon spun within an earthen cell.

Most species are small, but *Megaxyela* are around $\frac{9}{16}$ in (14–15 mm) long and with very long hind legs.



APOCRITA (PARASITICA) PARASITOID WASPS

NARROW-WAISTED WASPS (APOCRITA)

Historically this group of wasps was ranked at suborder level as a sister group (Apocrita) to the Symphyta, but the apocritan lineages have evolved from within the Symphyta, so the two groups cannot be considered as monophyletic suborders. The narrow-waisted wasps contain two groups, Aculeata and Parasitica, which were each historically regarded as infraorders in the classification, but the Aculeata have evolved from within the Parasitica, which means that they also cannot be considered to be sister groups at the same level of classification (see the phylogenetic tree on page 30).

The Apocrita are defined by the possession of a “wasp waist” that is absent in the symphytans. The waist is formed by a constriction between the first and second abdominal segments. The first abdominal segment is named the propodeum and is fused to, and effectively functions as part of the thorax. Consequently, these two body parts are referred to as the mesosoma (functional thorax) and the metasoma (functional abdomen).

The second, or second and third abdominal segments (therefore first or first and second metasomal segments), often form a petiole, which is a thinner segment than the remaining metasoma.

LEFT | A female parasitoid fig wasp, *Apocrypta guineensis* (Pteromalidae) ovipositing through the fig wall to reach the host fig wasp larvae already developing in the galled florets within the central fig cavity of *Ficus sur*.



Many ants have two petiolar segments. The evolution of this narrowed waist section, often with a distinct petiole, was an adaptive morphological response to enable improved mobility of the metasoma and more accurate positioning of the ovipositor for the parasitoid way of life.

We here maintain these two informal groupings Parasitica and Aculeata for ease of reference to historical classifications.

PARASITOID WASPS (PARASITICA)

The Parasitica have historically been classified as an infraorder of the Apocrita, but the Aculeata lineage evolved from parasitoid wasp ancestors, so the Parasitica cannot be a monophyletic group classified at the same level (infraorder) as the Aculeata. The Aculeata also contain many species, including several families, that are parasitoids, negating the circumscription of a Parasitica group based on their lifestyle strategy. This assemblage (the Hymenoptera, which are not sawflies or woodwasps, and not aculeates) comprises 12 superfamilies, of very different morphologies.

The majority of wasp species belong here, with their elevated species richness and diversity probably having been driven by their parasitoid existence. Most species of insects and spiders

(plus a few other arachnids) are attacked by one—but often more than one—species of parasitoid wasp. Although parasitoid wasps are often assumed to be frequently host-specific, this is not usually the case. Instead, a range of hosts is usually attacked by any given parasitoid species, although this range is tightly circumscribed by factors such as host taxonomy, host niche, seasonality, etc. Some are, of course, absolutely host-specific. The females lay their eggs on or inside the host, with the larvae consuming the host.

Parasitoids are differentiated from parasites as parasitoids kill their host, with each parasitoid consuming one (or part of one) host, so a mix of parasite and predator, whereas parasites (such as ticks feeding on vertebrates) do not usually kill their host, except sometimes indirectly via pathogen transmission.

Many parasitoid wasps are small, averaging $\frac{1}{32}$ – $\frac{1}{16}$ in (1–2 mm) in length, although some can be up to several centimeters long. The venoms of parasitoid wasps are often chemically and physiologically complex and some groups of Ichneumonoidea have co-opted viruses, all as adaptations to overcome hosts and their immune responses. Some of the larger Darwin wasps with short ovipositors (e.g., Ophioninae, some Ichneumoninae, *Netelia*) have fairly painful stings that can be used defensively. A few lineages of parasitoid wasps have lost their parasitoid lifestyle and are instead phytophagous (most notable in the gall wasps) or predatory, such as various Darwin wasps that consume spider egg sacs.

LEFT | A female *Gasteruption jaculator* ovipositing into a solitary bee nest.

TRIGONALYOIDEA: TRIGONALYIDAE

TRIGONALYID WASPS

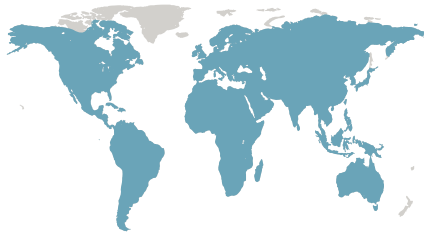
The family Trigonalyidae has a worldwide distribution and includes 2 subfamilies, Orthogonalyinae and Trigonalyinae, with 16 extant genera represented by around 120 species, and 4 extinct genera. The Cretaceous fossil genus *Maimetsha* (Maimetshidae) was originally believed to have affinities with the Megalyridae but is now considered to be related to the Trigonalyidae, and Maimetshidae is included in the superfamily Trigonalyoidea.

The elongate species mimic Darwin wasps (Ichneumonidae) in appearance and the more robust species mimic social wasps. Trigonalyids can be overlooked as aculeate wasps with very complete wing venation, but the antennae have more segments (usually 18–28), the mandibles are large and usually asymmetrical, the tarsal segments have plantar lobes (otherwise not found in the Apocrita), and the female antennae have unique white, scale-like setae.



LEFT | The North American *Taeniogonalos gundlachii*.

ABOVE RIGHT | An African species, *Trigonalys natalensis*.



DISTRIBUTION

Worldwide, except for the Arctic regions and New Zealand. Most species occur in the tropics

GENERA

Afrigonalys, *Bakeronymus*, *Bareogonalos*, *Ischnogonalos*, *Jezonogonalos*, *Lycogaster*, *Mimelogonalos*, *Nomadina*, *Orthogonalys*, *Pseudogonalos*, *Pseudonomadina*, *Seminota*, *Taeniogonalos*, *Teranishia*, *Trigonalys*, *Xanthogonalos*

HABITATS

Forests, woodland, grassland

SIZE

$\frac{1}{8}$ – $\frac{9}{16}$ in (3–15 mm) body length with much variation within species, depending on the size of the host; some elongate, others stout-bodied

ACTIVITY

Diurnal. Adults are usually rarely encountered but can be more common at higher altitudes in Asia and can be



These wasps are usually highly specialized hyperparasitoids of ichneumonoid wasp or tachinid fly parasitoids in plant-feeding caterpillars, or sometimes parasitoids of social wasps (Vespidae) when fed on parasitized caterpillars. However, at least one Australian species is known to be a primary parasitoid of pergid sawflies. The biology of trigonalysids is unusual for parasitoid wasps, because egg-laying does not occur directly into, or onto, the host.

Trigonalysids have an unusual life history as indirect hyperparasitoids. Females lay huge numbers of tiny eggs on or in slits in leaves,

which are then consumed by butterfly or moth caterpillars, or sawfly larvae. The eggs hatch within the caterpillar, and the larvae chew through the gut and into the body of the caterpillar, where they attack other parasitoid wasp larvae (Ichneumonidae or Braconidae) or parasitoid fly larvae (Tachinidae) already inside the host, thus developing as hyperparasitoids. If the plant-feeding caterpillar is fed to a social or potter wasp (Vespidae) larva, the trigonalysid then attacks the vespidae larva developing inside the social wasp nest. Trigonalysids complete their development in the host pupa.

There are a few other groups of parasitoid wasps who lay eggs on foliage, such as the chalcidoid family Eucharitidae and the Darwin wasp genus *Euceros*, but in these cases the larvae hatch before contacting hosts (or carriers). Note that Trigonalidae and Trigonalysidae (and equivalent family-group names) are both in use, based on different interpretations of the derivations of the genus name *Trigonalys*.

locally more numerous, such as in cacao plantations in Brazil. They are typically found in forests. Usually only a tiny proportion of reared caterpillars produce trigonalysids

REPRODUCTION

Females lay eggs on or in slits in leaves

DIET

Usually highly specialized hyperparasitoids of other parasitoid wasp or fly larvae

MEGALYRID WASPS

A largely southern-hemisphere family, the Megalyridae comprise 8 extant genera represented by 61 species, and 5 extinct genera. The family was named after the very long ovipositors of some Australian species (*Mega* meaning large and *lyra* a stringed instrument).

The hosts of most genera are unknown, but they are probably all parasitoids of concealed insect larvae, such as wood-boring beetles, or wasp larvae.



DISTRIBUTION

Mostly southern hemisphere, highest species richness in Australia and Madagascar, one species in Japan. Baltic amber and Cretaceous fossils demonstrate formerly more widespread distribution

GENERA

Carminator, *Cryptalyra*, *Dinapsis*, *Etchellsia*, *Megalyra*, *Megalyridea*, *Neodinapsis*, *Rigel*

HABITATS

Tropical or temperate forests, woodland, dry scrub, fynbos

SIZE

$\frac{1}{8}$ – $\frac{7}{8}$ in (3–22 mm) body length, excluding the ovipositor, which can be as long as $3\frac{1}{8}$ in (80 mm)

ACTIVITY

Diurnal. Adults are rarely encountered



ABOVE | The Madagascan *Dinapsis albicoxa*.

LEFT | The endemic South African genus and species *Megalyridia capensis*.

REPRODUCTION

Little is known about the biology. The female lays an egg on the host insect developing inside wood or mud nests using her long ovipositor

DIET

The parasitoid larva feeds on the host larvae of wood-boring beetles or wasps

The long ovipositors of the more conspicuous species are not used for drilling; instead, the ovipositor is inserted into pre-existing tunnels or holes to reach host larvae.

Little is known about the biology of most species, but a common Australian species, *Megalyra fasciipennis*, attacks large larvae of wood-boring beetles (Cerambycidae) and has been introduced to several countries to control pest longicorn beetle larvae (*Phoracantha*) developing in commercial Eucalyptus plantations. The female inserts her long ovipositor through the frass plug blocking the tunnel that the beetle larva has bored while feeding, laying an egg on the host beetle pupa. Another Australian species (*Megalyra troglodytes*) attacks the larvae of mud-nesting crabronid wasps.

Some distinctive characteristics of Megalyridae include the presence of subantennal grooves and highly reduced hindwing venation.

STEPHANOIDEA: STEPHANIDAE

CROWN WASPS

The Stephanidae contain 11 extant genera represented by 345 species, and 4 extinct genera.

They are easy to recognize by the distinctive crown of teeth on top of the globular head, and hind legs with bulbous first two segments, the second with large teeth on the underside. The crown of teeth on the head is shared with only one other wasp family, the Orussidae, and probably evolved to facilitate emergence of the adult wasp from deep inside wood.

OPPOSITE | A male of a *Foenatopus* species.

BELOW | The North American *Megischus bicolor* ovipositing into a host beetle larva developing inside a tree branch.



DISTRIBUTION

Worldwide, with most species occurring in tropical or subtropical forests

GENERA

Afromegischus, *Comnatopus*, *Foenatopus*, *Hemistephanus*, *Madegafoenus*, *Megischus*, *Parastephanellus*, *Profoenatopus*, *Pseudomegischus*, *Schlettererius*, *Stephanus*

HABITATS

Tropical or temperate forests, woodland, grassland, scrub

SIZE

$\frac{3}{16}$ – $1\frac{3}{8}$ in (3.5–35 mm) body length

ACTIVITY

Diurnal. Adults are rarely encountered

Females drill their ovipositor valves through wood to reach the targeted host larvae developing inside branches. They lay a single egg on the host larva. On hatching, the wasp larva develops as an external parasitoid. Species are parasitoids of mostly wood-boring beetle larvae (commonly Buprestidae and Cerambycidae), or occasionally sawflies or bees. Based on adaptations of the fore and hind tibiae, stephanids are presumed to have the ability to detect vibrations made by wood-boring larvae.

Adults live for three to four weeks. Individuals belonging to the same species can vary greatly in size, with the largest being twice the size of the smallest. This size variation is related to the size of the host insect larva that the crown wasp larva developed on.

Schlettererius cinctipes has been introduced to Tasmania from California as a biocontrol agent of the Sirex Woodwasp (*Sirex noctilio*, Siricidae).

REPRODUCTION

Females lay an egg directly onto host larvae developing inside branches

DIET

The parasitoid larvae feed on beetle, sawfly, or bee larvae



CERAPHRONID WASPS

OPPOSITE | *Ceraphron* searching for hosts to parasitize.

BELOW | A *Ceraphron* female—the twin fore-tibial spurs are visible on the front leg.

The family contains 16 genera represented by 304 described species and is widespread throughout the world. Most species are still undescribed.

These wasps are mostly commonly found in leaf litter and soil, with many being wingless, an adaptation for living in this environment.

Uniquely within Apocrita, Ceraphronoidea have two fore tibial spurs. A curious structure that is only found in Ceraphronidae, called the Waterston's evaporatorium, is present on the last (sixth) segment of the metasoma. This is



DISTRIBUTION

Worldwide

GENERA

Abacoceraphron, *Aphanogmus*,
Ceraphron, *Cyoceraphron*,
Donadiola, *Ectonetes*,
Elysoceraphron, *Gnathoceraphron*,
Homaloceraphron, *Kenitoceraphron*,
Masner, *Microceraphron*,
Pteroceraphron, *Retasus*, *Synarsis*,
Trassedia

HABITATS

Wide range of habitats, from forests to tundra

SIZE

$\frac{1}{64}$ – $\frac{1}{16}$ in (0.5–2 mm) body length

ACTIVITY

Probably mostly diurnal

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