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**A MAPLE WOOD WASP, *XIPHYDRIA MACULATA*, AND ITS INSECT ENEMIES (HYMENOPTERA: XIPHYDRIAE)**Mark A. Deyrup<sup>1</sup>

## ABSTRACT

A xiphydriid wood wasp, *Xiphydria maculata*, is very common in branches of *Acer* spp. in Indiana, and is frequently the proximate cause of branches falling from shade trees. *X. maculata* is attacked by seven parasitoids: *Aulacus burquei* (Aulacidae), *A. digitalis*, *Rhyssella nitida* (Ichneumonidae), *Xiphidriophagus meyerinckii* (Pteromalidae), *Coeloides rossicus betulae* (Braconidae), *Spathius elegans* (Braconidae), and *Orussus* sp. (Orussidae). The latter three parasitoids prior to this study had no confirmed hosts; *Xiphidriophagus* is new to N. America. This parasitoid complex is compared with that of the Palaearctic *Xiphydria camelus*, showing a series of pairs of closely related Palaearctic and Nearctic forms.

More than 20 years ago the British entomologists G. H. Thompson and E. R. Skinner produced their film on the alder wood wasp and its insect enemies (1961), a film that documents the complex story of *Xiphydria camelus* (L.) and four parasitoid wasps. This film has been shown to thousands of students in the United States as well as Great Britain; it must be the most widely disseminated study of insect parasitoids, now that the works of J. H. Fabre are no longer made required reading for young scientists. The film is also one of the earliest examples of a modern phenomenon: the scientific study that has been fully documented on film but not in print. As my study of a Nearctic species, *Xiphydria maculata* Say, is to a large extent dependent upon the Thompson and Skinner film, I will briefly recapitulate the alder wood wasp study as a prelude.

The alder wood wasp, *Xiphydria camelus*, oviposits in recently killed alder trees (*Alnus* spp.). The eggs, accompanied by propagules of a symbiotic fungus, are deposited at the interface between bark and wood. Upon hatching from the egg, the larva quickly bores into the wood, where it tunnels until fall. The larva pupates the following spring and emerges as an adult in late spring or early summer.

Four species of hymenopterous parasitoids are associated with *X. camelus*. The first of these, *Aulacus striatus* Jurine (Aulacidae), searches for the oviposition holes of *X. camelus* and lays its own egg inside the recently deposited egg of its host. When the host larva is fully grown the parasitoid larva begins to grow rapidly, soon killing its host. The aulacid larva forms a cocoon within the pupal cell of its host, overwintering in this cocoon and emerging as an adult the following spring. The second parasitoid, *Rhyssella approximator* (Fabricius) (= *R. curvipes* Gravenhorst), is a large ichneumonid that drills through bark and wood to intercept a large larva of *X. camelus*. After stinging and paralyzing its host, the wasp lays an egg externally on the larva. Like *A. striatus*, *R. approximator* grows rapidly on its mature host larva, overwinters in the wood, and emerges as an adult the following year. Another ichneumonid, *Pseudorhyssa alpestris* (Holmgren), is a cleptoparasitoid of *R. approximator*. *P. alpestris* uses the oviposition hole drilled by *R. approximator* to gain access to the larva of *X. camelus*. Upon hatching, the *P. alpestris* larva kills that of *R. approximator* and consumes the wood wasp larva. The fourth parasitoid, *Xiphidriophagus meyerinckii* (Ratzeburg) (Pteromalidae) is a gregarious external parasitoid that kills large larvae of *X. camelus*. The female *X. meyerinckii* enters old *Xiphydria* exit holes and burrows down through the frass in the abandoned larval

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gallery until she detects a *Xiphydria* larva boring nearby in the wood. *X. meyerinckii* then cuts a gallery through the intervening wood, stings the host, and lays about 30 eggs on its body.

Since 1961 there has been a quantitative study of the effect of ichneumonids of the tribe Rhyssini on various European Siricidae and Xiphydriidae (Kazmierczak 1979).

Inspired by the alder wood wasp film, I have been observing a native Nearctic wood wasp, *Xiphydria maculata*, and its insect enemies over a period of about three years. One goal of this study is descriptive: very little is known about the biology of Nearctic Xiphydriidae, or about their abundance, or about the amount of damage they cause, or about their insect associates. A second goal of this study is comparative: there are intriguing questions concerning parasitoid complexes of similar species found on separate continents. Are the parasitoids of the two *Xiphydria* closely related, or have unrelated species taken similar ecological roles in the two regions? Is there any evidence of apparently "empty" ecological niches? Is it possible to formulate any hypotheses on the biogeographical history of any of these groups of insects?

### MATERIALS AND METHODS

Most of the insects studied were collected in West Lafayette, Tippecanoe County, Indiana. *Xiphydria maculata* and its parasitoids were easily obtained from fallen maple (*Acer* spp.) branches in parks, in wooded areas, and under shade trees along city streets and on the Purdue University campus. Most of these branches were collected in winter and spring. The branches, which were usually 3 to 6 cm in diameter, were brought into the laboratory; some branches were split and the insects removed for examination, others were cut into sections and placed in plastic bags, into which the insects emerged. Each pinned specimen was given labels stating the date the branch was brought in, the date of emergence, and the host. When parasitoids emerged from wood known to have contained larvae of *X. maculata*, the host-parasitoid association was verified by splitting the wood and finding the head capsule and terminal abdominal spine of the host larva together with the shed skin or cocoon of the parasitoid. The head capsule and terminal spine of *Xiphydria* species are not easily confused with those of most other insects, though large Mordellidae larvae, occasionally occurring in maple, have a somewhat similar spine. Two additional *Xiphydria* species, *X. tibialis* Say and *X. polia* Smith, occur on maple in Tippecanoe County; neither of these species were reared from wood from which *X. maculata* emerged. For the purposes of this study, therefore, a firm host-parasitoid association was considered established by the combination of an emerged adult parasitoid, plus the cocoon or exuvia of the parasitoid and host remains at the bottom of an exit shaft, plus adult *Xiphydria maculata* reared from the same piece of wood. Voucher specimens of the insects discussed in this paper have been placed in the U.S. National Museum.

### SPECIES ACCOUNTS

#### *Xiphydria maculata* Say.

In central Indiana, if not elsewhere, the most surprising fact about *X. maculata* (Fig. 1) may be its abundance. My first finding of this species I considered an extraordinary piece of luck, but as my lucky finds were repeated day after day to the point of monotony and my office became filled with large branches containing these "rare" insects, it became evident that, although *X. maculata* adults are seldom seen, this species was by far the commonest of all wood boring larvae seen in branches of maple. It is not, however, established that this species is as common throughout its range, or whether it has cycles of abundance. The only author to remark on the abundance of *X. maculata* is Harrington (1884), who found *X. maculata* "far from being so rare as I then considered it," in Ottawa, Ontario.

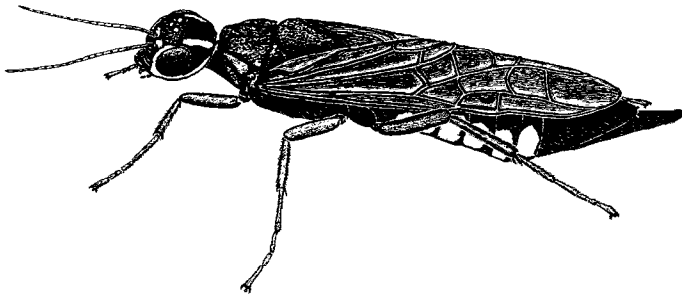


Fig. 1. *Xiphydria maculata*, female, natural stance, actual length 13 mm.

This species occurs in the northeastern United States and southeastern Canada, with isolated records as far west as Manitoba, Kansas, and eastern Texas, as well as a dubious record from California (Smith 1976).

Reported hosts of *X. maculata* are *Acer saccharinum* L. and *A. rubrum* L. (Smith 1976); I have reared specimens (103 voucher specimens) from many separate pieces of *A. saccharinum* and *A. saccharum* Marsh. Harrington (1884) found specimens attacking small to medium-sized trees, always on the bole below the branches. I have seen a series of 4–5-cm diameter *A. saccharum* saplings riddled with galleries of *X. maculata*, but most infested material is tops and branches from 2.5 cm to 9 cm in diameter. The galleries of *X. maculata* often weaken branches so extensively that the branches break off at the point where the galleries are most concentrated. The large number of such branches lying on the ground and showing the galleries of *X. maculata* in their broken ends suggests that *X. maculata* normally oviposits in branches that are still attached to the tree, or in the boles of small standing trees. I have actually observed oviposition on only six occasions; in two instances the material was fallen limbs, in four instances it was broken, bent-over trees or branches still attached to the tree.

Larval galleries usually run parallel to the grain and are filled with densely packed white frass composed of minute fibers. There is seldom any obvious evidence of fungus around the gallery, except for the pupal cell, which is usually lined with black fungus. The larva sometimes makes a bend in the gallery and approaches the surface of the wood before constructing a pupal cell (Fig. 2).

The mating of *X. maculata* has been described by Rohwer (1915), who stated that no courtship takes place. I found that males kept in isolation in small plastic dishes produced an audible tapping noise by striking the end of the abdomen very rapidly against the side

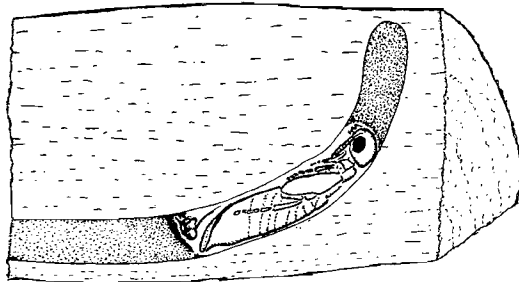


Fig. 2. pupa of *Xiphydria maculata*.

of the container, with bursts of tapping occurring at short intervals. By tapping lightly on the container with the point of a pencil I was sometimes able to induce the males to start tapping. On one occasion three males were observed walking up and down a small uprooted tree, making the characteristic tapping movements with the abdomen. On a few occasions females were heard tapping. It seems possible, therefore, that there are vibrational courtship signals preliminary to the rapid approach and mating observed by Rohwer and also observed in the present study. Male *X. maculata* have a brush of enlarged stiff, backward-pointing setae on abdominal sternites 6 and 7, with a smaller brush on sternite 5. These brushes have several conceivable functions, including sending or receiving signals through a substrate. Cooper (1953) described abdominal tapping in female Orussidae, and suggested the female was sounding out the wood to discover concealed larvae; the Orussidae, like the Xiphydriidae, are wood-inhabiting members of the superfamily Siricoidea (Ross 1937).

In the laboratory some pieces of maple produced series of at least 20 female *X. maculata* and no males, nor any evidence of an earlier emergence of males. The possible explanations for these all-female emergences are complete mortality of male larvae, or selective oviposition of female eggs in certain kinds of host material, or thelytoky in some individuals. None of these phenomena is known to occur in Xiphydriidae.

The life cycle probably normally requires one year, with adult emergence in early summer. Several large sugar maple branches broken during a spring storm in 1979 produced adult *X. maculata* the following summer. Most larvae I have seen in late winter and early spring are apparently nearly mature, but some are as small as 4 mm in length; it seems likely that these small individuals require two years to develop as there is no evidence of fall emergence of adults. Harrington (1884) observed adults (in Canada) from mid-June to the end of July. I have observed adults in the field in Indiana from 27 May to 1 July.

There is little evidence of competition between *X. maculata* and other species of *Xiphydria*. On two occasions I reared *X. tibialis* from *Acer saccharum* branches apparently similar to those often attacked by *X. maculata*. On one occasion I observed a specimen of *X. polia* ovipositing in an uprooted *A. saccharinum* with *X. maculata* females ovipositing nearby. Additional species collected in the study area are *X. scafa* Smith, *X. hickoriae* Rohwer, and *X. abdominalis* Say, none of which is known to attack maple.

It is still not clear whether *X. maculata* should be considered a beneficial insect promoting pruning of dead and unhealthy branches, or a pest that kills healthy and slightly stressed trees and branches. Harrington (1884) took the latter view; in an article gloomily entitled "A New Foe to the Maple" he described *X. maculata* attacking apparently healthy young shade trees. *X. maculata* was not discussed as a pest in any recent works on forest and shade tree entomology, but this does not prove that *X. maculata* is not causing considerable damage out of sight in the tops of shade trees. In siricids the ability to kill trees and branches depends entirely upon the phytotoxicity of a mucous secretion injected at oviposition and the virulence of a symbiotic fungus accompanying this secretion (Spradbery 1973); the same might be true of xiphydriids.

#### *Aulacus burquei* (Provancher)

*Aulacus burquei* is a parasitoid that was observed laying its egg in the egg of its host, in the manner of the European *A. striatus*. *A. burquei* varies in abundance from one maple branch to another, some branches kept in the laboratory produced more adult *A. burquei* than *X. maculata*, while other apparently similar branches produced no *A. burquei*. This suggests that this parasitoid is highly successful when it finds a batch of eggs, but often misses batches of eggs entirely.

*Aulacus burquei* is known to occur from Nova Scotia south to Maryland and west to Michigan (Carlson 1979). The only known host is *X. maculata*, though I have reared one specimen from the tree *Carpinus caroliniana* Walt., in which the host was probably *X. maculata*.

Almost all specimens seen were reared. Two specimens were collected in the field, on 6 June and 18 June respectively. Two larval specimens were removed from their cocoons on

7 July. I have prepared 44 voucher specimens. Published records of 14 specimens presumably taken in the field have collection dates from 17 June to 6 August (Townes 1950).

*Aulacus digitalis* Townes

*Aulacus digitalis* (Fig. 3), like *A. burquei*, occurs in maple branches, frequently emerging from the same branches as *A. burquei*. The two aulacids are easily distinguished morphologically (Townes 1950), but these differences, chiefly in coloration and the length of the metacoxal process, do not have any obvious ecological significance. The ovipositor lengths of the two species are similar.

*A. digitalis* is known to occur from New England west to northern Ohio (Carlson 1979). The only known host is *X. maculata*. Adults were taken in the field on 3 June and 7 June respectively; I have in addition 41 reared voucher specimens. Published records of three specimens taken in the field have collection dates of 20–30 June and 17 July (Townes 1950).

*Rhysella nitida* (Cresson)

*Rhysella nitida*, like the Palearctic *R. approximator*, attacks large *Xiphydria* larvae, drilling through bark and wood to reach its host. *R. nitida* is an abundant species that can be found in almost all pieces of maple that contain *X. maculata*.

*R. nitida* is distributed from Maine south to Georgia, and west to Minnesota; specimens have also been collected in British Columbia (Townes and Townes 1960). The only host reported for this species is *X. maculata* (Townes and Townes 1960) but the specimens from British Columbia must have had another host, almost certainly *X. mellipes* Harris, the only xiphydriid known from the area. I have reared *R. nitida* from *X. tibialis* as well as from *X. maculata*. The flight season is from early May to the end of August (Townes and Townes 1960). I have prepared 45 voucher specimens of this species. Townes and Townes (1960) provided an illustration of *R. nitida*.

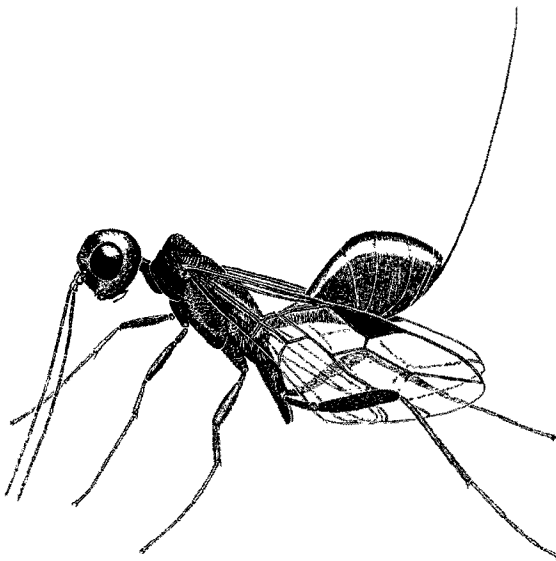


Fig. 3. *Aulacus digitalis*, female, natural stance, actual length 8.5 mm.

*Xiphydriophagus meyerinckii* (Ratzeburg)

On four occasions I have reared this species (Fig. 4) from larvae of *X. maculata* in *Acer saccharum*; this is the first Nearctic record of the genus *Xiphydriophagus*. The only described species of *Xiphydriophagus* is *X. meyerinckii*, mentioned above as a parasitoid of *Xiphydria camelus*. The Indiana specimens were identified as *X. meyerinckii* by Dr. Eric E. Grissell, (pers. comm.).

My limited studies of this species suggest that its life history is the same as that of European *X. meyerinckii*. Larvae were found clustered in the cell of the host. A tunnel could be seen in the wood, connecting the larval cell with a larva gallery and emergency hole of another *Xiphydria maculata*. Female *Xiphydriophagus* in the laboratory entered *Xiphydria* exit holes and commenced tunneling, presumably seeking host larvae.

The branches from which this species was reared contained only a few host larvae and did not appear suitable for another generation of wood wasps.

The geographic range and host range of *X. meyerinckii* in North America is unknown. In Europe, this species has been reared from *Betula* and *Ulmus*, as well as *Alnus* (Ferriere 1952), suggesting that several *Xiphydria* species may be hosts.

*Coeloides rossicus betulae* Mason

I have reared this braconid (Fig. 5) on 15 occasions from *X. maculata* and *X. tibialis* in *Acer saccharum*. The branches were found on the ground in deep shade in wooded areas. *Rhysella nitida* and, on two occasions, *Xiphydriophagus* were taken from material containing *C. rossicus*, and seem possible competitors of the latter. No *C. rossicus* were reared from the large number of branches found under shade trees along streets, branches in which *Aulacus* sp. and *R. nitida* are common.

*C. rossicus betulae* is the Nearctic subspecies of the Holarctic *C. rossicus* (Kokujev). Most reports of Nearctic specimens are from *Betula* (one from *Acer*), and Mason (1978) tentatively suggested that *Agrilus anxius* Gory might be the host; this suggestion is probably based on the host tree, a "birch borer" label on one specimen, and the fact that some other *Coeloides* do attack buprestids. There is no reason to rule out *Agrilus* spp. as

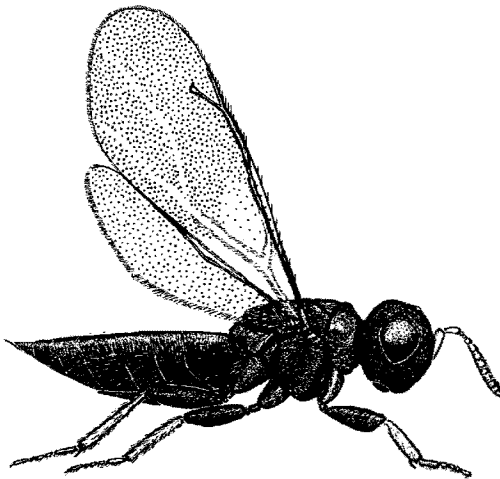


Fig. 4. *Xiphydriophagus meyerinckii*, female, actual length 2.8 mm.

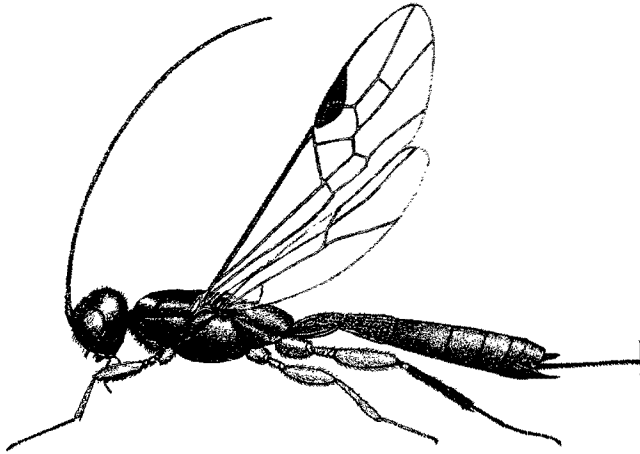


Fig. 5. *Coeloides rossicus*, female, actual length 9.5 mm.

hosts, but the only confirmed hosts at present are my records of *X. tibialis* and *X. maculata*, and on this basis there is a good possibility that *X. mellipes* is the host in *Betula*. In Europe the known host of *C. rossicus* is *Xiphydria prolongata* (Geoffroy) in *Salix* spp. (Balazy and Michalski 1977).

The geographic range of *C. rossicus betulae* includes southeastern Canada, the northeastern U.S., and British Columbia (Mason 1978).

I have taken one specimen in flight on 30 May; published collection records that presumably refer to adults collected in the field (Mason 1978) are from 28 May to 28 August. I have 15 voucher specimens.

#### *Spathius elegans* Matthews

On three occasions the braconid *Spathius elegans* (Fig. 6) was reared from small *Xiphydria* larvae, twice from *X. maculata*, once from *X. tibialis*. The larvae parasitized were near the surface of branches of *Acer saccharum* on the ground in dense shade in a wooded area. This species is undoubtedly an ectoparasitoid like other members of its genus (Matthews 1970) and like *Rhyssella* and *Coeloides*.

There are no other confirmed records of hosts of *S. elegans*. A tentatively identified teneral male was reared by Hopkins from wood infested with *Hadrobregmus* sp. (Matthews 1970); this possible host is almost certainly not *Hadrobregmus* according to current nomenclature, but some other genus of Anobiidae (see Knutson 1963). There is a record of a specimen reared from *Juglans nigra* L. (Matthews 1970), and I reared a specimen from *Celtis occidentalis* L.; neither of these hosts are likely to harbor xiphydriids. The admittedly unsatisfactory evidence on host relationships of *X. elegans* seems to suggest that this species is not a specialist dependent on *Xiphydria* but rather attacks a number of wood borers within a certain size range found in a particular habitat.

The geographic range of *X. elegans* is Quebec to Florida, west to Iowa and Minnesota; there is also a single specimen from San Juan Island, Washington (Matthews 1970). The flight season is 19 May to 7 September (the earlier date from Florida) (Matthews 1970). I have collected two adults in a flight trap, 24 June and 4 August, for a total of seven voucher specimens.



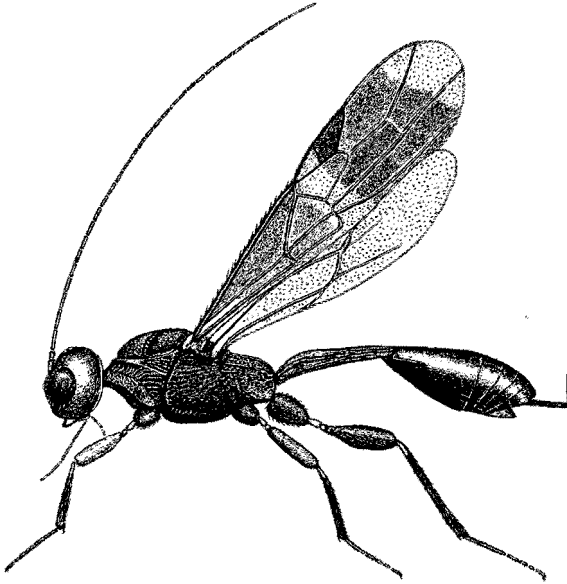


Fig. 6. *Spathius elegans*, female, actual length 5.5 mm.

*Orussus* sp.

Four separate branches of *Acer saccharum* containing *X. maculata* produced specimens of this undescribed orussid (Fig. 7). Three of these branches were split to reveal the larval skins of *X. maculata* together in the gallery with the larval and pupal skins of the orussid. Hosts of eastern Orussidae have not previously been identified, though the similar *O. sayii* is often associated with buprestids (Cooper 1953). On one occasion I reared specimens of *Agrilus obsoletoguttatus* Gory as well as *X. maculata* from *Acer saccharum* from which *Orussus* sp. emerged. A western species, *Orussus occidentalis* (Cresson), has been taken from the pupal cell of a buprestid (Burke 1917). The only report of *Orussus* associated with *Xiphydria* is Rudow's observation (cited in Rohwer 1925) that a European *Orussus* occurs together with *Xiphydria* on *Betula*. For the present it seems unwarranted to assume this orussid is a specialist associated only with *Xiphydria* in the manner of *Rhysella* spp. and some *Aulacus* spp.

*Orussus* sp. occurs together with *Rhysella nitida* and *Aulacus burquei* in branches from exposed trees. In the laboratory I found the orussids to be active only in bright light; in

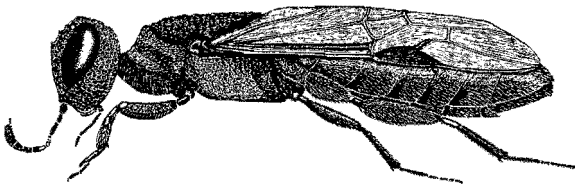


Fig. 7. *Orussus*, undescribed species, female, actual length 8 mm.

dim light and at night the adults sought open galleries (their own, or those of *X. maculata*) and backed into these holes until only the front of the head was visible.

#### GEOGRAPHIC RANGE NOTES

The following species of *Xiphydria* and parasitoids have not previously been reported from Indiana. All records are from Tippecanoe County, in the north-central part of the state.

*Xiphydria abdominalis* Say, *X. polia* Smith, *X. scafa* Smith, *X. hicoriae* Rohwer, *X. tibialis* Say, *Aulacus burquei* (Provancher), *A. digitalis* Townes, *A. lovei* (Ashmead), *Rhysella nitida* Cresson, *R. humida* Say, *Xiphidriophagus meyerinckii* (Ratzeburg), *Coeloides rossicus betulae* Mason, and *Spathius elegans* Matthews.

#### RELATIONSHIPS BETWEEN PARASITOIDS OF *X. MACULATA* IN INDIANA

Most parasitoids of *X. maculata* clearly differ in the way they exploit their host, but the term "resource partitioning," which often implies competitive displacement, may not be appropriate in this case. The parasitoids differ ecologically in ways that may be more simply explained as ecological differences that are inherent in the taxonomic groups to which they belong than as behavioral differences that coevolved among species utilizing the same species of host.

*Rhysella nitida* is limited by the length of its ovipositor, which can reach larvae at a depth no greater than 21 mm, the maximum length of the ovipositor. Small individuals have a proportionally short ovipositor as short as 11 mm. *X. maculata* larvae often occur at depths greater than 21 mm. Small *X. maculata* larvae are not suitable hosts, so that small species of parasitoids can pre-empt hosts before these hosts are large enough to be suitable for *R. nitida*.

*Coeloides rossicus*, though one of the largest members of the genus *Coeloides*, is considerably smaller than *R. nitida* and is able to utilize hosts that are suboptimal or too small for *R. nitida*. *C. rossicus*, however, is limited to hosts at a depth of 10 mm or less, and the smallest individuals have an ovipositor only 5.5 mm long. In addition, *C. rossicus* has thus far been found only in heavily shaded branches, whereas *R. nitida* occurs in both shaded and exposed branches.

*Spathius elegans* is one of the largest species of *Spathius*, but the largest individuals are only 6.5 mm long, about the size of the smallest *C. rossicus*. The ovipositor is 5–6 mm. *S. elegans* has been reared only from heavily shaded branches.

*Xiphidriophagus meyerinckii* can attack hosts at any depth in the wood, and can probably attack larvae of various sizes. *X. meyerinckii* however, attacks only the second and succeeding generations of *X. maculata* in a piece of wood, because exit holes of adult *X. maculata* must be present to provide access to host larvae in the wood. *X. maculata* attacks relatively sound branches, not soft and rotten branches, so some dead branches rot too rapidly to be suitable for the second host generation required by *Xiphidriophaga*, and few branches are likely to produce a third generation of hosts.

The two species of *Aulacus* are in no way limited by the depth at which the host occurs, as the eggs of *X. maculata* are always within the reach of *Aulacus*. The *Aulacus* species, however, have only a short time in which to find a batch of eggs of the host before the eggs hatch and the larvae bore into the wood. A few days of poor flight conditions, or any other factor that hinders efficient dispersal and host detection, allows the irretrievable escape of large numbers of potential hosts. The coexistence of *A. burquei* and *A. digitalis* is not explained by any known difference in ecological roles, but ecological differences could easily go unnoticed, especially in the important areas of dispersal and host detection. It may not be correct, however, to assume that an ecological difference must exist to explain the coexistence of *A. burquei* and *A. digitalis*. These two species utilize a resource (*Xiphydria* eggs) that is distributed in highly ephemeral patches in a habitat (dead branches) that is itself patchily distributed in time and space. The coexistence of two

ecologically similar species of *Aulacus* could be a small scale example of the diversity that may occur in temporary, disturbed habitats under conditions where numbers of colonizers are relatively independent of the numbers of offspring produced by the parent populations, and where the first colonizers can permanently preempt resources (Connell 1978).

*Orussus* sp., like the other species that oviposit on or near larvae in wood, is apparently limited in host utilization by the length of the ovipositor, which is normally retracted, and was not measured in use. It is not known whether the host is paralyzed or whether the larva of *Orussus* is able to tunnel in the wood looking for its host. This *Orussus* seems to have an ecological limitation in that it is active only under conditions of high light intensity.

The outcome of direct confrontation between any of these species of parasitoids is not known. The confrontation that is likely to occur most frequently is the attack by *R. nitida*, *X. meyerinckii*, *C. rossica*, *S. elegans*, or *Orussus* sp., on a *X. maculata* larva containing a small *Aulacus* larva.

### COMPARISON OF PARASITOID COMPLEXES

The parasitoid complexes in Europe and Indiana have in common parasitoids representing the genera *Aulacus*, *Rhyssella*, *Xiphidriophagus*, and *Coeloides*. There is no example of a species in one complex whose role is filled by a representative of a different genus in the other complex. There are, however, examples of ecological roles that are occupied in one complex and apparently vacant in the other. The best documented example is the Palearctic hyperparasitoid *Pseudorhyssa alpestris*, for which there is no Nearctic equivalent hyperparasitoid either in the genus *Pseudorhyssa* or in any other genus. The only Nearctic representative of *Pseudorhyssa*, *P. ruficoxis* (Kriechbaumer), is associated with Siricidae in conifers. No representatives of *Spathius* or *Orussus* are known to attack Palearctic Xiphidriidae. Of these two only *Spathius*, which attacks small *Xiphidria* larvae, has a demonstrably distinctive ecological role, a role apparently not occupied in Europe.

Some evidence of the biogeographical history of two *Xiphidria* species and their parasitoid complex can be seen from a number of cases of closely related species pairs. These species pairs show a Holarctic ecological complex that has diverged relatively little in the time since the species were isolated as Palearctic and Nearctic populations. *Xiphidria camelus*, which attacks *Alnus* spp., has as its counterpart *X. mellipes*, which attacks *Betula* spp. *X. mellipes*, the only transcontinental species of *Xiphidria*, more closely resembles *X. camelus* than any Nearctic *Xiphidria* (Smith 1976). *Aulacus striatus* is matched by *A. pallipes* Cresson, a transcontinental species attacking *X. mellipes*. *A. striatus* and *A. pallipes* are particularly closely related (Townes 1950). *Rhyssella approximinator* is matched by *R. nitida*, which probably has a transcontinental distribution and almost certainly attacks *X. mellipes*, at least in northwestern North America, *Rhyssella approximinator* and *R. nitida* may be only subspecifically distinct (Townes and Townes 1960). *Coeloides rossicus* and *Xiphidriophagus meyerinckii* are Holarctic species, though their connection with *X. camelus* and *X. mellipes* respectively have yet to be established.

In the case of *X. maculata*, this species is attacked by all of the Holarctic complex except for *A. pallipes*, and is also attacked by two apparently host-specific species of *Aulacus*, as well as by species of *Orussus* and *Spathius*, which may well be habitat-specific and host-generalist parasitoids.

This preliminary study raises a number of questions aside from the questions on host ranges and geographic ranges suggested in the paragraphs above. There is the general zoogeographic question of the origin of the host-parasitoid complexes in the Nearctic and Palearctic regions. There are the species of *Xiphidria* in both regions whose parasitoids have not been catalogued. There are questions of competitive interactions, particularly those involving aulacids. There are questions on how the various parasitoids locate their hosts. There is no consensus on the pest status of *X. maculata* or any other Nearctic *Xiphidria*. Finally, there is the ultimate and daunting task of revealing the population dynamics of *X. maculata* and the quantitative impact of its insect enemies.

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