

ORIGINAL RESEARCH



Insect Herbivores of Ferns along the Pacific Northwest Coast of North American

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ABSTRACT

Fifteen species of insect herbivores were discovered on ferns growing along the Pacific northwest coast of North America. These included insects from the orders: Diptera in the families Anthomyiidae, Cecidiomyiidae and Syrphidae; Lepidoptera in the families Erebidae, Tortricidae and Noctuidae; Hymenoptera in the family Tenthredinidae; Hemiptera in the family Aphididae and Coleoptera in the family Curculionidae. The present study illustrates these associations that provides new world and North American host records of fern herbivores. The fossil record of these families is used to determine if the most ancient of these insects (dating from the Mesozoic) are now mostly restricted to ferns and the most recent ones (dating from the Cenozoic) are mostly polyphagous, feeding on ferns as well as various angiosperms. Results indicate that the insect clades belonging to the most ancient families, such as *Aneugmenuss* and *Strongylogaster* in the Tenthredinidae and *Dasineura* and *Mycodiplosis* in the Cecidiomyiidae, appear to be monophagous on ferns.

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Introduction

The present paper discusses insect herbivores of ferns along the Pacific Northwest coast of North America. While insects on ferns have been studied in many parts of the world (Balick et al., 1978; Cooper-Driver, 1978; Gerson, 1979; Hendrix, 1980; Lawton, 1976, 1982, 1984; Lawton & MacGarvin, 1985; Ottosson & Anderson, 1983), this is the first discussion of fern insects along this geographic region. Included are representatives of the dipteran families Anthomyiidae, Cecidiomyiidae and Syrphidae, the lepidopteran families Erebidae, Tortricidae and Noctuidae, hymenopteran family Tenthredinidae, hemipteran family Aphididae and the coleopteran family Curculionidae. Some of these associations represent new world and North American host records.

When ferns first appeared in the upper Devonian (Pryer et al., 2004), they possessed morphological features, such as rigid thick-

walled sporangia with indusia and paraphyses and hard multiple-layered spores as well as various chemical compounds, for protection from herbivores. Over time, insect herbivores adapted to ferns and some became able to complete their development on these plants (Cooper-Driver, 1978; Gerson, 1979; Hendrix, 1980; Ottosson & Anderson, 1983).

A previous hypothesis (Cooper-Driver, 1978) suggested that today, the insects dependant on ferns are more “primitive” than those that use ferns intermittingly for their development. To test this hypothesis, the insects collected in the present study were arranged into “primitive” and “advanced” categories depending on the fossil record on their respective families. The insects on Pacific Northwest ferns support this hypothesis, showing that “primitive” insects such as members of the Tenthredinidae, Cecidiomyiidae and Aphididae that first appear in the Mesozoic appear to be monophagous on ferns while “advanced” insects that first appear

in the Cenozoic are polyphagous, feeding on ferns as well as various angiosperms.

Method and materials

The study area included dunes, dune forests and dune wetlands within 0.25 miles from the Pacific ocean from northern California through Oregon to northern Washington. The ferns examined were: northern wood fern (*Dryopteris expansa* (C. Presl) Fraser-Jenk. & Jermy), western sword fern (*Polystichum munitum* (Kaulf.) C.Presl) and bracken (*Pteridium aquilinum* (L.) Kuhn). Observations were made every 1-2 months over a 4 year period. Developmental stages of fern insects were maintained in petri dishes or small cages supplied with fern foliage until adults were obtained. Photos were taken with a Sony digital still camera, model no. DSC-H-10.

Results

Insects found on Pacific northwest ferns included members of the Diptera, Lepidoptera, Hemiptera, Hymenoptera and Coleoptera (Table 1) (Figs.1-10). Representatives of the Diptera included two genera of Cecidiomyiidae. The larvae of *Dasineura* Rondani were easily noticeable since they stimulated gall formation on the leaf

margins of bracken. These galls became quite black as the spore-feeding larvae matured (Fig. 6A). While such galls of *Dasineura* spp. are found on bracken in England and Europe (Gerson, 1979; Spencer, 1973, Ottosson & Anderson, 1983), they apparently have not been reported previously in North America (Gagne 2004a, 2004b). The second genus of Cecidiomyiidae on bracken was *Mycodiplosis* Rübssaamen. The larvae of this species developed with fungi in small compartmentalized mines in the pinna (Fig. 6B). While members of this genus occur on angiosperms in both New and Old worlds, no *Mycodiplosis* spp. have been reported from ferns (Gagné, 2004, 2010). A dipteran on the northern wood fern (*Dryopteris expansa*) was *Chirosia idahensis* Stein (Anthomyiidae) with a completely different developmental pattern. The female deposits eggs in the coiled fronds of the fern, the action which prevents the frond from unwinding (Fig.1A). The hatched larvae feed inside the coiled fronds, becoming surrounded with moist fecal material and decomposed plant material (Fig. 1B). Adult flower flies (Diptera: Syrphidae) fed on spores of northern wood fern (*Dryopteris expansa*) (Fig. 10B). Syrphid larvae were especially common on bracken when aphids were present.

Insect	Stage	Plant damage
<i>Chirosia idahensis</i> (Diptera: Anthomyiidae) (Fig.1A,B)	larva	circinate frond
<i>Strongylogaster</i> sp. (Hymenoptera:Tenthredinidae)(Fig.2A,B)	larva, adult	foliage, spores
<i>Spilosoma virginica</i> (Lepidoptera: Erebidae) (Fig.3A, B)	larvae	foliage
Geometridae (Lepidoptera) (Fig.4A,B)	larvae	foliage
<i>Phlogophora</i> spp. (Lepidoptera; Noctuidae) (Fig.5A, B)	larva	foliage
<i>Dasineura</i> sp. (Diptera: Cecidiomyiidae) (Fig.6A)	larva	spores
<i>Mycodiplosis</i> sp. (Diptera: Cecidiomyiidae) (Fig. 6B)	larva	pinna
<i>Nemocestes tuberculatus</i> (Coleoptera:Entiminae) (Fig.7A)	adult	foliage
<i>Sciopithes obscurus</i> (Coleoptera: Entiminae) (Fig.7B)	adult	foliage
<i>Acleris</i> sp. (Lepidoptera:Tortricidae)(Fig.8A)	larva	pinna, spores
Various Tortricidae (Lepidoptera)(Fig.8B)	larva	foliage
<i>Aneugmenuss</i> sp. (Hymenoptera:Tenthredinidae)(Fig.9A)	larva	foliage
<i>Macrosiphum</i> sp. (Hemiptera:Aphididae)(Fig.9B)	all stages	foliage
<i>Orgyria antiqua</i> (Lepidoptera: Erebidae) (Fig.10A)	larva	foliage
<i>Eupodes lapponicus</i> (Diptera: Syrphidae) (Fig.10B)	adult	spores

Table 1. Insects feeding on ferns along the Pacific northwest coast of North America.

Several families of Lepidoptera occurred on ferns in the sampling area. Included were representatives of the families Noctuidae (Fig. 5), Erebidae (Figs. 3, 10A), Geometridae (Fig.4) and Tortricidae (Fig. 8). The larvae demonstrated a range of developmental patterns. Feeding completely exposed on the fronds was the most

common behavior but some geometrids covered themselves with webbing (Fig. 4A). Tortricid larvae had their typical leaf-rolling behavior on pinnules of western sword fern (Fig.8B) and some *Acleris* spp. Hübner sp. developed in galls on bracken (Fig. 8A).



Figure 1. A. Coiled tip of northern wood fern frond (*Dryopteris expansa*) containing a larva of *Chirosia idahensis* (Diptera: Anthomyiidae). Bar = 10 mm. B. Larva of *Chirosia idahensis* (Diptera: Anthomyiidae) protruding from coiled tip of frond of northern wood fern (*Dryopteris expansa*). Bar = 4.6 mm.



Figure 2. A. Larvae of the tenthredinid, *Strongylogaster* sp. (Hymenoptera: Tenthredinidae) feeding on western sword fern (*Polystichum munitum*). Bar = 4.0 mm. B. Adult *Strongylogaster* sp. (Hymenoptera:

Tenthredinidae) on western sword fern (*Polystichum munitum*). Bar = 4.1 mm.

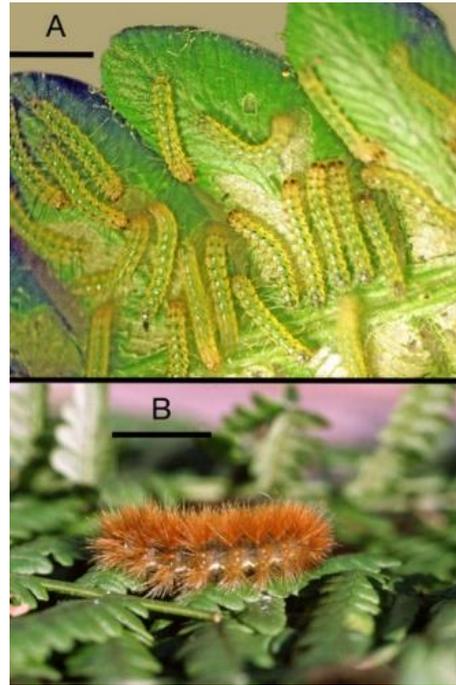


Figure 3. A. Recently hatched larvae of *Spilosoma virginica* (Lepidoptera:Arctiidae) feeding on bracken (*Pteridium aquilinum*) pinna. Bar = 2.5mm. B. Mature larva of *Spilosoma virginica* (Lepidoptera:Arctiidae) feeding on bracken (*Pteridium aquilinum*). Bar = 5.0 mm.



Figure 4. A. Geometrid larva (Lepidoptera: Geometridae) under protective webbing while feeding on western sword fern (*Polystichum munitum*). Bar = 1.5 mm. B. Geometrid larva

feeding on bracken (*Pteridium aquilinum*). Bar = 2.0 mm .



Figure 5. A. Larva of *Phlogophora* sp. (Lepidoptera: Noctuidae) feeding on bracken (*Pteridium aquilinum*). Bar = 4.6 mm. B. Different larva of *Phlogophora* sp. (Lepidoptera: Noctuidae) feeding on bracken (*Pteridium aquilinum*). Bar= 4.8 mm.

Cecidiomyiidae) with fungi infecting veinlets of a bracken pinna (*Pteridium aquilinum*). Note white spore clusters (urediospores?) on surface. Bar= 1.3 mm.



Figure 7. A. Adult *Nemocystes* sp. weevil (Coleoptera: Curculionidae) feeding on bracken (*Pteridium aquilinum*). Bar = 1.0 mm B. Adult *Sciopithes* sp. weevil (Coleoptera: Curculionidae) feeding on western sword fern (*Polystichum munitum*) pinna. Bar= 2.3 mm.

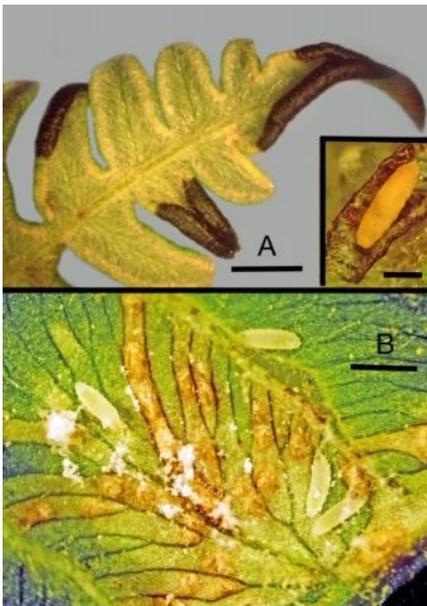


Figure 6. A. Black, in-rolled edges of leaf margin galls on bracken pinna (*Pteridium aquilinum*) protecting larvae of *Dasineura* sp. (Diptera: Cecidiomyiidae). Bar= 6.0 mm. Insert shows mature *Dasineura* larva inside gall. Bar= 0.5 mm. B. Larvae of *Mycodiplosis* sp. (Diptera:

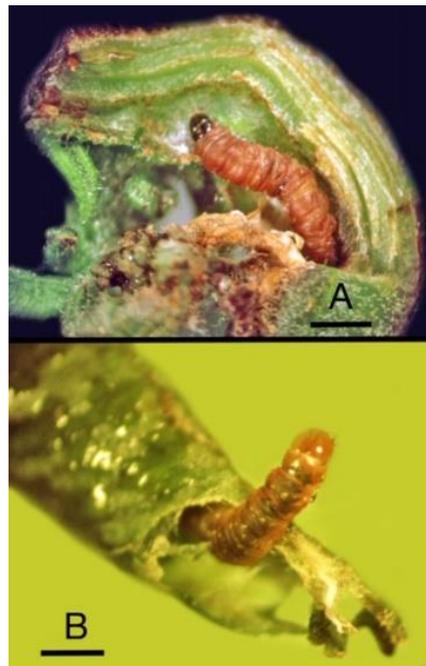


Figure 8. A. *Acleris* sp. (Lepidoptera:Tortricidae) larva developing in a

leaf gall on bracken (*Pteridium aquilinum*). Bar = 2.5 mm. B. A tortricid larva (Lepidoptera:Tortricidae) emerging from a hole in a rolled up pinnule of western sword fern (*Polystichum munitum*). Bar= 2.8 mm.

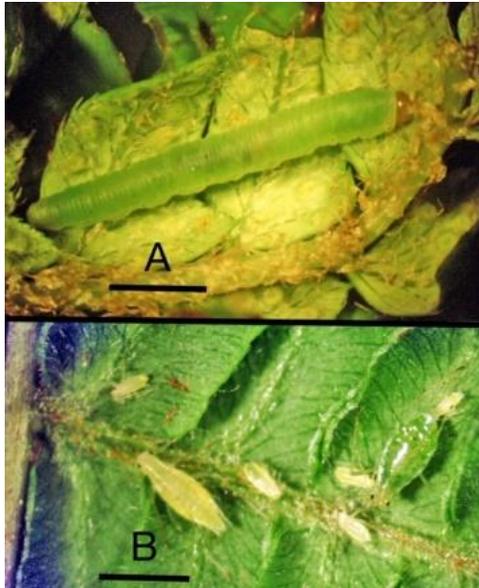


Figure 9. A. Larva of *Aneugmenus* sp. (Hymenoptera:Tenthrednidae) feeding on western sword fern (*Polystichum munitum*). Bar = 2.5 mm. B. Group of *Macrosiphum* sp. (Hemiptera: Aphididae) developing on bracken (*Pteridium aquilinum*). Bar = 3.0 mm.



Figure 10. A. *Orgyria antiqua* (Lepidoptera: Erebidae) feeding on bracken (*Pteridium*

aquilinum). Bar= 4.2 mm. B. Adult *Eupeodes lapponicus* (Diptera: Syrphidae) feeding on spores of northern wood fern (*Dryopteris expansa*). Bar= 3.3 mm.

The only Coleoptera encountered were adult *Nemocestes* Van Dyke (Fig. 7A) and *Sciopithes* Horn (Fig. 7B), both broad-nosed weevils of the subfamily Entiminae (Curculionidae). The adults fed on the foliage and occasionally spores of bracken and western sword fern. Hymenopteran herbivores consisted of larval sawflies (Hymenoptera: Tenthredinidae) of the genera *Strongylogaster* Dahlbom (Fig. 2A) and *Aneugmenus* Hartig (Fig. 9A). These developed on the foliage of western sword fern although adult *Strongylogaster* (Fig. 2A) consumed spores of western sword fern. Most Hemiptera were species of *Macrosiphum* Passerini (Fig. 9B) that often covered the entire surface of the pinna of bracken (Fig. 9B). They were often accompanied by syrphid larvae and small parasitic wasps. Spittlebugs (Cercopidae) and mirids (Miridae) were less abundant.

Discussion

Ferns carry a diverse assemblage of chemicals, some of which are known to affect vertebrates. These compounds have been most studied in bracken, since this fern has a nearly cosmopolitan distribution, is known to poison cattle and horses, and is consumed by humans in various parts of the world (Lewis & Elvin-Lewis, 1977; Muenscher, 1951; Connor, 1977; Cooper-Driver, 1990).

While bracken possesses compounds poisonous to vertebrates, it has not been shown if these or in fact, compounds in any fern, protect them from insect herbivores. It is quite possible however and could explain why many primitive insects, geologically speaking, that are found on ferns today, would have had time to adjust to the chemical and physical defenses of ferns. While bracken evolved many anti-herbivore compounds, a number of insects throughout the world can develop on this fern (Douglas,1983; Cooper-Driver, 1990; Lawton, 1976,1982,1984; Lawton & MacGarvins, 1985; Ottosson & Anderson, 1983).

Cooper-Driver (1978) suggested that there may be more “primitive” insects associated with ferns than “advanced” or recent forms. And that today these “primitive” insects are the ones now

specific on ferns, while the “advanced” insects are polyphagous. To test this hypothesis, the insects collected in the present study were arranged into “primitive” and “advanced” categories depending on the fossil record on their respective families. The grouping in the present work defines “primitive” insect herbivores as those first appearing in the Mesozoic and

“advanced” insect herbivores emerging in the Cenozoic (Table 2). As an example, sawflies as a group, can be considered “primitive” since their fossil record dates back to the Lower Cretaceous and the two sawfly genera reported here, namely *Strongylogaster* and *Aneugmenus* that are called “fern sawflies” have species now restricted to ferns (Hogh, 1966).

Insect family	Earliest known fossil	Source
Anthomyiidae (Diptera)	Eocene	Rasnitsyn & Quicke (2002)
Cecidiomyiidae (Diptera)	Upper Jurassic	Rasnitsyn & Quicke (2002)
Aphididae (Hemiptera)	Lower Jurassic	Rasnitsyn & Quicke (2002)
Tenthredinidae (Hymenoptera)	Lower Cretaceous	Rasnitsyn & Quicke (2002)
Noctuidae (Lepidoptera)	Eocene	Rasnitsyn & Quicke (2002)
Tortricidae (Lepidoptera)	Eocene	Rasnitsyn & Quicke (2002)
Geometridae (Lepidoptera)	Eocene	Rasnitsyn & Quicke (2002)
Erbidae (Lepidoptera)	Eocene	Rasnitsyn & Quicke (2002)
Curculionidae (Entiminae) (Coleoptera)	Pleistocene	Legalov, 2015
Syrphidae (Diptera)	Eocene	Rasnitsyn & Quicke (2002)

Table 2. Fossil ages of insect groups associated with ferns along the Pacific northwest coast of North America.

A similar pattern occurs with Cecidiomyiidae that date back to the Lower Jurassic (Table 2). It is quite likely that at least some species of *Dasineura*, such as the species that forms dark, marginal leaf galls on bracken, are now restricted to ferns. Aphids are another ancient group and it is likely that members of the genus *Macrosiphum* are restricted to ferns today (Cooper-Driver, 1978; Gerson, 1979).

While species of *Chirosia* are considered to be monophagous on ferns (Balick et al., 1978; Gerson, 1979), the earliest fossil record of the Anthomyiidae is the Eocene (Table 2), however it is likely that this family does extend back to the Mesozoic since fossils of this family are rare (Rasnitsyn & Quicke, 2002). The lepidopterans in the families Noctuidae, Tortricidae, Geometridae and Erbidae are all polyphagous and attack ferns as well as angiosperms. A number of other genera of angiosperm feeding moths in Northwestern North America in the families Noctuidae, Crambidae, Micropterigidae and Hepialidae also develop on ferns (Powell & Opler, 2010).

Short-nosed weevils of the subfamily Entiminae, which are polyphagous, have a very poor fossil record, extending back only to the Pleistocene (Legalov, 2015). However fern weevils of the genera *Syagrius* Pasc. and *Neosyagrius* Lea may have had a much more ancient fossil record since they are restricted to ferns today. Members of

these genera are native to Australia, but species of the former genus were introduced into England, Ireland and Hawaii, where they caused much damage to the native ferns (Marshall, 1922; Gerson, 1979). Thus the hypothesis of Cooper-Driver (1978) is basically supported by herbivores occurring on Pacific Northwest ferns.

The present study provides previously unknown records of fern herbivores of the genera *Orygia* (Fig. 10A), *Mycodiplosis* (Fig. 6B), *Nemocestes* (Fig. 7A), *Sciopithes* (Fig. 7B), *Acleris* (Fig. 8A), *Macrosiphum* (Fig. 9B) and representatives of the family Geometridae (Fig. 4).

New records for North America include *Spilosoma* (Fig. 3) and *Dasineura* (Fig. 6A) (Balick et al., 1978; Cooper-Driver, 1978; Gerson, 1979). The association of larval *Mycodiplosis* with spores of what appears to be a rust fungus is also unique. The rust fungus, *Uredinopsis pteridis*, is a well known pathogen of bracken in Western North America (Ziller, 1974) and the larvae of *Mycodiplosis* have been reported to commonly feed on spores of rust fungi (Henk et al., 2011). This would be the first case of a *Mycodiplosis* sp. associated with a rust fungus on a fern.

The present study provides new information on fern herbivores, thus increasing the data base of an already wide selection of both monophagous and polyphagous insects feeding on ferns

throughout the world (Cooper-Driver, 1978; Gerson, 1979).

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