

**A REVIEW OF THE NEARCTIC FERN-FEEDING SAWFLIES
(HYMENOPTERA: TENTHREDINIDOIDEA), WITH NEW HOST
RECORDS AND LARVAL DESCRIPTIONS**

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Abstract.—The North American sawflies (Hymenoptera) occurring north of Mexico with larvae feeding on ferns (Polypodiopsida) are reviewed. They include the introduced European stipe borer *Heptamelus dahlbomi* (Thomson) (Heptamelidae) and 21 external feeders in the tribes Aneugmenini and Strongylogastrini (Tenthredinidae: Selandriinae). Host and distribution records are summarized for each species, and descriptions of larvae are provided where available. The first USA records are given for the introduced Palearctic species *Strongylogaster macula* (Klug) (previously known from Canada). New host records include: *Athyrium asplenioides* var. *angustum* (Willd.) T. Moore (Athyriaceae) for *Aneugmenus flavipes* (Norton), *S. macula*, and *Thrinax albidopicta* (Norton); *Onoclea sensibilis* L. (Onocleaceae) for *S. impressata* Provancher; and *Osmunda claytoniana* L. (Osmundaceae) for *S. polita* Cresson. A list of fern species and their sawfly associates is provided, including descriptions of unidentified larvae.

Key Words: interrupted fern, lady fern, sensitive fern, rearing

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Twenty-two species of North American sawflies occurring north of Mexico are known or presumed to feed on ferns as larvae, but little is known of their specific hosts and habits. With the exception of *Heptamelus* Haliday (1 sp.), which is now considered to constitute the distinct family Heptamelidae (Malm and Nyman 2015), all belong to the subfamily Selandriinae (Tenthredinidae), including members of the tribes Aneugmenini (*Aneugmenus* Hartig, 4 spp.) and Strongylogastrini (*Eriocampidea* Ashmead, 1 sp.; *Strongylogaster* Dahlbom, 12 spp.; *Thrinax* Konow, 4 spp.). There are no host records for *A. floridella* (Ross) (GA, FL, *NC), *S. lata* Smith and Naito

(ON, MD), *S. remota* Rohwer (NS, ON, QC, PA, MD, VA, AR, TN), *S. rufigastrea* (Kincaid) (*AB, BC, NF, NS, *YT, AK), *S. tuberculiceps* Rohwer (FL), or *T. primaria* (Smith) (BC, OR, CA) (distribution records from Smith 1979, 2006, 2008a, 2008b; Smith and Naito 1995; Skvarla et al. 2016; Goulet and Bennett 2021; * = previously unpublished records based on specimens in USNM). As far as is known, members of the other selandriine genera feed on mosses (Bryopsida), horse-tails (Equisetaceae: *Equisetum* L.), grasses (Poaceae), and sedges (Cyperaceae), but there are no host records for the aneugmenine genera *Eustromboceros* Rohwer

(3 spp., AZ), *Liliacina* Malaise (1 sp.; SC, LA, GA, FL), and *Stromboceridea* Rohwer (1 sp., AZ), or for the monotypic dolerine genus *Prionourgus* Goulet (southern CA). Hogh (1966) alluded to bracken fern (Dennstaedtiaceae: *Pteridium aquilinum* (L.) Kuhn) being a host for *Tenthredo* Linnaeus (Tenthredininae) in Michigan. We are unaware of any authentic records of *Tenthredo* from ferns in North America, although several species in this genus are recorded from *Pteridium* in Europe (Lorenz and Kraus 1957, Macek et al. 2020).

On 6 June 2020, one of us (CSE) noticed lightly nibbled pinnae on a clump of lady fern (Athyraceae: *Athyrium asplenoides* var. *angustum* (Willd.) T. Moore) in his yard, which led to the discovery of a nearly full-grown sawfly larva resting on one of the fronds. When CSE bent down to photograph it, it dropped to the ground, and while searching for it a second, smaller larva was found. After both larvae had been placed in a jar along with a piece of the fern, a third larva appeared by 10 June, having hatched from an unseen egg. All three larvae were successfully reared to adults; the first represents the first North American rearing record (and southernmost locality) for *Strongylogaster macula* (Klug), and the others represent new host records for *Thrinax albidopicta* (Norton) and *Aneugmenus flavipes* (Norton). Collections of larvae from other ferns yielded new rearing records for additional species. Here we describe the larvae of these species and review the other North American sawflies that have been associated with ferns, summarizing their recorded hosts, distributions, and what is known of their larvae.

MATERIALS AND METHODS

Early to late feeding stage sawfly larvae found on ferns were placed in vials or jars, with slightly moistened pieces of toilet paper or paper towels packed into the bottoms, along with leaves of their host

plants. These containers were kept indoors, away from direct sunlight, and were checked daily. Larvae were photographed throughout their development, and fresh leaves were added as needed. When mature or nearly so, the larvae were provided with some combination of wine corks, pieces of corrugated cardboard, and segments of ~1.5 cm diameter dead, dry staghorn sumac stems (Anacardiaceae: *Rhus typhina* L.). The leaves were removed after the larvae bored into these substrates or spun cocoons under the paper. Jars containing overwintering prepupae were stored in a refrigerator at 1–3 °C from 16 October 2020 to 1 March 2021, except for a few (identified in the Comments sections) that were instead kept in an unheated shed until 12 March. Photos were taken by CSE using a Canon EOS Rebel XSi DSLR camera, MP-E 65 mm macro lens, and Macro Twin Lite MT-24EX flash unit. Larval measurements were estimated from photographs, based on the lens' field of view being 22 mm at 1× magnification, 11 mm at 2×, and 7 mm at 3×.

Specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). DRS identified them using Smith (1969) and comparison with specimens in the USNM. New host and distribution records are preceded by an asterisk (*); these incorporate caught specimens in the USNM in addition to those reared as part of this study.

CSE located online photographs of fern-feeding sawfly larvae primarily by perusing images that had already been identified as Selandriinae on BugGuide (<https://bugguide.net/node/view/102194/bgimage>) and iNaturalist (https://www.inaturalist.org/observations?place_id=97394&taxon_id=324454). A few additional examples were found on iNaturalist by conducting a search of all Symphyta images with the word “fern” in their descriptions (https://www.inaturalist.org/observations?place_id=97394&q=fern&taxon_id=84643). Records

annotated with “BG” followed by a number can be found online by adding that number to the end of this URL: <https://bugguide.net/node/view/>. For those annotated with “iNat”, the number is added to the end of <https://www.inaturalist.org/observations/>.

Additional records of fern-associated sawfly larvae were gleaned from unpublished notes provided to CSE by H. Goulet (Canadian National Collection of Insects, Ottawa, Ontario). Early in his career (c. 1978), H. Goulet swept thousands of ferns in eastern Ontario (as far west as the Bruce Peninsula on Lake Huron), sampling about 40 species of ferns and collecting larvae from them. He intended to begin a rearing program to associate larvae with adults, but the project was abandoned. The frozen larvae are preserved at the CNC. His notes include a dichotomous key to 26 distinct types of mature larvae, of which 15 were found regularly and 11 rarely; some of the latter may represent larvae that were only on the ferns incidentally. For each of the 26 types, H. Goulet drew the maculation pattern on a photocopied template showing lateral, frontal, and dorsal views of the head as well as a posterior view of the last abdominal segment.

RESULTS AND DISCUSSION

Based on the key to Selandriinae genera provided by Lorenz and Kraus (1957), larvae of the three groups that are confirmed as fern feeders in North America can be distinguished as follows:

- 1 Body with minute bristles; integument not granular 2
- Body without bristles, integument granular *Aneugmenus*
- 2 Antennae 5-segmented Strongylogastrini
- Antennae 3-segmented and short; femur with large lobes *Heptamelus*

Some of these characters may not be evident in even reasonably high-quality photographs. In nature, *Heptamelus* is easily distinguished by its feeding internally in the stipe rather than externally on foliage. *Aneugmenus* larvae possess a pair of fleshy protuberances on the anterior margin of the pronotum (Fig. 4), which we have not observed in any Strongylogastrini. *Eriocampidea* differs from other known fern-feeding larvae in having minute blackish tubercles on the body. We are not aware of generic characters for *Strongylogaster* and *Thrinax*, but individual species may be immaculate (*Strongylogaster* spp.) or have various patterns of dark markings on the head or on the terminal abdominal segment (both genera), and at least two *Strongylogaster* species have yellow sublateral spots on the thorax and abdomen.

In Europe, many fern feeders enter a substrate other than soil to complete their metamorphosis, and none are known to make a clearly identifiable cocoon according to Vikberg and Liston (2009), although Lorenz and Kraus (1957) stated that *Aneugmenus* species transform in a cocoon in the soil. Diapausing Strongylogastrini are commonly found in decomposing wood and bark (Vikberg and Liston 2009); Lorenz and Kraus (1957) also mention plant stems and peat as pupation sites. In our experience, Strongylogastrini will enter pithy twigs, corks, or corrugated cardboard to pupate (and die if only provided with soil to burrow into), while *Aneugmenus* larvae form thin brown cocoons under toilet paper in rearing containers.

Aneugmenus flavipes (Norton)
(Figs. 1–4, 10)

Reared specimens.—MASSACHUSETTS: Franklin Co., Northfield, 42.647085, -72.425111, 10.vi.2020, em. 29.vi.2020, C.S. Eiseman, ex *Athyrium*



Figs. 1–9. Fern-feeding sawflies. 1, *Aneugmenus flavipes* egg. 2, *Aneugmenus flavipes* early instar. 3, *Aneugmenus flavipes* late feeding stage. 4, Same, showing pair of protuberances behind head. 5, *Strongylogaster impressata* mid-instar. 6, *Strongylogaster impressata* late feeding stage. 7, Same, showing head pattern. 8, *Strongylogaster macula*, late feeding stage. 9, *Strongylogaster polita*, late feeding stage.

angustum, #CSE6323 (USNM); 42.646787, -72.425392, 17.vi.2020, em. by 7.viii.2020 [adult found alive but possibly emerged earlier without being noticed], C.S. Eiseman, ex *Athyrium angustum*, #CSE6477 (USNM); NORTH CAROLINA: Scotland Co., Laurinburg, St. Andrews University, 28.iv.2021, em. 22.v.2021, T.S. Feldman, ex *Pteridium aquilinum*, #CSE7025 (USNM).

Larva.—*Early instars* (Fig. 2): Length ~3–7 mm. Head amber (pale brown in first instar) with black eyespots; otherwise unmarked. Body uniformly colored, transitioning from unpigmented (first instar) to yellow to yellow-green; first annulet behind head with a pair of fleshy dorsal tubercles. *Late feeding stage* (Figs. 3, 4): Length ~7–14 mm. Head very pale brown with black eyespots; otherwise unmarked. Body uniformly pale green; in a few photographs, minute points (~.02 mm) are evident at the tips of the paired dorsal tubercles behind the head, and dorsally on several other thoracic and abdominal annulets. Also see Yuasa (1922) (as *Selandria flavipes*).

Hosts.—This species has been repeatedly reported from *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae) (Yuasa 1922, Hogh 1966, Smith 1969, Schreiner et al. 1984), the host of our North Carolina specimen. Our Massachusetts specimens were reared from *Athyrium asplenoides* var. *angustum* (Willd.) T. Moore (*Athyriaceae), and in Virginia DRS has caught adults in Malaise traps where *Athyrium* is common and there is no *Pteridium* in sight. According to Smith (2008b), *Thelypteris* Schmidel (Thelypteridaceae) is also a probable host; H. Goulet (in litt.) has found larvae on *T. palustris* Schott in Ontario.

Distribution.—Canada: MB, NB, NF, NS, ON, QC; USA: *AL, CO, CT, FL, GA, IL, MA, MD, ME, MI, MN, *MO, NC, NH, NJ, NY, OH, PA, *RI, *SC, TN, *TX, VA, VT, WI, WV (Smith 1969, 2008b).

Comments.—Several eggs of this species were observed, all deposited on the lower surfaces of pinnae rather than inserted in plant tissue as is more typical for sawfly eggs (Fig. 1).

Although offered corks and sumac twigs to bore into, both successfully reared larvae rejected these and instead spun thin brown cocoons in or under the crumpled toilet paper that was stuffed in the bottoms of the rearing containers. Adults (Fig. 10) emerged without diapause, and DRS has trapped adults throughout the year, so there is evidently more than one generation. Smith and Marshall (2003) reported an observation of nuptial feeding in this species, in which the female appeared to feed on glandular secretions from a depression in the male's seventh tergite.

Aneugmenus padi (Linnaeus)

Larva.—Described in German by Lorenz and Kraus (1957), and Macek et al. (2020) provide color illustrations. No differences from *A. flavipes* are evident in the illustrations. Lorenz and Kraus (1957) give a length of 17 mm.

Host.—*Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae) (Smith 1969, Macek et al. 2020).

Distribution.—Canada: BC; USA: OR, WA; Europe; Asia; North Africa (Smith 1969).

Comments.—This parthenogenetic species is presumed to be introduced in western North America, where it has become common in coastal regions (Smith 1969). Both Lorenz and Kraus (1957) and Macek et al. (2020) state that *A. padi* is univoltine in Europe.

Aneugmenus scutellatus Smith

Larva.—According to Smith and Lawton (1980), the larva of this species can be distinguished from that of *Eriocampidea arizonensis* Ashmead (the

only other Arizona fern feeder whose larva has been observed) “by the presence of a pair of fleshy protuberances on the anterior margin of the pronotum, presence of numerous, long hairs on the head, lack of winged spiracles, lack of minute black protuberances on the body, and the uniform, pale coloration of the head.”

Hosts.—Adults of the type series, and associated larvae, were swept from unspecified ferns (Smith 1969). Smith and Lawton (1980) referred to this species as “another bracken fern sawfly,” indicating that it has been found on *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae).

Distribution.—USA: AZ; Mexico (Smith 1969, 1979).

Comments.—This species has not been reared, and larvae were associated with adults based on their being collected together and on there being just one *Aneugmenus* species known from the southwestern USA.

Eriocampidea arizonensis Ashmead

Larva.—Early and late feeding stages were described in detail by Smith and Lawton (1980). Older larvae are up to 17 mm long; the head is amber with darker brown mottled areas especially on the vertex, upper half of frons, and behind the black eyespots; the body is green with minute blackish tubercles, and the tarsal claws, tibiae, and wings of the spiracles are also black. Younger larvae are much darker, with larger tubercles and with black head, thoracic legs, prolegs (at least on the outer surfaces), apex of 9th tergum, and most of the 10th tergum. There are 7 annulets on abdominal segments 2–8, and prolegs are present on segments 2–8 and 10.

Host.—*Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae) (Smith and Lawton 1980).

Distribution.—USA: AZ, NM; Mexico (Smith 1979).

Comments.—This species is bivoltine, with adults present in the last two weeks of May and in the first two weeks of July. Larvae have been found from 11 to 28 June and from 16 July to 2 August (Smith and Lawton 1980). The pupation habits are unknown, as this species has not been reared, and it can only be assumed that the observed larvae were the progeny of the adults found on the same ferns shortly before they appeared.

Heptamelus dahlbomi (Thomson)

Larva.—Described by Vikberg and Liston (2009). Larvae are whitish when young, later grayish and finally reddish-violet or violet-gray. The first four instars have short, laterally directed thoracic legs and no abdominal prolegs. The head of the fourth instar is mostly brown with an inverted whitish V-shaped marking on the lateral frons. The fifth and final instar is 8–12 mm long and has longer, more downward-directed thoracic legs and well-developed prolegs, with which it wanders in search of a pupation site. Its head lacks the fourth-instar pattern; the vertex and temples are covered with brownish flecks and the frons is pale.

Hosts.—Confirmed in Europe from *Athyrium filix-femina* (L.) Roth (Athyriaceae). This species was previously confused with the strictly Palearctic *H. ochroleucus* (Stephens), and it is unknown to which species older host records apply: *Blechnum spicant* (L.) Roth (Blechnaceae), *Dryopteris dilatata* (Hoffm.) A. Gray (Dryopteridaceae), *Matteuccia struthiopteris* (L.) Tod. (Onocleaceae), and *Polypodium vulgare* L. (Polypodiaceae) (Vikberg and Liston 2009). There are no North American host records.

Distribution.—Canada: BC, QC; USA: MD, NY, VA, *VT; introduced from Europe (Smith 2003, Vikberg and Liston 2009, Goulet and Bennett 2021).

Comments.—Females of this species fly in spring, inserting eggs in the convex surface of the rachis or stipe of the host plant. Larvae are internal feeders, boring downward in the stipe. In captivity, they bore into rotten wood when finished feeding; in nature, they are said to favor the lower, dead parts of ferns growing near the feeding site for pupation, and one specimen was reared from a spruce cone. Flight periods suggest this species is bivoltine in most of its range (Vikberg and Liston 2009). Since 1985, DRS has caught 89 specimens in his backyard trap in Virginia: 15 in April, 43 in May, 11 in June, 5 in July, 12 in August, 2 in September, and 1 in October.

Strongylogaster distans Norton

Larva.—The larva was first described by Dyar (1894) (as *S. pacificus* MacGillivray), and later in more detail by Beer (1955). Early instars transition from colorless to pale green, with slight infuscation of the head that becomes concentrated on the vertex in the third instar. In the fourth and fifth instars, the head is opaque white with a greenish tinge, with black eyespots and with two small fuscous patches on the dorsum of the vertex. Vessels give the appearance of a dark green median dorsal stripe flanked by conspicuous white stripes, and a threadlike, white lateral line connecting the spiracles; the conspicuousness of the dorsolateral stripes is the most obvious feature distinguishing older *S. distans* larvae from those of *S. tibialis* Cresson, which are frequently found feeding side by side, but the two fuscous head patches and entirely white antennae are more reliable characters for identifying *S. distans* (*S. tibialis* has a single central dark patch on the dorsum of the vertex, reduced to a narrow middorsal line in the fourth instar and absent in the fifth, and its antennae are mostly black). The fifth instar is 19 mm

long and becomes purplish-brown when finished feeding and ready to seek a pupation site (Beer 1955).

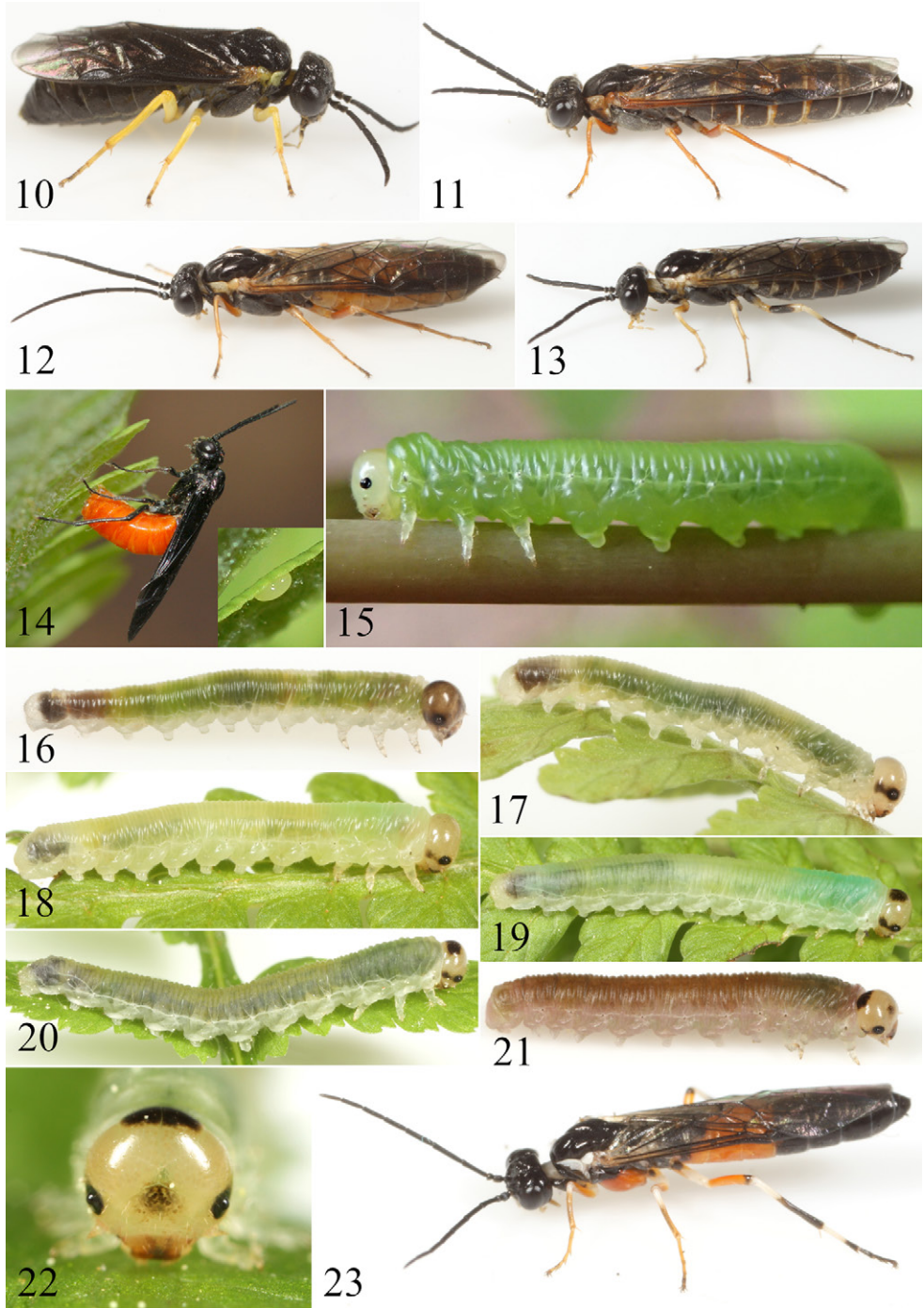
Host.—*Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae), apparently exclusively (Dyar 1894, Beer 1955). However, photographed adults have been observed ovipositing in unfurling fiddleheads of *Athyrium filix-femina* s.l. (Athyriaceae) in British Columbia (BG 915899) and *Woodwardia fimbriata* Sm. (Blechnaceae) in Washington (BG 397649).

Distribution.—Canada: BC; USA: CA, CO, ID, NV, OR, UT, WA (Smith 1969).

Comments.—Beer (1955) made extensive observations of this univoltine species. Adults emerge in early spring; in captivity they feed on sap from the host plant. Females insert eggs singly in the rachis, exclusively in the tight curls at the tips of fronds. The egg is often only slightly covered by the plant epidermis, being also protected by the dense trichomes. Larvae feed in this portion of the plant until the fourth instar, then descend the frond to feed on more mature leaflets of lateral branches. The body is usually stretched out flat against the underside of the leaflet, but when disturbed, the larva drops to the ground or whips its abdomen back and forth. Mature larvae bore into dead wood to overwinter, pupating the following spring. The pupal cell is almost 16 mm by 3.5 mm, is sealed off at the entrance with a frass plug, and is not lined with silk or any other secretion. The egg stage lasts about a week; larvae are active for two to four weeks, in diapause for about ten months, and the pupal period is about two weeks.

Strongylogaster impressata Provancher
(Figs. 5–7, 11)

Reared specimen.—MASSACHUSETTS: Franklin Co., Northfield, 42.646994, -72.426232, 4.vi.2020, em. 10.iv.2021, C.S. Eiseman, ex *Onoclea sensibilis*, #CSE6833 (USNM).



Figs. 10–23. Fern-feeding sawflies. 10, *Aneugmenus flavipes* reared adult. 11, *Strongylogaster impressata* reared adult. 12, *Strongylogaster macula* reared adult. 13, *Strongylogaster polita* reared adult. 14, *Strongylogaster tacita* adult ovipositing (inset, egg). 15, *Strongylogaster tacita* larva (photo by P. Woods). 16, *Thrinax albidipicta* early instar, 6 June 2020. 17, Same larva, 8 June. 18, Same larva, 13 June. 19, Same larva, 17 June. 20, *Thrinax albidipicta* late feeding stage with darker green dorsally. 21, *Thrinax albidipicta* mature larva, purplish. 22, *Thrinax albidipicta* late feeding stage, head pattern. 23, *Thrinax albidipicta* reared adult.

Larva.—*Late feeding stage* (Figs. 6–7): Length 25–26 mm (Yuasa 1922). Head ground color whitish, spotted with pale brown except for a narrow horizontal band between the eyes; shining black patch on vertex, sharply delineated by the lateral sutures, abruptly tapering just above the eyes and then widening to a round spot at the upper edge of the frons; black spots around eyes and extending backward a short distance. Body green dorsally, whitish below and on prothorax, with large yellow sublateral spots on thoracic segments and around/below each abdominal spiracle; a pair of black spots on last abdominal segment; tibiae and tarsal claws black dorsally. Previous instar (Fig. 5) with fainter green and yellow coloration, last two abdominal segments whitish and lacking black spots, and with dusky coloring instead of black on thoracic legs. Our description agrees in all details with Dyar's (1895b, as *S. luctuosus* Provancher). Yuasa (1922) (under the names *Thrinax impressatus* and *T. pulatus* [sic] MacGillivray) described similar markings on the head and tenth tergum, but made no mention of the yellow spots, stating that the body is uniformly greenish.

Hosts.—Dennstaedtiaceae: *Pteridium aquilinum* (L.) Kuhn (Dyar 1895b, Schreiner et al. 1984); DRS has collected adults and larvae on *Dennstaedtia punctilobula* (Michx.) T. Moore in West Virginia (Smith and Strazanac 2016). Our new specimen was reared from *Onocleaceae: *Onoclea sensibilis* L. Larvae resembling *Strongylogaster impressata* have been found on other ferns as noted in the comments below, but these potential hosts require further investigation.

Distribution.—Canada: LB, NB, NS, ON, QC; USA: AR, CO, CT, IA, IL, *KS, *KY, MA, *MD, ME, *MI, MN, NC, NH, NM, NY, PA, TN, *VA, *VT, WI, WV (Dyar 1895b; Smith 1969, 1979; Skvarla

et al. 2016; Smith and Strazanac 2016; Goulet and Bennett 2021).

Comments.—Our reared larva entered a piece of corrugated cardboard on 10 June, behaving just as Gordh (1975) described for *Thrinax dubitata* (Norton); its entry point was marked by a loose mass of chewed or rasped bits of cardboard. It was kept in an unheated shed over the winter, emerging as an adult (Fig. 11) a month after being brought indoors.

On 31 May 2016, at the same location in Northfield, MA where our reared specimen was collected, identical larvae were found on *Osmunda claytoniana* L. (Osmundaceae) (iNat 100382616), and a shed skin with the same head pattern was found on *Polystichum acrostichoides* (Michx.) Schott (Dryopteridaceae), but the body coloration of the larva that left it is unknown (iNat 100381050). A similar larva with less distinct yellow spots was photographed on *Cystopteris protrusa* (Weath.) Blasdell (Cystopteridaceae) in Missouri (Monroe Co., Mark Twain State Park) on 28 April 2020 (BG 1806072). Other larvae resembling *S. impressata*, but with a large black spot extending behind the eye, were photographed on *Dryopteris* Adans. (Dryopteridaceae) on 27 May 2019 in Virginia (Grayson Co., Jefferson National Forest) (iNat 25942704), and on *Osmundastrum cinnamomeum* (L.) C. Presl (Osmundaceae) on 9 May 2019 in North Carolina (Swain Co., along Blue Ridge Parkway) (iNat 24935803); H. Goulet's unpublished notes record such larvae from *Pteridium* in Ontario and identify them as *S. impressata*. H. Goulet found larvae that instead had a narrow stripe extending from the eye to the back of the head (and sometimes lacked dark spots on the last abdominal segment) on *Athyrium asplenoides* var. *angustum* (Athyraceae) and *Homalosorus pycnocarpus* (Spreng.) Pic.Serm. (Diplaziopsidaceae). According

to Dyar (1895a, 1895b), the yellow (orange) sublateral spots are not present in *S. multicincta* Norton and *S. soriculatipes* Cresson, which he also reared from *Pteridium aquilinum*, nor have any other fern feeders been described as having them. Based on our observations, *S. polita* Cresson has rather indistinct yellow spots; it is easily distinguished from *S. impressata* by its head pattern. Unidentified larvae with more or less distinct yellow spots—and still other head patterns—have been found on *Homalosorus* Pic. Serm. (Diplaziopsidaceae), *Phegopteris* (C.Presl) Fée (Thelypteridaceae), and *Woodsia* R.Br. (Woodsiaceae); see Host Summary below for details.

Strongylogaster macula (Klug)
(Figs. 8, 12)

Reared specimen.—MASSACHUSETTS: Franklin Co., Northfield, 42.6473, -72.4253, 6.vi.2020, em. 16.iv.2021, C.S. Eiseman, ex *Athyrium angustum*, #CSE6856 (USNM).

Larva.—*Late feeding stage* (Fig. 8): Length 16–20 mm (Lorenz and Kraus 1957). Head mostly amber, paler cream-colored around eyespots, on genae and along lower edge of frons; eyespots black. Body green dorsally, pale green below; tibiae and tarsal claws dusky dorsally. Also see Lorenz and Kraus (1957) and Macek et al. (2020).

Hosts.—Recorded in Europe from *Athyrium filix-femina* (L.) Roth (Athyriaceae), *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae), *Dryopteris filix-mas* (L.) Schott, and *Polystichum aculeatum* (L.) Roth (Dryopteridaceae) (Lorenz and Kraus 1957, Macek et al. 2020). Our specimen was reared from *Athyrium *asplenioides* var. *angustum* (Willd.) T. Moore.

Distribution.—Canada: BC, NS, ON, QC; *USA: MA, ME, NH, VT; Europe to Japan (Smith 1969, Goulet and Bennett 2021). Introduced in North America.

Comments.—The first known North American specimens, both females, were collected in Ontario in mid-May and in British Columbia in early June (Smith 1969). The Massachusetts larva was found resting on top of a lady fern frond on 6 June, and it dropped to the ground when CSE approached—a behavior not observed in the *Aneugmenus* and *Thrinax* larvae found on this host. It bored into a piece of sumac twig within a few days after it was collected, excavating a channel in the pith that was 3 cm long with no enlargement for a pupal cell. The adult (Fig. 12) emerged the following spring, 46 days after being removed from refrigeration.

Strongylogaster multicincta Norton

Larva.—Dyar (1895b) reared this species (as *S. annulosus* Norton) along with *S. soriculatipes* Cresson (as *S. soriculatus* Provancher) and did not distinguish the larvae of the two, although he noted some differences that he suspected were characteristic of species rather than representing individual variation. In a larval key, Dyar (1895a) indicated that the head of *S. multicincta* is black-spotted and *S. soriculatipes* is immaculate green, but with a footnote stating that it may be the other way around. Yuasa (1922) described the head of *S. multicincta* (as *S. annulosus*) as pale or light brown with blackish brown markings: “vertex with a pair of diverging spots over the vertical furrows directed toward ocellaræ and a spot caudad of each ocellaræ; vertical markings sometimes faint, sometimes very distinct and large, merging into a continuous vertical marking; front never with spot.” He indicated that the larva is 18 mm long, uniformly green, rarely with a pair of faint spots on the tenth abdominal tergum. According to Hogh (1966), the fifth instar “has a green body and an amber head capsule marked with a characteristic black mask.” Thus,

all authors agree that *Strongylogaster multicincta* has black markings on the head, and DRS has examined larvae identified as *S. multicincta* in the USNM and found that all have distinct black markings on the head as described by Yuasa (1922).

Host.—*Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae) (Dyar 1895b, Yuasa 1922, Hogh 1966, Schreiner et al. 1984).

Distribution.—Canada: NB, NS, ON, QC; USA: FL, IL, MA, MD, ME, MI, MN, NC, NH, NJ, NY, PA, *SC, VA, VT, WV (Smith 1969, 1979; Smith and Strazanac 2016).

Comments.—Hogh (1966) briefly summarized the biology of this species. Adults emerge in early spring, and females insert eggs in the midribs of fiddleheads and young, unfurling fronds, 3–10 days after fiddlehead emergence (late May and June in Michigan). Eggs hatch in June, and there are five larval instars. In July or August, mature larvae move onto the ground litter and burrow into small pieces of wood or dried fern stipes of the previous season's growth, where they enter diapause, pupating the following spring.

Strongylogaster polita Cresson
(Figs. 9, 13)

Reared specimens.—IOWA: Winneshiek Co., 43°25'55.97"N, 92°0'34.78"W, 1.vi.2018, em. 4.v.2019, MJ Hatfield, ex *Osmunda claytoniana* (USNM); PENNSYLVANIA: Cumberland Co., Boiling Springs, 1.vi.2020, em. 18.iv.2021, L. DeHart, ex *Osmunda claytoniana*, #CSE6865 (USNM).

Larva.—*Late feeding stage* (Fig. 9): Length ~14 mm. Head amber above and on frons and clypeus, elsewhere pale cream-colored, with diffuse-margined black patch on vertex extending to just above the black eyespots. Body pale green with indistinct sublateral yellow spots on thorax and abdomen and a diffuse-margined central black spot on last abdominal segment; thoracic legs and abdominal

prolegs whitish except for minute brown tips on tarsal claws. The feeding stage larva photographed on 1 June by MJ Hatfield (BG 1529053) has the head uniformly cream-colored except for the black eyespots; it is unknown whether this represents an earlier instar or individual variation, but the two mature larvae or prepupae photographed on 30 September (BG 1620177, 1620178) each have a black patch on the vertex as with the larva from Pennsylvania, as does another larva photographed at the time of collection (MJ Hatfield, in litt.).

According to Yuasa (1922), the length is 21–23 mm, the head is uniformly pale brown, rarely with a pair of faint spots on the dorsal part of the vertex, and the body is uniformly green, with the legs brownish distad of the trochanter. In comparison with *S. tacita* (Norton), Yuasa stated that *S. polita* has the trochanter not distinctly shorter than the femur, and the distal segment of the labial palpi is shorter than the preceding segment, and subequal to the distal segment of the maxillary palpi.

Hosts.—Our specimens were reared from *Osmunda claytoniana* L. (*Osmundaceae). Similar larvae have been found on *Osmundastrum cinnamomeum* (L.) C. Presl in Ontario (H. Goulet), Ohio (BG 933685), and Pennsylvania (iNat 48543137). The host given by Yuasa (1922) is *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae), but no adult specimens are available to verify the identity of the larvae he studied.

Distribution.—Canada: NS, ON; USA: CT, *IA, *MD, *MI, NC, *NH, NY, *PA, TN, VA, *VT, *WV (Smith 1979, Goulet and Bennett 2021).

Comments.—The two Iowa larvae that were successfully reared bored into a cork by mid-June (the two discussed above were found loose in the rearing container; they were still alive on 30 September but ultimately died without pupating). The

Pennsylvania larva bored 2 cm into the pith of a piece of sumac twig by 21 June; it was kept over the winter in an unheated shed and emerged as an adult (Fig. 13) 37 days after being brought indoors.

Strongylogaster soriculatipes Cresson

Larva.—As noted above, Dyar (1895b) reared this species along with *S. multincta* and did not distinguish the larvae, but descriptions by later authors agree with Dyar's (1895a) guess that *S. multincta* larvae have markings on the head; it may be that larvae of *S. soriculatipes* are always "immaculate green" (Dyar 1895a), but this requires confirmation. According to Dyar (1895b), in the larvae that gave rise to adults of both species, the head is "whitish, with sordid testaceous tinge, shining, eye black, mouth brown;" and the body is "not shining, whitish waxy, appearing green, except subventrally, from the food showing by transparency; in later stages actually green; segments finely 6–7 annulate; spiracles dark, tracheal line white; feet on joints 6–13."

Host.—*Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae) (Dyar 1895b, Smith 1969).

Distribution.—Canada: MB, NB, NS, ON, QC; USA: *AL, IL, MA, MD, ME, *MI, MN, NC, *NH, NY, PA, TN, VA, *VT, WV (Smith 1969, 2006, 2008b; Smith and Strazanac 2016; Goulet and Bennett 2021).

Comments.—According to Dyar (1895b), the larva is "solitary, sitting flat on the venter, or on the edge of a leaf." Diapause and pupation take place in a cell excavated in soft wood.

Strongylogaster tacita (Norton)
(Figs. 14, 15)

Larva (Fig. 15).—Yuasa (1922) stated that the larva of this species is 19 mm long, with the head uniformly pale brown and the body and legs uniformly green,

without markings. In comparison with *S. polita*, Yuasa indicated that *S. tacita* has the trochanter distinctly shorter than the femur (8:13), and the distal segment of the labial palpi is as long as the preceding segment, and shorter than the distal segment of the maxillary palpi.

DRS has found larvae on royal fern in the same area where numerous adults of *S. tacita* were collected. The later instar larvae are similar to what Yuasa (1922) described for this species: The head is amber to pale brown with a black ocellar spot; the legs and body are uniformly green when alive except the 10th tergum which is usually more brownish. The unpublished notes of H. Goulet indicate that the larvae he found on royal fern had a pair of weak spots at the back of the vertex, and these are evident in the live larva photographed by P. Woods (Fig. 15, iNat 49747981), which shows amber spots on a whitish ground. In our experience *S. polita* is easily distinguished by the black patch on the vertex and the yellow sublateral spots on the body.

Hosts.—*Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae) (Yuasa 1922; Smith 1979, 2006). DRS has collected adults and larvae from *Osmunda spectabilis* Willd. (Osmundaceae) (Smith 2006), and P. Woods has reared adults from this host (iNat 49747981). CSE photographed a female ovipositing on *O. claytoniana* L. (Fig. 14); DRS has swept adults from (or near) *Osmundastrum cinnamomeum* (L.) C.Presl., and H. Goulet found larvae on this host that matched those found on *Osmunda spectabilis*.

Distribution.—Canada: NB, NS, ON, QC; USA: AL, CT, FL, GA, IL, MA, MD, ME, MI, *MN, NC, NH, NJ, NY, PA, SC, VA, VT, WI, WV (Smith 1969, 1979; Smith and Strazanac 2016; Goulet and Bennett 2021).

Comments.—On 14 May 2016, CSE observed a female ovipositing on

interrupted fern in Northfield, MA. The whitish egg was deposited on the lower surface of a pinnule (not inserted), against its curled margin (Fig. 14). Larvae collected by P. Woods (in litt.) in Fulton Co., Pennsylvania on 13 June 2020 pupated in punky wood, and they emerged as adults beginning 19 days after the collection date.

Strongylogaster tibialis Cresson

Larva.—Beer (1955) described the larvae in detail. First instars are very pale yellowish-white. The second instar is still almost transparent but with the dorsum greenish; the head capsule is opaque white with a small, fuscous, V-shaped area on the dorsum of the vertex and another fuscous masklike patch on the front, extending over the distance between the eyes. The third and fourth instars have a distinctly green body with a darker median dorsal band, with the head capsule white to faintly amber, lacking the mask of the second instar; on the vertex is a “middorsal, dark area” in the third instar, becoming a “narrow, fuscous, middorsal line” in the fourth. The fifth instar is 17 mm long and similarly colored, but the head is opaque white with a greenish, amber, or faintly fuscous tinge, without the mid-dorsal fuscous line on the vertex. When the larva is finished feeding, the body becomes reddish, especially in the abdomen. Antennal segments 2–5 are black, with the first segment white and with a narrow white distal margin on segments 2–4.

Hosts.—*Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae), apparently exclusively (Beer 1955).

Distribution.—Canada: BC; USA: CA, ID, OR, WA (Smith 1969).

Comments.—This species is univoltine, with adults emerging in April and early May in the San Francisco Bay area. Captive adults were often observed to

feed on sap exuding from *P. aquilinum* fronds that were kept in vases in the rearing chambers. Beer (1955) reported that females insert eggs singly beneath the epidermis of the stems and branches of the host plant, usually in grooves of the most succulent portions (rarely on stems less than 1/8” in diameter), and always at least 2” above ground level. The egg causes the epidermis to bulge conspicuously, and one end is exposed where the incision slit is made. Upon hatching 4–8 days later, the larva immediately moves up the frond to feed on the small, curled tip of tender new growth, usually positioning itself on the underside of the pinna, and remaining in or near the curl until the fourth instar. Fourth and fifth instars may be found on exposed branchlets, resting on either the upper or the lower surfaces of pinnae. Larvae of all ages vigorously wave their abdomens back and forth when disturbed, and late instars frequently drop to the ground. They have usually all disappeared into rotten wood by early June, excavating frass-plugged tubular cavities (about 13 mm by 3 mm) where they remain until the following spring. Many enter old, dead fern stems instead of wood, often boring 2–3 inches before constructing the frass plug.

Thrinax albidopicta (Norton)
(Figs. 16–23)

Reared specimens.—MASSACHUSETTS: Franklin Co., Northfield, 42.646965, -72.425069, 10.vi.2020, 4 black-headed larvae, em. 22.vi.2020, C.S. Eiseman, ex *Athyrium angustum*, #CSE6280 (USNM); same collection, em. 8.vii.2020, #CSE6367 (USNM); 42.647086, -72.425112, 10.vi.2020, larva with eye stripe, em. 23.vi.2020, C.S. Eiseman, ex *Athyrium angustum*, #CSE6285 (USNM); 42.6473, -72.4253, 6.vi.2020, em. 7.iv.2021, C.S. Eiseman, ex *Athyrium angustum*, #CSE6820 (USNM); 42.646815, -72.426917, 8.vi.2020, em. 10–12.iv.2021,

C.S. Eiseman, ex *Athyrium angustum*, #CSE6837 (2 specimens, USNM).

Larva.—The first collected larva (CSE6820) was isolated and photographed throughout its development. The descriptions for different dates may each represent a separate instar, but actual timing of molts was not recorded. *6 June* (Fig. 16): Length ~5 mm. Head brown with diffuse-margined blackish patch on vertex and diffuse blackish stripe extending backward from black eyespot. Body transparent, colorless except for green gut contents. *8 June* (Fig. 17): Length ~7 mm. Head pale cream-colored with small, indistinct dusky patch on vertex and distinct blackish stripe extending backward from black eyespot. Body as previous. *11–13 June* (Fig. 18): Length ~8.5–10 mm. Head pale cream-colored with only a slight hint of dark pigment on vertex; irregular black stripe extending backward from black eyespot; indistinct brown spot at upper edge of frons. Body milky-translucent, the green gut contents less distinctly visible. *14–18 June* (Fig. 19): Length ~9.5–12 mm. Head amber with lower half of frons whitish, distinct black patch on vertex, distinct black stripe extending back from black eyespot, and diffuse-margined black spot at upper edge of frons. Body as previous, but with pale blue-green tint dorsally on thorax and pale yellow-green tint on abdomen except for last two segments. This larva bored into a sumac twig on 19 June.

In general, early instars consistently have a blackish stripe behind the eye, a brown or dusky spot on the frons, and may or may not have a dark spot on the vertex. The head pattern of final instars appears to be consistent (Fig. 22; see 14–18 June above), but the body color varies; some larvae are dorsally forest green on the thorax and about the color of pea soup on the abdomen (Fig. 20), and when ready to bore into a substrate for overwintering, some are a dull olive green while

others become entirely suffused with a rosy to purplish color (Fig. 21). None of our photographed larvae have spots on the last abdominal segment as reported for the two other *Thrinax* species below.

Host.—Our new specimens were reared from *Athyrium asplenoides* var. *angustum* (Willd.) T. Moore (Athyriaceae). Ross (1951) indicated that the host of this species is *Osmunda* L. (Osmundaceae), but the origin of this record is unclear. Dyar (1897) reported rearing *T. albidopicta* from *Onoclea sensibilis* L. (Onocleaceae), but Smith (1969, 1986) determined that all adults Dyar reared from *Onoclea* and *Osmunda* (under his “5G” code) were in fact *T. dubitata*. In Ontario, H. Goulet collected two larvae resembling *T. albidopicta* from *Deparia acrostichoides* (Sw.) M.Kato (Athyriaceae), but their identity requires confirmation.

Distribution.—Canada: NB, NF, NS, ON, QC; USA: AL, AR, CT, DC, IA, IL, IN, KS, MA, MD, ME, MI, MN, MO, NH, NJ, NY, OH, PA, *TN, VA, *VT, WI, WV (Smith 1969, Skvarla et al. 2016, Smith and Strazanac 2016, Goulet and Bennett 2021).

Comments.—The mature larvae all bored into the pith of dead sumac twig pieces to pupate or overwinter; the excavation made by #CSE6820 was 15 mm long. The four black-capped larvae collected on 10 June had all bored by 14 June, with one adult emerging on 22 June and another on 8 July. The early-instar larvae collected on 6 June bored into twigs on or before 17–19 June and did not emerge as adults (Fig. 23) until the following year: one emerged 37 days after being removed from refrigeration, and two emerged 29–31 days after being brought indoors from an unheated shed. DRS has collected adults from April to September, indicating multiple generations per year.

One of the larvae collected on 8 June 2020 yielded an undetermined

ichneumonid parasitoid on 6 April 2021 (CSE6819, BG 2059028). It is deposited in the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa.

Thrinax dubitata (Norton)

Larva.—The first reference to this larva is in Dyar (1895a), as the unidentified “5G”: “On *Onoclea*; head and anal segment black spotted.” Dyar (1897) described larvae of “*Taxonus dubitatus*” and *T. “albidopictus,”* noting that they could not be distinguished with certainty, but Smith (1969, 1986) reported that all of Dyar’s reared adults associated with both names represented *T. dubitata*. Under the first heading, Dyar (1897) described the “Stage before last” as having a pale yellowish head with black eyespots and a very small brown dot in the apex of the clypeus and behind the eye; the body was dull, waxy, green from the gut contents, with 7-annulate segments (the first two annulets largest), and unmarked except for the small black spiracles, antennae, palpi, jaws, and claws of the thoracic legs. The “Last stage” had a pale brownish head with a big black patch behind the eye (“Others have more spots on the head”); the body was still green from the gut contents, faintly yellowish, paler below, and unmarked except for a large black subdorsal patch on segment 13 anterior to the anal flap. Under the second heading, without specifying the stage, Dyar described the head as shining pale brownish with a large triangular black patch on the vertex connecting to a similar one on the clypeus, and “another patch at its apex on the black eye reaching back to the occiput; these three patches have diffuse edges and the vertical and lateral ones are connected by a dark cloud”; the body was smooth and slightly shining, dark green from the dorsum to the spiracles, translucent whitish below, with a large, round, smoky black

lateral patch on segment 13; the spiracles were black and there were black markings on the thoracic legs.

Hosts.—Reared by Dyar (1897) and Smith (1969) from *Onoclea sensibilis* L. (Onocleaceae). Dyar’s observations were associated with his “5G” code, which also included an adult of *T. dubitata* reared from *Osmunda* L. (Osmundaceae) and a collection of a larva from *O. claytoniana* L. (Smith 1986). Ross (1951) indicated that the host of *T. dubitata* is *Osmunda*, and did not mention *Onoclea*; the reason for this is unclear. Krombein (1960), who only observed prepupae in their overwintering sites, stated, “in the locality of my research I suppose that they feed on bracken (*Pteridium*) which is common along the railroad tracks.”

Distribution.—Canada: MB, NB, NS, ON, QC; USA: CT, DC, IL, IN, MA, MD, ME, MI, MN, NC, NH, NJ, NY, OH, PA, TX, VA, *VT, WI, WV (Smith 1969, Smith and Strazanac 2016, Goulet and Bennett 2021).

Comments.—Smith (1969) stated that adults fly early in spring, and that in Maryland larvae are most abundant in late May into June. DRS has since caught adults throughout the growing season, indicating multiple generations per year. Dyar (1897) reported that the larvae bore into wood to pupate. Smith (1969) found that they readily pupate in corrugated cardboard in rearing containers, and adults emerged during the same summer, indicating that there may be more than one generation. Gordh (1975), who described the sexual behavior of reared adults, stated that the larvae crawled between laminae of the cardboard and did not spin cocoons, but did seal the apertures through which they entered. In Virginia, Krombein (1960) collected sumac stems containing prepupae beginning in mid-September; the one he succeeded in rearing pupated between April 6 and 10 and

emerged on April 13. He noted that the larva does not spin a cocoon, instead constructing a narrow plug of fine particles of pith just above itself, and occasionally beneath itself; it does not construct a plug at the boring entrance. *Cubocephalus alacris* (Cresson) (Ichneumonidae) (as *C. canadensis* (Provancher)) was reared from one prepupa; the parasitoid larva spun its cocoon within its host's pith boring.

Thrinax multicincta (Hall)

Larva.—According to Hall (1917), the larva is about 10 mm long when mature, and is “[l]ight green with black spots on the head and a light line along each side of the body.” He additionally noted that the “last feeding-stage larvae preserved [in] alcohol have a large brownish spot on the anal plate, the vertex, occiput and front medianly brownish, and a blackish spot behind the eye.”

Host.—*Deparia acrostichoides* (Sw.) M.Kato (Athyraceae) (Hall 1917, as *Athyrium thelypteroides* (Michx.) Desv.). Smith (1969) collected several specimens “by sweeping ferns, most of which were *Onoclea*.”

Distribution.—Canada: ON, QC; USA: AR, MD, ME, *NY, OH, TN, *VA, WV (Smith 1969, 2008b; Skvarla et al. 2016; Smith and Strazanac 2016; Goulet and Bennett 2021).

Comments.—Hall (1917) stated that the “eggs are attached on end to the upper side of the leaf, often as many as ten or twelve on a frond.” Oviposition occurred around 22 May in Ohio. Larvae feed for 11–12 days, and there is one generation per year. A puparium of an undetermined dipteran parasitoid was found in a rearing vial (Hall 1917).

Host Summary

The host records given above are summarized below by host plant, along with notes on unidentified larvae (mostly

Strongylogastrini) found on various North American ferns.

Athyraceae

Athyrium asplenioides var. *angustum* (northern lady fern).—*Aneugmenus flavipes*, *Strongylogaster macula*, *Thrinax albidopicta*. Undetermined larva found on 23 August 2020 on Cape Breton Island, Nova Scotia (resting in coiled position, iNat 57395204): Head apparently blackish on vertex and fading to brown laterally; body dorsally green with dark green dorsal or addorsal line and a series of oblique subdorsal lines of the same color (possibly the inverted “V” markings H. Goulet described on fern-associated tenthredinines; see *Thelypteris palustris* below), ventrally mottled with pale yellow. On lady fern in Ontario, H. Goulet commonly found larvae he identified as *Strongylogaster*, with a pair of large, dark spots on the vertex, a pair of small, very pale spots on the frons, and usually a pair of dark spots on the last abdominal segment. He found two additional types of Strongylogastrini larvae with head patterns like that of *S. impressata*, one of which lacked dark spots on the last abdominal segment and apparently also lacked sublateral yellow spots; the other had a dark stripe extending from the eye to the back of the head, sometimes had dark spots on the last abdominal segment, and did have sublateral yellow spots. He also collected larvae on lady fern that were doubtfully fern feeders, including a single individual identified as “Blennocampinae nr. *Mesoneura*” (but *Mesoneura* Hartig is a nematine genus) and two individuals identified as *Allantus* Panzer (Allantinae).

Heptamelus dahlbomi feeds on *Athyrium filix-femina* in Europe and presumably also occurs on *A. asplenioides*.

Athyrium cyclosorum (Rupr.) Maxon (subarctic lady fern; we presume plants identified as *A. filix-femina* in the Pacific

Northwest to represent this species).—*Strongylogaster distans* (oviposition observed). *Undetermined larva found on 24 September 2013 in Snohomish Co., Washington* (BG 853093): Head amber, apparently unmarked except for black eyespots; body pale green with paired, broken yellow subdorsal lines.

Deparia acrostichoides (silvery spleenwort).—*Thrinax multicincta*. On this host in Ontario, H. Goulet collected two larvae resembling *T. albidopicta*, and he collected many examples of two different tenthrudinines, both of which had the dorsum of the body gray-banded. One of these was of the type described below under *Homalosorus pycnocarpus*, and the other was of the type described under *Thelypteris palustris* (without inverted “V” markings on the dorsum).

Blechnaceae

Woodwardia fimbriata (giant chain fern).—*Strongylogaster distans* (oviposition observed).

Cystopteridaceae

Cystopteris protrusa (southern fragile fern).—Unidentified larva similar to *Strongylogaster impressata*.

Dennstaedtiaceae

Dennstaedtia punctilobula (hay-scented fern).—*Strongylogaster impressata*.

Pteridium aquilinum (bracken fern).—*Aneugmenus flavipes*, *A. padi*, *A. scutellatus*, *Eriocampidea arizonensis*, *Strongylogaster distans*, *S. impressata*, *S. macula*, *S. multicincta*, *S. polita* (according to Yuasa 1922; questionable record), *S. soriculatipes*, *S. tacita*, *S. tibialis*, *Tenthredo* sp.?. *Thrinax dubitata* has been circumstantially associated with bracken fern.

Diplaziopsidaceae

Homalosorus pycnocarpus (narrow-leaved glade fern).—*Unidentified larva*

found on 8 May 2011 in Boone Co., Missouri (BG 629203): Head pale cream-colored with large, shining black patch on vertex, extending behind and confluent with black eyespots; body pale green above, whitish below with distinct yellow sublateral spots, and with pair of black spots on last abdominal segment. In Ontario, H. Goulet collected two types of larvae from this host. One was similar to the Missouri larva, but with the dark patch on the vertex bounded by the lateral sutures; the head pattern was like that of *Strongylogaster impressata*, but with a dark stripe extending from the eye to the back of the head (this type was also found on *Athyrium*). The other was a tenthridine, thought to represent *Aglaostigma* Kirby or *Macrophya* Dahlbom, which had the upper half of the head covered with numerous minute, pale brown spots, and a rufous patch along the dorsal portion of the coronal suture; the dorsum of the body was gray-banded (this type was also found on *Deparia*).

Dryopteridaceae

Dryopteris carthusiana (Vill.) H.P. Fuchs (spinulose wood fern).—Dyar collected larvae on this host (as *Aspidium spinalosum*) in New Hampshire but did not succeed in rearing adults (Smith 1986). *Larva photographed on 27 May 2020 in Erie Co., Pennsylvania* (dorsal view only, iNat 47890000): Head with black patch on vertex; body pale green above with pale yellow sublateral spots. On 16 June 2016 in Massachusetts, CSE observed (but did not photograph) a larva at least superficially resembling *Strongylogaster impressata* beginning to bore into a stump next to a clump of *D. carthusiana* near the edge of a beaver meadow.

Dryopteris cristata (L.) A.Gray (crested wood fern).—*Strongylogaster larva photographed on 3 June 2019 in Leeds and Grenville Co., Ontario* (dorsal view only,

iNat 26360899): Head pale cream-colored with bold black patch on vertex; body pale green above, whitish below with distinct yellow sublateral spots.

Dryopteris filix-mas (L.) Schott (male fern).—*Strongylogaster macula* is recorded from this host in Europe, as well as from *Polystichum aculeatum* (L.) Roth (hard shield-fern), which does not occur in North America.

Polystichum acrostichoides (Christmas fern).—Possibly *Strongylogaster impressata* (based on head pattern on shed skin).

Polystichum munitum (Kaulf.) C.Presl (western sword fern).—Poinar (2021) reported larvae of *Aneugmenus* and *Strongylogaster* developing on this fern in the Pacific Northwest, but these records require confirmation. DRS is thanked in the paper's acknowledgments for assistance with identification, but he did not actually examine any specimens, and as stated in his correspondence with Poinar, the photographs of larvae are not of sufficient detail to determine the genera. The illustrated adult that purportedly was reared from *P. munitum* (G. Poinar *in litt.* to DRS, 28 May 2012) and consumed its spores as an adult (Poinar 2021) is in fact a *Nematus* Panzer (Tenthredinidae). It presumably fed as a larva on some nearby tree or shrub and happened to spin its cocoon on the fern.

Onocleaceae

Matteuccia struthiopteris (L.) Tod. (ostrich fern).—On 19–22 June 2009 in Massachusetts, CSE photographed larvae on this fern that were bluish-green with more or less distinct yellow-orange sublateral spots and a large black spot on the last abdominal segment. The head was black with brown genae and clypeus (BG 350738). H. Goulet recorded three distinct types of larvae from ostrich fern in Ontario. One had a head pattern like that of *Strongylogaster impressata* but lacked

spots on the last abdominal segment, and apparently also lacked sublateral yellow spots. Another had a pair of large, dark spots on the vertex and a pair of dark spots on the last abdominal segment. The head of the third type (of which just two examples were found) lacked distinct dark spots, but was dorsally pale brown except along the coronal suture.

Onoclea sensibilis (sensitive fern).—*Strongylogaster impressata*, *Thrinax dubitata*.

Osmundaceae

Osmunda claytoniana (interrupted fern).—*Strongylogaster polita*, *S. tacita* (oviposition observed), *Thrinax dubitata*. Larvae identical to *S. impressata* found, but not reared.

Osmunda spectabilis (royal fern).—*Strongylogaster tacita*.

Osmundastrum cinnamomeum (cinnamon fern).—No rearing records, but larvae similar to *Strongylogaster impressata* (but with large black spot behind eye), *S. polita*, and *S. tacita*.

Pteridaceae

Adiantum pedatum L. (maidenhair fern).—*Unidentified larvae found on 5 September 2016 in Delaware Co., Pennsylvania* (lateral view only, iNat 13230936): Head pale amber with brown stripe on vertex directed toward black eyespot; body uniformly green. H. Goulet recorded four types of larvae from maidenhair fern in Ontario. One was a strongylogastrine with a large dark spot on the vertex (~bounded by the lateral sutures), a spot in the upper portion of the frons, and a small spot extending backward from each eye (this type also found on *Athyrium*, *Matteuccia*, and *Pteridium*). Another was the tenthredinine described below under *Thelypteris palustris* (rarely with inverted "V" markings on the dorsum). The other two were each encountered just once and

had immaculate heads; one had a gray body and was possibly a tenthredinine, and the other had a green body and its head was tinted pale rufous dorsally.

Thelypteridaceae

Phegopteris connectilis (Michx.) Watt (long beech fern).—*Strongylogaster* larvae found on 4–7 June 2017 in Northfield, Franklin Co., Massachusetts (iNat 100384883): Head pale cream-colored with two bold black dorsal spots (broken by a medial line of ground color); body green above, whitish with indistinct yellow spots sublaterally (darker yellow to yellow-orange on thorax); no spots on last abdominal segment; tibiae and tarsal claws blackish dorsally, sometimes also with thin, oblique dusky line on coxae and paired dusky spots on femora. Larvae found on 27 May 2015 in Franklin Co., New York (BG 1625898; iNat 9508556): Head pale cream-colored with bold black central patch on vertex, tapering abruptly just above the eyes and then widening to a round spot at upper edge of frons; body milky whitish, appearing pale green dorsally due to gut contents; dusky to blackish patches on trochanters, femora, tibiae, and tarsal claws.

Phegopteris hexagonoptera (Michx.) Fée (broad beech fern).—*Strongylogaster* larvae as described above, found 27 April 2019 in Conover, Catawba Co., North Carolina (iNat 23405137) and 25 May 2020 at Catoctin Mountain Park, Frederick Co., Maryland (iNat 47849503).

Thelypteris palustris (marsh fern).—*Aneugmenus flavipes*. H. Goulet's unpublished notes record six additional types of larvae from this host, although some were rarely encountered and seem unlikely to have been actual fern feeders (two examples of a larva identified as *Pristiphora* Latreille (Nematinae); a single individual identified as Blennocampinae; and another singleton tentatively identified as *Brachythops* Haliday (Selandriini)). A

commonly encountered larva was said to be a *Tenthredo*-like tenthredinine; its head had a large reddish-brown spot on the dorsal third, and its body was gray dorsally, banded and often with inverted "V" markings (this type was also found on *Adiantum* and *Deparia*). A selandriine known from four examples had an arrow-shaped central dark spot on the vertex, extending from the back of the head and tapering to a point at the frontal suture; a dark spot extending behind the eye; the body dorsally gray and unbanded; and a small, black apical spot on the last abdominal segment. A more common one, identified as *Strongylogastrini*, had a broader spot on the vertex, not reaching the frontal suture; a spot on the upper portion of the frons; a stripe extending from the eye to the back of the head; and the body was gray dorsally, without a spot on the last abdominal segment.

Woodsiaceae

Woodsia oregana D.C.Eaton (Oregon cliff fern).—*Strongylogaster* larva found 27 May 2021 at Brown Ecological Reserve, Vernon, British Columbia (dorsal view only, iNat 98582851): Head entirely shining black on dorsal half, pale whitish below. Body dark green dorsally, whitish behind head and sublaterally, with distinct yellow sublateral spots and a pair of black spots on last abdominal segment; femora with dusky patches, tibiae and tarsal claws shining black dorsally.

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