PROC. ENTOMOL. SOC. WASH.
123(2), 2021, pp. 314–333

A NOVEL ORIGIN OF PTERIDIVORY AMONG THE NEW WORLD NOCTUOIDEA: FERN-FEEDING "LITTER MOTHS" (EREBIDAE: HERMINIINAE)

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Abstract.—Surveys of the caterpillars of Area Conservacion de Guanacaste (ACG), northwestern Costa Rica, documented an array of litter moths (Erebidae: Herminiinae) feeding on ferns in at least 17 families. This represents the first documentation of extensive oligophagous fern-feeding among Herminiinae and possibly within New World Erebidae. Collectively, the taxonomic composition of foodplants of pteridivorous Herminiinae in ACG differs markedly from those of corresponding fern foodplants of sympatric Noctuidae: they are less concentrated in Polypodiales and tree ferns (Cyatheaceae) are among the primary foodplants of several herminiines. These have been recorded only rarely as foodplants of ACG noctuids. Pteridivorous herminiines also appear closely related to species variously recorded from dead leaves, algae, mosses (Bryophyta), spikemosses (Selaginaceae), palms (Arecaceae), and the exclusively New World family Cyclanthaceae. Feeding on monocots and mosses by caterpillars with pteridivorous congeners may even represent a more general pattern that is shared, for example, with certain sawflies (Tenthredinidae).

Key Words: diet breadth, Polypodiaceae, Polypodiopsida, *Selaginella,* tropical caterpillars

DOI: 10.4289/0013-8797.123.2.314

Although a range of polyphagous herbivorous insects feed incidentally or opportunistically on ferns, specialized fern-feeding (pteridivory) invites questions concerning plant-herbivore coevolution due to the considerable age and complex allelochemistry of ferns (Balick et al. 1978, Cooper-Driver 1980). A first step towards—and an empirical prerequisite of—addressing any such questions is the resolution of the number and sequence of independent origins of pteridivory in a given lineage, and their timing relative to the origins of and relationships among major fern groups. Polypodiopsida date back nearly 400 mya and there is evidence of at least isolated stasis in chromosomal arrangements (Bomfleur et al. 2014), However, recent phylogenetic work has characterized the extant leptosporangiate orders (subclass Polypodiidae) as having originated much more recently during the Cretaceous, following the explosion of

dominance by flowering plants (Schneider et al. 2016).

Obligate pteridivory by insects also draws interest because of its alleged ecological rarity in nature, which has been variously asserted and inferred from observations of low herbivore loads on ferns in nature. This general paradigm was reviewed and challenged by Hendrix's (1980) summary of apparently independent origins of specialized pteridivory in each of the most species-rich herbivorous insect orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera). Although it has yet to be assessed critically, evolutionary colonization events by herbivorous insects onto ferns may have taken place over a span of 250 my or more. These include cases within the Hemiptera and Coleoptera (ages of origin ~ 290–285 mya) relative to Hymenoptera (189 mya), Diptera and Lepidoptera (both ~ 160 mya). Among the most conspicuous of the early holometabolan origins is that of sawflies (Symphyta), a primitive hymenopteran lineage in which pteridivory appears to have arisen multiple times (Schneider et al. 2016). Within the macro-heteroceran Lepidoptera, pteridivory is perhaps most commonly associated with Musotiminae (Pyraloidea: Crambidae), Lithinini (Geometridae: Ennominae), and Eriopinae (Noctuidae). Several of the Geometridae and Erebidae: Arctiinae (= Arctiidae) in Balick et al.'s (1978) review represent incidental feeding records of highly polyphagous species (e.g., *Cingilia catenaria* (Drury)). Within the Noctuoidea, pteridivory has not been reported widely, if at all, from within the 'deltoid' subfamilies. These are all formerly Noctuidae and now placed within the Erebidae, including Herminiinae, or litter moths. They are so named because many of their caterpillars are detritivores, feeding on dead leaves and soft substrates within leaf litter. Within the Noctuidae, pteridivory is most commonly observed by caterpillars of Eriopinae (Noctuidae), a cosmopolitan subfamily with substantial species richness in tropical Asia and significant number of Neotropical species. An exception is *Pseudobryomima* Barnes & Benjamin (Noctuinae), at least two species of which feed on ferns, first as early-instar leafminers that then construct shelters in later instars (McCabe et al. 2002). As the boundaries of the Herminiinae are re-evaluated, a growing body of evidence based in large part on the rearing of caterpillars in Area Conservacion de Guanacaste, Costa Rica (ACG), suggests greater complexity in the extent of noctuid fern-specialization outside the Eriopinae.

Here we characterize the fern associations among several genera of tropical Herminiinae. This represents the first discussion of a substantial group of related fern-feeding species within Erebidae. Our purpose is to characterize the botanical associations of herminiine pteridivore caterpillars observed at ACG with reference to the most current understanding of fern classification, and to contrast the taxonomic and phylogenetic distributions of these foodplants with those of hosts records for sympatric pteridivorous Noctuidae, in which fern-feeding was derived independently. A more expansive treatment of the larvae and their hosts will accompany ongoing taxonomic revisionary work as in Goldstein et al. (2018a, 2018b, 2019) and Goldstein and Zilli (2019).

Herminiinae comprise a diverse and cosmopolitan array of more than 140 recognized genera, many of which are poorly circumscribed and polyphyletic. Many of the species reared at ACG are undescribed, and herminiine genera represent one of the more abyssal gaps in

our current understanding of noctuoid systematics. A systematic treatment of the group is beyond the scope of this paper and consequently many of the generic assignments used here are provisional and will likely change following revision. Inference of the number of origins of fern-feeding within the subfamily awaits comparative phylogenetic analyses.

Materials and Methods

Caterpillars have been, and still are being, sampled in the course of general inventory efforts undertaken at ACG since 1978 (Janzen and Hallwachs 2011, 2016; Diaz et al. 2018, Metz et al. 2020). Identification of foodplants (and their confirmation by professional plant taxonomists), rearing of larvae and parasitoids, and DNA barcoding were undertaken by the parataxonomist team in collaboration with the Consortium for the Barcode of Life (CBOL) and the Centre for Biodiversity Genomics (CBG), University of Guelph. Provisional barcode analyses (NJ, Kimura 2-parameter) were used to differentiate species; and among these, provisional determinations were made for specimens matching recognizable species morphologically and provisional generic assignments were made for others. All ACG vouchered specimens included in this assessment were found on and had to continue feeding on their associated foodplants. Original adult species identifications were made by examination of morphology and DNA barcodes, followed up with identifications by R. W. Poole and refined subsequently by P. Z. Goldstein. Adult voucher specimens are deposited at the U. S. National Museum of Natural History, Washington, DC, USA and identified by unique voucher codes referring to the inventory master database at http://janzen.sas.upenn.edu, a FileMaker Pro copy of which is deposited in the Department of Entomology, NMNH; much of the collateral data are also available in the BOLD public database of the CBG.

A survey of ACG rearing records quickly revealed repeated records of novel fern feeding records in both the Noctuidae and Herminiinae. Among the noctuids, primarily pteridivorous larvae were documented for at least three genera within the likely boundaries of Eriopinae (*Argyrosticta* Hübner, *Callopistria* Hübner, and *Phuphena* Walker), and were newly reported from three Noctuinae genera considered incertae sedis (*Leucosigma* Druce, *Lophomyra* Schaus, 1911b, and *Aprica* Goldstein). Provisional generic assignments of fern-feeding Herminiinae include *Dusponera* Dognin, *Ipanephis* Nye, *Mamerthes* Druce, *Nicetas* Druce, *Rejectaria* Guenée, *Salia* Hübner, *Scopifera* Herrich-Schäffer, *Strathocles* Druce, and *Tarista* Schaus. Just as the discovery of several *incertae sedis* Noctuidae feeding on ferns raises questions that require taxonomic resolution at the supra-generic levels, the numerous herminiine fern-feeders highlight specific nomenclatural problems that require extensive taxonomic revision in the subfamily. Specifically, fern-feeding species of ACG include described and undescribed species distributed among several genera that are either polyphyletic or pending synonymy, most prominently among the *Mamerthes-Nicetas-Rejectaria* complex. While clustering of DNA barcodes suggest prospective groups of closely related species with shared suites of foodplant records, their ultimate taxonomic placement awaits proper revision. Given our current understanding, based on type specimens and type species, we have endeavored to minimize our use of provisional generic names, but retain

provisional morphospecies names for undescribed species. Undescribed species bear an interim, informal, non-italicized species-specific epithet that contains numerals and capital letters. Such names are constructed as to be computer- and database-friendly, not containing spaces and indicating, where possible, the taxonomist or parataxonomist who coined the name (e.g., *Rejectaria* Poole03).

Prior to collating foodplant data, we initially arranged specimens according to NJ dendrograms generated from DNA barcode sequences, then collated and labeled specimens with available metadata (additional metadata are in the individual data base record for each specimen, as located by its unique voucher code). Species generally match Barcode Index Numbers (BINs; Ratnasingham and Hebert 2013), though some BINs contain more than one species. Species determinations and provisional generic assignments for undescribed morphospecies were retained or revised on the basis of ongoing revisions, with the understanding that herminiine nomenclature is in a state of flux. Records of unvouchered or unavailable specimens (such as all of those that die of disease, parasites, or mistreatment, although they do have their own records in the master data base) and specimens with foodplants that could not be assigned to genus were excluded from this paper. We examined all foodplant records, including non-pteridophytes, for species and putative congeners of species recorded from ferns. Foodplant records were arranged taxonomically following the Pteridophyte Phylogeny Group (PPG I, 2016) and the Angiosperm Phylogeny Group (APG IV, 2016).

Since field caterpillar capture methods at the massive scale of the ACG effort cannot be standardized, we do not attempt to quantify or even assert species-level oligophagy beyond that which is obvious in the data analysis. For example, if *Callopistria floridensis* (Guenée, 1852) caterpillars are found 1,370 times out of roughly 720,000 wild caterpillars during 43 years of inventory, and all were feeding on ferns (which they were), we consider them pteridivores. Although in many specific cases the distributions of foodplant records were heavily weighted towards a particular taxonomic group of plants, implying some level of oligophagy, the recorded feeding records of most species are dispersed across multiple plant families. We summarize repeated observations of foodplant as a step towards constructing diet breadths, and use ensembles of foodplant records to generate coarse comparisons between two unrelated groups of noctuoids. For the purposes of this paper, we avoid the conventional use of 'hostplant', which often includes random encounters of caterpillars starving or searching for cocooning foliage. Again, our usage of "foodplant" is restricted to documented feeding at the time of and after capture, not incidental occurrence, and in general we restrict the usage of 'host' to parasitized caterpillars.

We examined the taxonomic distributions of parasitoids (excluding hyperparasitoids) reared from pteridivorous Herminiinae and Noctuidae species and their putative congeners. Parasitoid records were arranged taxonomically by caterpillar host genus and plant genus; parasitoids that were not assigned to family were excluded.

Results

We examined 2,298 foodplant records of 42 species of Herminiinae fern-feeders

and 18 putative congeners with foodplant records outside Polypodiopsida (Table 1, Figs. 1–10) and 2,545 records of 27 species of Noctuidae fern-feeders (Table 2). The taxonomic distributions of feeding records among species and families of foodplants are non-uniform among among both Herminiinae and Noctuidae taxa; both recorded diet breadths and taxonomic concentrations of recorded foodplants vary widely. Excluding pteridivore species for which only a singleton feeding record species exists, most fern-feeders were recorded from more than one fern family (29/35 herminiines and 17/24 noctuids), and the mean number of fern families represented in the recorded diet of a given fern-feeder is 3 for herminiines ($n = 35$, $\bar{x} = 3$, $M = 3$, Range 1–9) and 2 for noctuids ($n = 24$, $\bar{x} = 2$, $M = 3$, Range 1–13). We hasten to point out that in contrast to non-ferns, we have no idea of how distinctive are the allochemical signatures of individual fern families, although they may be more homogeneous than those of dicotyledonous angiosperms. Despite the paucity of potentially species-level or family-level fern specialists, several well-sampled species of both Herminiinae and Noctuidae have records limited to a narrow taxonomic range of foodplants, just as the collective feeding records on certain ferns and fern families are narrowly concentrated within a small number of herbivore species. We stress that while all of these species are "fern specialists" in the sense that they feed only on ferns, most appear to be 'fern-polyphagous' with respect to multiple fern taxa.

Collectively, Herminiinae are recorded from a greater taxonomic breadth of fern foodplants (17 families in 5 orders) than Noctuidae (13 families in 3 orders) (Figs. 11, 12; Tables 1, 2). However, there are very few records of herminiine foodplants within the primitive leptosporangiate fern orders Hymenophyllales, Gleicheniales, and Schizeales.

The contrast between the taxonomic distributions of foodplants of ACG Noctuidae versus those of Herminiinae can be visualized coarsely at the ordinal level and with reference to the two largest suborders of Polypodiales, Aspleniineae and Polypodiineae (Fig. 12). Of 42 ACG Herminiinae species captured and reared on ferns, all but one were recorded from Polypodiales, 20 of them exclusively from the order; 21 herminiine species have foodplant records in four families in the suborder Aspleniineae (Aspleniaceae, Blechnaceae, Thelypteridaceae, and Athyriaceae), including 7 with all their foodplant records confined to Aspleniineae (Table 1). Of the 27 fern-feeding Noctuidae, eight species have foodplant records in Aspleniineae, with only *Phuphena multilinea* recorded exclusively from the suborder (220 records from *Salpichlaena volubilis,* Blechnaceae; a single specimen from Polypodiineae (*Polybotrya osmundacea,* Dryopteridaceae) was parasitized so its identification is questionable) (Table 2). Among the noctuid fern feeders, the Polypodiineae represents a majority of all the foodplant records. All 27 pteridivorous Noctuidae species examined were recorded from foodplants in Polypodiineae: 16 of these were recorded exclusively from the suborder, and 19 were recorded from Polypodiaceae, including 12 chiefly or exclusively from that family (Table 2). Only three species of noctuid fern-feeders had foodplant records in addition to Polypodiales, and these included two of the three least oligophagous fern-feeders in terms of foodplant families, *C. floridensis* and *Phuphena cilix* (Druce, 1898) (Godman and Salvin 1898); all three species were recorded from Cyatheaceae (Cyatheales) and one

Table 1. Taxonomic distribution of foodplant records for ACG Herminiinae (Erebidae). Genus assignments are provisional.
(Abbreviations: HYM = Hymenophyllaceae, GLE = Gleicheniaceae, SCH = Schizaeaceae, CYA = Cyatheaceae, SAC = Saccolomataceae, PTE = Pteridaceae, DEN = Dennstaedtiaceae, ASP = Aspleniaceae, THE = Thelypteridaceae, ATH = Athyriaceae, BLE = Blechnaceae, DID = Didymochlaenaceae, DRY = Dryopteridaceae, LOM = Lomariopsidaceae, NEP = Nephrolepidaceae, TEC = Tectariaceae, POL = Polypodiaceae. DL = Dead leaves, ALG = Algae, BRY = Bryophyta, SEL = Selaginellaceae, CYC = Cyclanthaceae, ARE = Arecaceae)

		HYMENOPHYLLALES	GLEICHENIALES	SCHIZAEALES	CYATHEALES	POLYPODIALES													Non-fern Plants & Substrates						
HERMINIINAE									Aspleniineae				Polypodiineae												
Provisional Genus Assignment	Provisional Species	HYM	GLE	SCH	CYA	SAC	PTE	DEN	ASP	THE	ATH	BLE	DID	DRY	LOM	NEP	TEC	POL	DL	ALG	BRY	SEL	CYC	ARE	TOTAL
Dusponera	Poole01 (= *D. fannia*)								12																12
Ipanephis	*esperanzalis*				6			52							1										59
"Ipanephis"	sp.				6			35				1		1	2										45
Mamerthes	*nigrilinea*				40								4		5										49
Mamerthes	Poole01DHJ01											7	1				1								9
Mamerthes	Poole01DHJ02				1					5	2	7	1	2		1	1	1							21
Nicetas	*annon*		1		2		11											1							15
Nicetas	*antonalis*				2					1				4	2		16	1							26
Nicetas	Biolep214																					1			1
Nicetas	Biolep218																					66			66
Nicetas	Janzen02										3														3
Nicetas	Janzen238					2		1																	3
Nicetas	Janzen239																					3			3
Nicetas	Poole01DHJ01									2															2
Nicetas	Poole01DHJ02			1			3	8		23						1									36
Nicetas	Poole03						1																		1
Nicetas	Poole04													1						5					6
Nicetas	Poole05				10									7	1										18
Nicetas	Poole06				22				1	9		3						6							41
Nicetas	Poole07									14					17										31
Nicetas	Poole08									14	1				2										17
Nicetas	Poole09														1									1	2
Nicetas	Poole10																			1				1	2
Nicetas	Poole11																			12					12

Table 1. Continued.

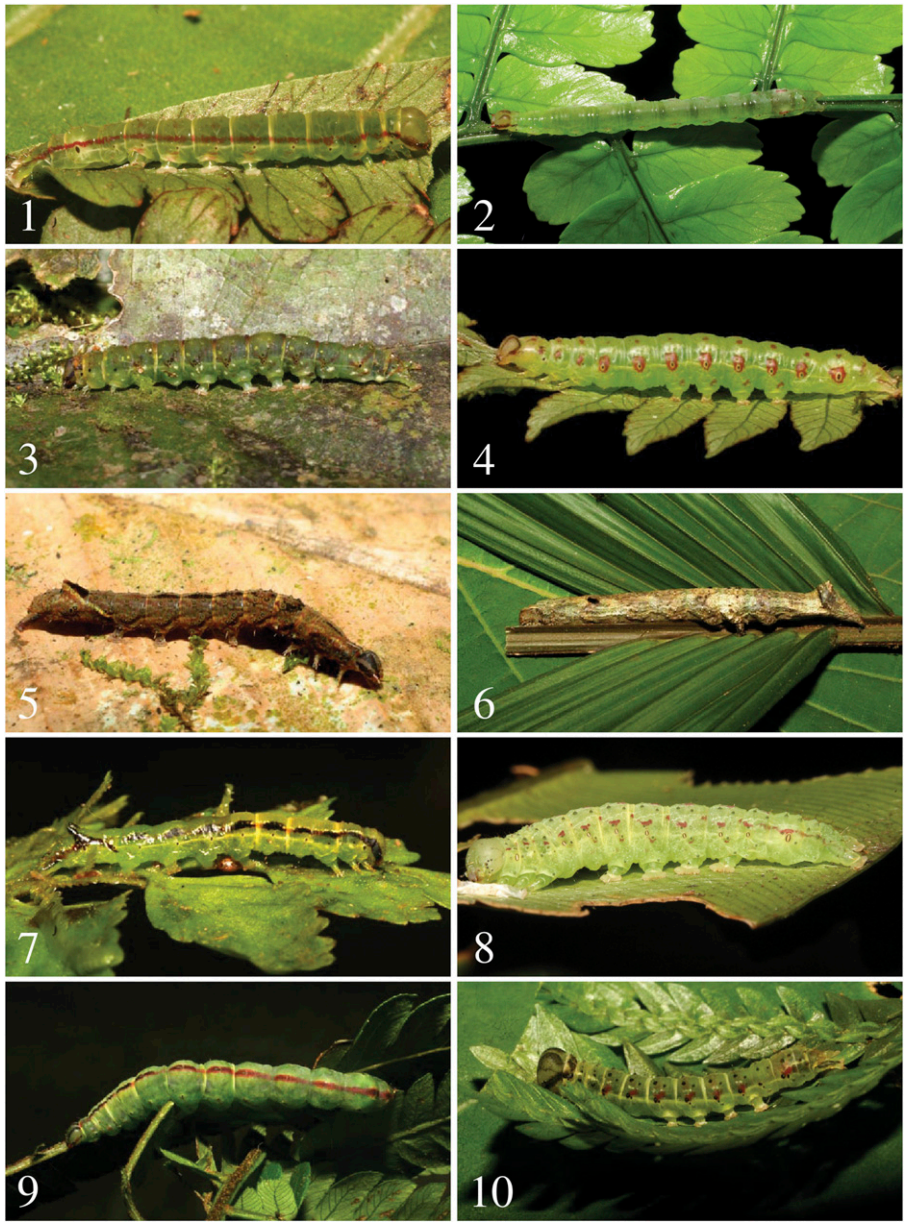
		HYMENOPHYLLALES	GLEICHENIALES	SCHIZAEALES	CYATHEALES	POLYPODIALES													Non-fern Plants & Substrates						
HERMINIINAE									Aspleniineae				Polypodiineae												
Provisional Genus Assignment	Provisional Species	HYM	GLE	SCH	CYA	SAC	PTE	DEN	ASP	THE	ATH	BLE	DID	DRY	LOM	NEP	TEC	POL	DL	ALG	BRY	SEL	CYC	ARE	TOTAL
Nicetas	Poole12									4															4
Nicetas	Poole13	1							5																6
Nicetas	Poole14						14					1		1	1			56							73
Nicetas	Poole15		4																						4
Nicetas	Poole16																							2	2
Nicetas	Poole18				67					4					12										83
Nicetas	Poole19																				1				1
Nicetas	Poole20				581		4	5		13	1			15	110										729
Nicetas	Poole21				2								52												54
Nicetas	Poole22													25	13		1	12							51
Nicetas	Poole23						13							19											32
Rejectaria	*craftsalis*																		2						2
Rejectaria	*funebris*																		1						1
Rejectaria	Janzen01													1						1					2
Rejectaria	Poole05																						2		2
Rejectaria	Poole08																						1		1
Rejectaria	Poole09																						4		4
Rejectaria	Poole10																						151		151
Rejectaria	Poole11																						166		166
Rejectaria	Poole12																						10		10
Rejectaria	Poole14																		1	1					2
Rejectaria	*villosa*																						13		13
Salia	BioLep454								1																1
Salia	Janzen10				1			1		6															8
Salia	Janzen235																					4			1

Table 1. Continued.

		POLYPODIALES																							Non-fern Plants & Substrates							
		HYMENOPHYLLALES		GLEICHENIALES	SCHIZAEALES	CYATHEALES				Aspleniineae					Polypodiineae																	
HERMINIINAE																																
Provisional Genus Assignment	Provisional Species	HYM	GLE	SCH	CYA	SA	PTE	DEN	ASP	THE	ATH	BLE	DID	DRY	LOM	NEP	TEC	POL	DL	ALG	BRY	SEL	CYC	ARE	TOTAL
Salia	Janzen305									62															62
Salia	*Ivsizona*						2							2											4
Salia	Poole01															10		1							11
Salia	Poole02											1													1
Salia	Poole03					1				36															37
Scopifera	*antelia*					242		3					1		9										255
Scopifera	Poole01					6	1								5										12
Scopifera	Poole16					2		1																	3
Stradtocles	*imitata* (= *"Dasponera fannia"*)					3								12	5										20
Tarista	Poole01													1											1
Tarista	Poole02					1								4	4										9
	TOTAL	1	5	1	995	2	49	106	19	193	7	20	59	95	190	12	19	78	4	20	1	74	347	4	2298

from Lygodiaceae (Schizeales) (Table 2). In contrast, 28 species of the 42 Herminiinae fern-feeders have host records among six families of Polypodiineae (Didymochlaenaceae, Dryopteridaceae, Lomariopsidaceae, Nephrolepidaceae, Tectariaceae, and Polypodiaceae), of which the foodplant records of three species are confined entirely to the suborder (Table 1).

Among the most conspicuous differences in the suites of fern foodplants in Herminiinae versus Noctuidae is that 995 foodplant records for tree ferns (Cyatheales, Cyatheaceae; e.g., *Alsophila, Cyathea*) are widespread among Herminiinae species (18 species) (Table 1), but are nearly absent (7 records) from Noctuidae and confined to only 3 species) (Table 2). Both Dennstaedtiaceae (e.g., *Hypolepis, Pteridium*) and *Didymochlaena* (Didymochlaenaceae) are also well-represented among herminiine foodplant records, but records of Blechnaceae (e.g., *Blechnum, Salpichlaena*) and Pteridaceae (e.g., *Adiantum, Pityogramma, Pteris*) are few among Herminiinae relative to Noctuidae, and almost all records of noctuids feeding on Pteridaceae are of *Callopistria floridensis*. Although tree ferns (Cyatheaceae), represent perhaps the most conspicuous difference between the collective diet breadths of Herminiinae versus Noctuidae, the herminiine larvae that feed on them are rarely if ever specialists at the fern family level (Table 1). Every one of the 18 species of Herminiinae feeding on tree ferns also had foodplant records for at least one other fern species. None of these 18 hermeniines, however, had foodplant records from non-ferns (Table 1). Again, we clarify that although most fern-specialists do not appear restricted to a given group of ferns, the near absence of tree ferns from the spectrum of noctuid foodplants is noteworthy.



Figs. 1–10. Representative examples of fern-feeding larvae and their relatives (Erebidae: Herminiinae) with food substrate records outside Polypodiopsida. 1, 05-SRNP-33660 DHJ424715 *Tarista* Poole02 on *Polybotrya osmundacea* (Dryopteridaceae). 2, 06-SRNP-32792 DHJ415934 *Tarista* Poole02 on *Lomariopsis vestita* (Lomariopsidaceae). 3, 07-SRNP-65271-DHJ429409 *Nicetas* Poole19 on moss (Bryophyta). 4, 08-SRNP-41994-DHJ446615 *Scopifera antelia* on *Lomariopsis vestita* (Lomariopsidaceae). 5, 09-SRNP-31750-DHJ455150 *Rejectaria* Poole14 on algae. 6, 09-SRNP-32562-DHJ464251 Herminiinae sp. on *Calyptrogyne trichostachys* (Arecaceae). 7, 11-SRNP-40811-DHJ482826 *Nicetas* Poole13 on *Trichomanes collariatum* (Hymenophyllaceae). 8, 14-SRNP-44574 DHJ724243 *Dusponera* Poole01 (= *D. fannia*). 9, 05-SRNP-4748-DHJ403124 *Nicetas* Poole18 on *Alsophila firma* (Cyatheaceae). 10, 09-SRNP-73178-DHJ465672 *Nicetas* BioLep218 on *Selaginella arthritica* (Selaginellaceae).

Table 2. Taxonomic distribution of foodplant records for ACG Noctuidae (Table 2). Genus assignments are provisional.
(Abbreviations: LYG = Lygodiaceae, CYA = Cyatheaceae, PTE = Pteridaceae, DEN = Dennstaedtiaceae, ASP = Aspleniaceae, THE = Thelypteridaceae, ATH = Athyriaceae, BLE = Blechnaceae, DRY = Dryopteridaceae, LOM = Lomariopsidaceae, NEP = Nephrolepidaceae, TEC = Tectariaceae, POL = Polypodiaceae)

		SCHIZAEALES	CYATHEALES	POLYPODIALES											
HERMINIINAE						Aspleniineae				Polypodiineae					
Provisional Genus Assignment	Provisional Species	LYG	CYA	PTE	DEN	ASP	THE	ATH	BLE	DRY	LOM	NEP	TEC	POL	TOTAL
Aprica	*patula*			13	1		3		5		2	3			27
Argyrosticta	*aurifundens*									1				103	104
Argyrosticta	*bellinita*						1			4			5	197	207
Argyrosticta	ditissimaPoole02													14	14
Argyrosticta	*eubotes*								2					13	15
Argyrosticta	Janzen01													5	5
Argyrosticta	Janzen05													9	9
Argyrosticta	*meres*						2		1		5			3	11
Argyrosticta	Poole01													3	3
Argyrosticta	scionePoole01			1										2	3
Argyrosticta	*vauaurea*												1	60	61
Callopistria	*floridensis*	27	1	585	35	18	15	39	473	12	20	35	9	2	1271
Callopistria	Poole01											1			1
Callopistria	*mexicana*						3		16	6			82	2	109
Callopistria	mexicanaDHJ01												6		6
Callopistria	mexicanaDHJ02									4	2		63	1	70
Leucosigma	*albimixta*									1					1
Leucosigma	*Chloe* (= Poole02)									8				12	20
Leucosigma	*Poolei* (= Janzen242)									1				2	3
Leucosigma	*reletiva*									1					1
Leucosigma	*Schausi* (= Janzen839)										1			9	10
Lophomyra	*Commixta* (= Poole02)													74	74
Lophomyra	*Tacita* (= Poole01)													48	48
Phuphena	*cilix*		1					12	126	3	44		1	5	192
Phuphena	*zelotypa* (= cilixDHJ02)		5							1	48				54
Phuphena	*multilinea*								220	1					221
Phuphena	*tura* (=Poole02)				1							4			5
	TOTAL	27	7	599	37	18	24	51	843	43	122	43	167	564	2545

Within Herminiinae, *Mamerthes nigrilinea* Druce, 1891 (Godman and Salvin 1891), *Scopifera antelia* (Druce, 1891) (Godman and Salvin 1891), and two putative *Nicetas* account for most of the records of tree ferns (Cyathaceae) (predominantly *Alsophila firma* (Baker) D.S. Conant.). *Ipanephis esperanzalis* (Schaus, 1913) and an indeterminate species "*Ipanephis*" account for most herminiine feeding records on Dennstaedtiaceae, predominantely *Hypolepis repens* (L.) C. Presl. *Thelypteris* species (Theylypteridaceae), primarily *T. palustris* Schott and *T. nicaraguensis* (E. Fourn.) C.V. Morton are primary or shared primary foodplant records for a number of *Nicetas* and two species of *Salia* Hübner, [1818] that may be specialists. Records for *D. fannia* Schaus, 1916 (= *D.* Poole01) are confined to *Asplenium serratum* L.; Aspleniaceae account for multiple foodplant records of only one other herminiine species (*Nicetas* Poole13). *Nicetas* Poole21 is recorded predominantly from *Didymochlaena*

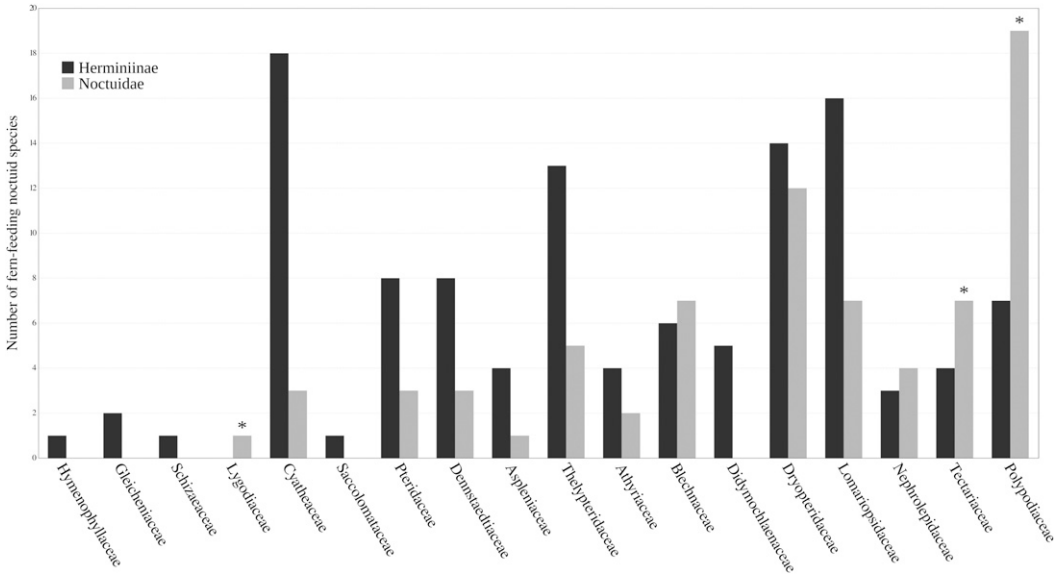


Fig. 11. Taxonomic distribution of fern foodplant records by family of 60 species of fern-feeding Herminiinae (based on 1851 foodplant records; See Table 1) and 27 species of Noctuidae (based on 2545 foodplant records; See Table 2) at ACG. These records represent the total number of plant family feeding records per caterpillar species, and are not mutually exclusive (i.e., The number of plant families exceeds the number of caterpillar species they represent.). No ACG noctuid species are recorded feeding on five fern families (Hymenophyllaceae, Gleicheniaceae, Schizaeaceae, Saccolomataceae, and Didymochlaenaceae). Columns marked with * indicate three of eighteen fern families with more noctuid species than herminiine species (Lygodiaceae, Tectariaceae, and Polypodiaceae).

truncatula and accounts for most of the ACG herminiine records on Didymochlaenaceae. The records for *Salia* Poole01 on *Nephrolepis brownii* and *N. biserrata* represent most of the herminiine records on Nephrolepidaceae. Likewise the 16 records of *Nicetas antonalis* Schaus, 1916 on *Tectaria* spp. account for most of the records of ACG Herminiinae on Tectariaceae, which are more widespread among recorded noctuid foodplants. *Nicetas* Poole14 is recorded predominantly on *Polypodium* and *Serpocaulon,* and accounts for a majority of the herminiine records on Polypodiaceae.

Among the Noctuidae, aside from the fern-polyphagous *C. floridensis,* three species of *Phuphena* Walker, 1858 account for most of the noctuid foodplant records on Blechnaceae and Lomariopsidaceae. Most of the feeding records on Blechnaceae are accounted for by *P. cilix* on *Blechnum occidentale* L. and by *Phuphena multilinea*, a possible specialist on *Salpichlaena volubilis* J. Sm.; both *P. cilix* and *P. zelotypa* Schaus, 1911a were encountered repeatedly on *Lomariopsis vestita* (Lomariopsidaceae), on which *P. zelotypa* is a possible specialist. Excluding *C. floridensis, Phuphena* species also account for a majority of the noctuid records on Cyatheaceae, Athyreacae, and Nephrolepidaceae; *Lophomyra* and *Argyrosticta* Hübner, [1821] account for most of the noctuid records from Polypodiaceae genera. *Aprica* Goldstein, 2019 (Goldsteain et al. 2019) accounts for almost all the records on Pteridaceae.

The many records of the fern-polyphagous and highly abundant

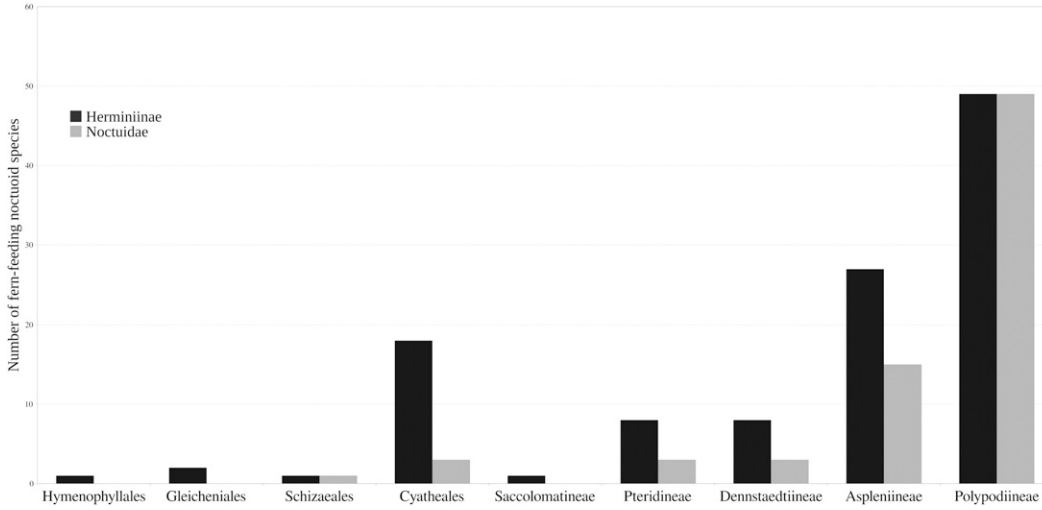


Fig. 12. Taxonomic distribution of fern foodplant records by order and suborder (for Polypodiales only) of 60 species of fern-feeding Herminiinae (based on1851 foodplant records; See Table 1) and 27 species of Noctuidae (based on 2545 foodplant records; See Table 2) at ACG. These records represent all the plant groups recorded per caterpillar species, and are not mutually exclusive (i.e., The number of plant groups exceeds the number of caterpillar species they represent.). No ACG noctuid species are recorded from Hymenophyllales, Gleicheniales, or Saccolomatineae.

species *Callopistria floridensis* accounted for 1271/2545 (50%) of all the successfully reared adult noctuid foodplant records examined, and represent all 13 of the fern families recorded for *Callopistria* species at ACG. Like other *Callopistria, C. floridensis* is considered a fern-specialist, but it is highly fern-polyphagous. It accounts for all the Schizeales and Aspleniaceae records and most of the Pteridineae (all Pteridaceae) records among the Noctuidae.

The families represented by foodplants of putative fern-oligophages among the Herminiinae are more numerous than among the noctuid pteridivores (Figs. 11, 12) outside as well as within Polypodiales. Non-pteridophyte foodplants recorded for putative congeners of pteridivorous species are distributed asymmetrically among ACG Noctuidae and Herminiinae. Among Noctuidae, they consist of records of angiosperm-feeding by *C. carmioli* on Gesneriaceae (Lamiales) and *C. dapsilis* on Bombacaceae (Malvales), but these species are probably misplaced in *Callopistria* and are excluded from Table 2 and Fig. 12.

Among the Herminiinae, however, several primary non-fern hosts of apparent oligophages appear repeatedly. Records of grazing on algae, mosses (Bryophyta), Selaginellaceae (Lycophyta), and dead leaves, as well as palms (Arecaceae) and the New World family Cyclanthaceae are conspicuous among Herminiinae, either as alternative foodplants of fern-feeders or (particularly in the case of the cyclanth-feeders) as primary foodplants of their congeners (Table 1). The non-fern foodplant groups most frequently recorded for herminiine fern-feeders and their putative congeners are as follows, with numbers of species of Herminiinae recorded from group of plant or substrate in parentheses: 20 (5) Algae, 1 Bryophyta, 4 (3) dead leaves, 74 (4) Selaginellaceae (Lycophyta); and among the monocot angiosperm

Table 3. Taxonomic distribution of parasitoid (Hymenoptera and Diptera) among ACG Herminiinae (Erebidae) and Noctuidae.

FAMILY Subfamily Tribe	PARASITOID SPECIES	# RECORDS (# Host spp.) NOCTUIDAE	# RECORDS (# Host spp.) HERMINIINAE	TOTAL # Records	NOCTUIDAE FOODPLANT Family, Genera	HERMINIINAE FOODPLANT Family, Genera
ICHNEUMONIDAE	IchJanzen01 Janzen01	2(2)	1	3	Dennstaedtiaceae, *Pteridium* Blechnaceae, *Salpichlaena*	Selaginaceae, *Selaginella*
Ophioninae	*Enicospilus maculipennis*	27(3)		27	Pteridaceae, *Ceratopteris* (24) Thelypteridaceae, *Thelypteris* Blechnaceae, *Salpichlaena* *Nephrolepidaceae, Nephrolepis*	
	Enicospilus Janzen46		1	1		Polypodiaceae, *Serpocaulon*
Campopleginae	*Charops* GauldA		2(2)	2		Aspleniaceae, *Alsophila* Lomariopsidaceae, *Lomariopsis*
	Charops GauldADHJ04	8(2)	8(3)	16	Tectariaceae, *Tectaria* (4) Blechnaceae, *Salpichlaena* (3) Dryopteridaceae, *Bolbitis*	Cyatheaceae, *Cyathea* (5) Aspleniaceae, *Alsophila* Thelypteridaceae, *Thelyptris* Lomariopsidaceae, *Lomariopsis*
	Charops GauldADHJ05		1	1		Aspleniaceae, Alsophila
	Charops GauldADHJ06	1		1	Tectariaceae, *Tectaria*	
	Charops Janzen03	4(1)		4	Blechnaceae, *Salpipchlaena*	
	Charops Janzen04	3(1)		3	Polypodiaceae, *Niphidium*	
	Charops Janzen05	3(1)	1	4	Polypodiaceae, *Niphidium*	Polypodiaceae, *Serpocaulon*
	Dusona W-1	1		1	Lomariopsidaceae, *Lomariopsis*	
	Dusona GAU-07		1	1		Lomariopsidae, *Lomariopsis*
	Dusona INB-099		2(1)	2		Cyclanthaceae, *Asplundia*
	Microcharops Janzen30	5(1)		5	Aspleniaceae, *Asplenium* (4) Dennstaedtiaceae, *Pteridium* (1)	
Cremastinae	*Eiphosoma* Janzen38	1		1	Nephrolepidaceae, *Nephrolepis*	
Metopiinae	*Colpotrichia* Wahl02		1	1		Polypodiaceae, *Serpocaulon*
	Colpotrichia veriga	1		1	Polypodiaceae, *Microgramma*	
Cryptinae	*Isdromas* Wahl01	1		1	Blechnaceae, *Salpichlaena*	
	Cryptanura sp.	3(1)		3	Lomariopsidaceae, *Lomariopsis*	
Banchinae	*Diradops* Wahl01NEW	1		1	Polypodiaceae, *Microgramma*	
	Diradops opeva		1	1		Polypodiaceae, *Serpocaulon*
	Diradops Wahl03OLD		1	1	Cyclanthaceae, *Asplundia*	
BRACONIDAE	bracJanzen01 Janzen01		1	1		Cyatheaceae, *Cyathea*
Microgastrinae	*Apanteles raulacevedoi*		1	1		Thelypteridaceae, *Thelypteris*
	Diolcogaster Choi215		1	1		Cyatheaceae, *Cyathea*

Table 3. Continued.

FAMILY Subfamily Tribe	PARASITOID SPECIES	# RECORDS (# Host spp.) NOCTUIDAE	# RECORDS (# Host spp.) HERMINIINAE	TOTAL # Records	NOCTUIDAE FOODPLANT Family, Genera	HERMINIINAE FOODPLANT Family, Genera
Microgastrinae cont.	*Glyptapanteles nealweberi*		8(4)	8		Cyatheaceae, *Cyathea* (6) Aspleniaceae, *Asplenium* Polypodiaceae, *Serpocaulon*
	Glyptapanteles Janzen03		1	1		Thelypteridaceae, *Thelypteris*
	Glyptapanteles Janzen447		1	1		Polypodiaceae, *Serpocaulon*
	Glyptapanteles Whitfield103		4(2)	4		Dryopteridaceae, *Elaphoglossum* (2) Lomariopsidaceae (2)
	Glyptapanteles Whitfield118		12(1)	12		Selaginellaceae, *Selaginella*
	Glyptapanteles Whitfield147	2(2)		2	Polypodiaceae, *Microgramma, Niphidium*	
	Glyptapanteles Whitfield150	31(1)		31	Blechnaceae, *Salpichlaena* (30) Dryopteridaceae, *Polybotrya*	
	Glyptapanteles Whitfield252	2(2)		2	Tectariaceae, Tectaria Polypodiaceae, *Niphidium*	
	Glyptapanteles Whitfield309	10(2)		10	Blechnaceae, *Salpichlaena*	
	Hypomicrogaster Whitfield46		1	1		Thelypteridaceae, *Thelypteris*
	Hypomicrogaster Whitfield55		1	1		Aspleniaceae, *Asplenium*
	mgJanzen01 Janzen01	2		2	Blechnaceae, *Salpichlaena*	
Agathidinae	agaJanzen01 Janzen01		1	1	Cyatheaceae, *Cyathea*	
	Zelomorpha nigriceps	1		1	Blechnaceae, *Blechnum*	
	Zelomorpha paulgoldsteini	3(2)	26 (7)	29	Blechnaceae, *Blechnum* Nephrolepidaceae, *Nephrolepis* Dryopteridaceae, *Bolbitis*	Cyclanthaceae, *Asplundia* (5), *Carludovica* (5) Aspleniaceae, *Alsophila* (6) Cyatheaceae, *Cyathea* (3) Lomariopsidaceae, *Lomariopsis* (3) Dennstaedtiaceae, *Hypolepis* (1) Athyreaceae, *Diplazium* (1) Didymochlaenaceae, *Didymochlaena* (1) Dryopteridaceae, *Elaphoglossum* (1)
Rogadinae	*Aleiodes* Janzen125		1	1		Algae
CHALCIDIDAE	chalJanzen01 Janzen01		1	1		Cyclanthaceae, *Asplundia*
EULOPHIDAE Eulophinae	*Euplectrus alvarowillei*	4(1)		4	Pteridaceae, *Ceratopteris* (3) Polypodiaceae, *Niphidium*	
	Euplectrus eowilsoni	19(4)		19	Polypodiaceae, *Campyloneurum* (8), *Niphidium* (6), *Polypodium* (3), *Microgramma, Phlebodium*	

Table 3. Continued.

FAMILY Subfamily Tribe	PARASITOID SPECIES	# RECORDS (# Host spp.) NOCTUIDAE	# RECORDS (# Host spp.) HERMINIINAE	TOTAL # Records	NOCTUIDAE FOODPLANT Family, Genera	HERMINIINAE FOODPLANT Family, Genera
EULOPHIDAE Eulophinae cont.	*Euplectrus paulhansoni*		2(2)	2		Dryopteridaceae, *Bolbitis* Cyclanthaceae, *Asplundia*
	Euplectrus Janzen01	3(2)		3	Polypodiaceae, *Microgramma, Campyloneurum, Niphidium*	
TACHINIDAE	tachJanzen01 Janzen01	1		1	Polypodiaceae, *Microgramma*	
Exoristinae Goniini	*Atactosturmia* Janzen04	5(1)		5	Polypodiaceae, *Microgramma, Polypodium*	
	Chrysoexorista Janzen35		7(5)	7		Aspleniaceae, *Alsophila* (3) Lomariopsidaceae, *Lomariopsis* (3) Dennstaedtiaceae, *Hypolepis*
	Houghia aurifera	1		1	Polypodiaceae, *Polypodium*	
	Houghia crypta	58(3)		58	Blechnaceae, *Blechnum* (38), *Salpichlaena* (1) Dennstaedtiaceae, *Pteridium* (6) Athyriaceae *Diplazium* (4) Lygodiaceae, *Lygodium* (2) Pteridaceae, Ceratopteris (3) Aspleniaceae, *Asplenium* (2) Thelypteridaceae, *Thelypteris* (1) *Pityogramma* (1)	
	Houghia Janzen22		2(1)	2		Polypodiaceae, *Polypodium, Serpocaulon*
	Hyphantrophaga blandaDHJ06		3(2)	3		Pteridaceae, *Adiantum* (2) Thelypteridaceae, *Thelypteris*
	Winthemia aureonigra		6(5)	6		Dennstaedtiaceae, *Hypolepis* (2) Aspleniaceae, *Alsophila* (2) Cyatheaceae, *Cyathea* Lomariopsidaceae, *Lomariopsis*
	Winthemia Janzen34	2(2)	1	3	Polypodiaceae, *Campyloneurum, Microgramma*	Polypodiaceae, *Polypodium*
Eryciini	*Lespesia* Janzen29	1		1	Blechnaceae, *Salpichlaena*	
Blondeliini	*Calolydella virginiajamesae*	2(1)		2	Thelypdteridaceae, *Thelypteris*	
	Lixophaga Janzen58		1	1		Cyatheaceae, *Cyathea*
Tachininae Tachinini	*Archytas* Janzen44	1		1		
	Jurinella Wood05		1	1	Arecaceae	
Siphonini	*Siphona* Janzen59	2(1)		2	Dryopteridaceae, *Megalastrum* Nephrolepidaceae, *Nephrolepis*	
	Siphona Janzen60	1		1	Polypodiaceae, *Niphidium*	
	Siphona Janzen62		1	1		Dryopteridaceae, *Bolbitis*
	Siphona Janzen63		2(1)	2		Selaginellaceae, *Selaginella*

families 4 (3) Arecaceae and 347 (7) Cyclanthaceae.

From the database of over 73,000 parasite records we culled 322 records of 67 species of parasitoids reared from ACG noctuoid pteridivores and their congeners (Table 3). There was little taxonomic overlap among suites of noctuid versus herminiine parasitoids, nor do we expect any. Of 46 parasitic wasps and 21 flies, herminiine caterpillars hosted 26 and 9, respectively, and noctuid caterpillars 24 and 13; but only 5 parasitoid species (3 ichneumonids, 1 braconid, and 1 tachinid) were recorded from species in both groups, and all of these require more DNA barcoding of larger samples to determine conspecificity. The disparity between suites of parasitoids attacking herminiine versus noctuid herbivores is consistent across parasitoid taxa. Nineteen of 22 species of ichneumonids, 18 of 19 braconids, all five of the remaining recorded wasps and 20 of 21 recorded flies were exclusive to either noctuids or herminiines. Although a majority of these are singleton records, several of the more frequently sampled parasitoids; including species of braconids, eulophids, ichneumonids, and tachinids, were not recorded from any Lepidoptera other than pteridivorous species treated here. Among the species recorded only from pteridivorous Noctuidae are *Enicospilus maculipennis* (Cameron) (Ichneumonidae), 24 of which were from one batch of caterpillars and were probably siblings); the braconids *Glyptapanteles* Whitfield150 (29 of which recorded from one batch of 31 *Phuphena multilinea*) and *G.* Whitfield309; *Euplectrus eowilsoni* Hansson (Eulophidae); and *Houghia crypta* (Townsend) (Tachinidae). Both *G.* Whitfield309 and *H. crypta* are recorded only from *Callopistria* and *Phuphena* species. Parasitoids specific to Herminiinae appear to include at least two more species of *Glyptapanteles* and the tachinids *Winthemia aureonigra* Thompson

Table 3. Continued.

FAMILY Subfamily Tribe	PARASITOID SPECIES	# RECORDS (# Host spp.) NOCTUIDAE	# RECORDS (# Host spp.) HERMINIINAE	TOTAL # Records	NOCTUIDAE FOODPLANT Family, Genera	HERMINIINAE FOODPLANT Family, Genera
Siphonini cont.	*Siphona* Janzen66	1		1	Tectariaceae, *Tectaria*	
	Siphona Janzen67	2(1)		2	Dennstaedtiaceae, *Pteridium*	
SARCOPHAGIDAE	sarcJanzen01 Janzen18	1		1	Pteridaceae, *Ceratopteris*	
	TOTAL	216 (11)	106 (17)	322		
	TOTAL # Parasitoid spp.	37	35	67		

and *Chrysoexorista* Janzen35. One of the *Glyptapanteles* (Whitfield118) is recorded only from an undescribed *Nicetas* species (BioLep218) feeding on *Selaginella*. At least two well-sampled species, *Charops* GauldADHJ04 and *Zelomorpha paulgoldsteini* Meierotto recorded from multiple species of both Herminiinae and Noctuidae and have not been reared from any non-pteridivorous species.

Discussion

Many species of Herminiinae caterpillars are generally thought of as ground-dwelling detritivores because they feed on leaf litter where drably colored adults also conceal themselves. Our focus here has been the documentation of pteridivory among multiple Neotropical herminiine species, and a coarse comparison of their feeding habits with similarly inclined noctuid relatives in ACG. The documentation of a substantial number of fern-feeding and all the fern-obligate Herminiinae found in this study represents a significant expansion of our understanding of fern-feeding insects. To our knowledge, the breadth of these associations is considerably broader than that documented for any group of New World noctuid pteridivores, although the data and folklore to date is based almost entirely on extratropical feeding records. It is a considerable challenge to evaluate the reliability, much less the generalizability, of literature-based foodplant records, and the rearing efforts reflected in this paper present a rare opportunity to document behavioral observations while enabling the corroboration of taxonomic identities through vouchered specimens, images and DNA barcodes.

Many pteridivorous insects appear to specialize on ferns in the broad sense (Balick et al., 1978), and this is certainly the case for many of the noctuoids examined here. As in Herminiinae, fern-feeding noctuids exhibit a range of oligophagy, with foodplant records for some species indicating considerable breadth across fern families. Excepting singleton foodplant records, rarely do we see in either group or a species recorded exclusively from a single foodplant. *Callopistria,* the most species-rich of fern-associated noctuids, accounts for a dominant number of reared pteridivorous ACG larvae, and the highly fern-polyphagous *C. floridensis* includes all of the recorded plant family diversity among pteridivorous Noctuidae at ACG, yet does not feed on angiosperms. Although inferences of subspecialization on particular ferns or fern groups are often unwarranted because of the difficulty of parsing records scattered across a wide taxonomomic array of plants, the non-uniform distributions of feeding records among ferns and fern families for ACG Herminiinae and Noctuidae suggests a range of foodplant preferences for species in both groups. And although this is to be expected from any large group of tropical caterpillars, those encountered in the ACG inventory represent the first opportunity to examine noctuoid fern foodplant records with any precision. What all of this may suggest is that while some of the chemical traits that "matter" most to numerous pteridivorous caterpillars may be distributed throughout leptosporangiate fern families, different suites of those that matter differently to noctuids versus herminiines may vary among families.

Although several of the more frequently sampled parasitoids have not been recorded from any Lepidoptera other than pteridivorous species treated here, this is not unusual for any given taxonomic group of caterpillars; in general, ACG parasitoids tend to be recorded exclusively from one or a few host species. We note the differences not

because two unrelated groups of host insects have minimally overlapping suites of parasitoids, but because this pattern persists despite the hosts' shared foodplants and ecological space.

The available foodplant records of fern-feeding among the Geometridae are more limited than among the noctuoids, but based on ACG foodplant records and observations of North American species (e.g., *Cingilia catenaria,* mentioned earlier), several geometrids recorded from ferns tend towards polyphagy within fern families. If this is the case, and fern-feeding is facultative in such species, it represents a broadening of dietary tolerance, and not an evolved exploitation of a novel resource. We refrain from opining further because the Geometridae feeding records from ACG are only now beginning to receive the taxonomic attention required to address this kind of question empirically.

Non-fern plants and substrates, primarily algae, Cyclanthaceae, Arecaceae, bryophytes, *Selaginella,* and dead leaves, are fed upon by many herminiines at ACG, including documented fern-feeders and their congeners. This assemblage may loosely parallel that of selandriine sawflies (Hymenoptera: Symphyta: Tenthredinidae: Selandriinae), in which unspecified monocots and mosses are both hosts of species related to fern-feeders (Schneider et al. 2016).

The establishment of monophyly for the major fern groups and the increasingly refined understanding of their relationships represent a critical tool for evaluating the extent to which herbivore diets are evolutionarily constrained. Although it will not be possible to address with precision the origins or evolutionary lability of such associations until the muddled state of herminiine generic taxonomy is further refined, the documentation of unusual and potentially conserved foodplant associations presents a welcome taxonomic tool.

Acknowledgments

We thank Ben Proshek for extracting specimen data, labeling specimens, and configuring plates; Charlie Eiseman for his thoughtful comments on an earlier draft of this manuscript; and Mark Metz for his especially careful editorial attention. Above all, we express our deep gratitude and admiration for the ACG team of parataxonomists (Janzen and Hallwachs 2011) and the Guanacaste Dry Forest Conservation Fund, Wedge Foundation, and Costa Rican government for supporting them to generate the fundamental observations that made this paper possible. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA; USDA is an equal opportunity provider and employer.

Literature Cited

APG IV [Angiosperm Phylogeny Group; Byng, J. W., M. W. Chase, M. J. M. Christenhuesz, *et al.*]. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnaean Society 181: 1–20.

Balick, M. J., D. G. Furth, and G. Cooper-Driver. 1978. Biochemical and evolutionary aspects of arthropod predation on ferns. Oecologia (Berlin) 35: 55–89. https://doi.org/10.1007/BF00345541.

Bomfleur, B., S. McLoughlin, and V. Vajda. 2014. Fossilized nuclei and chromosomes reveal 180 million years of genomic stasis in royal ferns. Science 343: 1376–1377. DOI: 10.1126/science.1249884.

Cooper-Driver, G. A. 1980. The role of flavonoids and related compounds in fern systematics. Bulletin of the Torrey Botanical

Club 107(2): 116–127. https://doi.org/10.2307/2484216.

Diaz, F. M. S., Janzen, D. H., Hallwachs, W., Chacon, I., Willmott, K., Ortiz-Acevedo, E., Mielke, O. H. H., and Casagrande, M. M. 2018. DNA barcodes uncover hidden taxonomic diversity behind the variable wing patterns in the Neotropical butterfly genus *Zaretis* (Lepidoptera: Nymphalidae: Charaxinae). Zoological Journal of the Linnean Society 20:1–61. https://academic.oup.com/zoolinnean/advance-article/doi/10.1093/zoolinnean/zly036/5066255?guestAccessKey=e443010e-cd38-49ee-b61b-8efb48903ea8.

Godman, F. D. and O. Salvin. 1891. Biologia Centrali-Americana; or Contributions to the Knowledge of the Fauna of Mexico and Central America. Zoology. Lepidoptera. Heterocera by H. Druce. Volume . London. Taylor and Francis. 490 pp., plates 1–64.

Godman, F. D. and O. Salvin. 1898. Biologia Centrali-Americana; or Contributions to the Knowledge of the Fauna of Mexico and Central America. Zoology. Lepidoptera. Heterocera by H. Druce. Volume 2. London. Taylor and Francis. 692pp., plates 65–101.

Goldstein, P. Z., D. H. Janzen, W. Hallwachs, B. Proshek, and T. Dapkey. 2018a. A review of *Leucosigma* Druce, 1908 (Lepidoptera, Noctuidae): A newly discovered case of fern-feeding and a description of three new species. ZooKeys 788: 87–133. https://doi.org/10.3897/zookeys.788.21222.figures105-110.

Goldstein, P. Z., D. H. Janzen, B. Proshek, T. Dapkey, and W. Hallwachs. 2018b. Review of *Lophomyra* Schaus, 1911 (Lepidoptera, Noctuidae): a new combination and redescriptions of species newly associated with ferns (Polypodiaceae), pp. 135–165. *In* Schmidt, B. C. and J. D. Lafontaine, eds. Contributions to the systematics of New World macro-moths VII. ZooKeys 788. 252 pp. https://doi.org/10.3897/zookeys.788.21235.

Goldstein, P. Z., D. H. Janzen, and W. Hallwachs. 2019. *Aprica*: A new genus and life history for the pteridivore *Xanthia patula* Druce, 1898 (Lepidoptera: Noctuidae). ZooKeys 866: 127–145.

Goldstein, P. Z. and A. Zilli. 2019. *Thraumata,* a new genus from South America with description of a new species from Peru (Lepidoptera: Noctuidae). ZooKeys 867: 139–160.

Guenée, A. 1852. Histoire naturelle des insectes; spécies général des lépidoptères. Roret, Paris. Vol. 5: Noctuéites 1: i-xcvi; 1–407.

Hendrix, S. D. 1980. An evolutionary and ecological perspective of the insect fauna of ferns. American Naturalist 115: 171–196. https://doi.org/10.1086/283554.

Hübner, J. [1818]. Sammlung exostisher Schmetterlinge. Volume 1. Augsburg. 213 plates, 36 pp.

Hübner, J. [1821]. Verzeichniss bekannter Schmettlinge. der Verfasser, Augsburg. 432pp.

Janzen, D. H. and W. Hallwachs. 2011. Joining inventory by parataxonomists with DNA barcoding of a large complex tropical conserved wildland in northwestern Costa Rica. PLoS ONE 6 (8): e18123. https://doi.org/10.1371/journal.pone.0018123.

Janzen, D. H. and W. Hallwachs. 2016. DNA barcoding the Lepidoptera inventory of a large complex tropical conserved wildland, Area de Conservacion Guanacaste, northwestern Costa Rica. Genome 59: 641–660. https://doi.org/10.1139/gen-2016-0005.

McCabe, T. L., W. D. Patterson, and J. Debenedictis. 2002. Pseudobryomima fallax (Hampson) and P. muscosa (Hampson) (Lepidoptera: Noctuidae) leaf-mining noctuids on ferns. Proceedings of the Entomological Society of Washington 104 (1–2): 505–509.

Metz, M. A., Hallwachs, W. and Janzen, D. H. 2020. Four new gelechioid species to honor Costa Rica's conservation of wild biodiversity (Lepidoptera). Zootaxa 4810(1): 045–064. https//doi.org/10.11646/zootaxa.4810.1.2.

PPG I [Pteridphyte Phylogeny Group; Schuettpelz, E., H. Schneider *et al.*]. 2016. A community-derived classification for extant lycophytes and ferns. Journal of Systematics and Evolution 54(6): 53–603.

Ratnasingham, S., P. D. N. Hebert. 2013. A DNA-based registry for all animal species: the Barcode Index Number (BIN) system. PLoS ONE 8(8): e66213. DOI:10.1371/journal.pone.0066213.

Schaus, W. 1911a. New species of Heterocera from Costa Rica. –IV. Annals and Magazine of Natural History, series 8, 7: 33–84.

Schaus, W. 1911b. New species of Heterocera from Costa Rica. –IX. Annals and Magazine of Natural History, series 8, 8: 90–117.

Schaus, W. 1913. New species of Heterocera from Costa Rica. –XIX. Annals and Magazine of Natural History, series 8, 11: 1–44.

Schaus, W. 1916. A generic revision of the American moths of the subfamily Hypeninae, with descriptions of new genera and species. Proceedings of the United States National Museum, 50: 259–399.

Schneider, H. 2016. The ghost of Cretaceous terrestrial revolution in the evolution of fern-sawfly associations. Journal of Sytematics and Evolution 54 (2): 93–103.

Walker, F. 1858. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. Volume 15. London. Edward Newman. pp. 1521–1888.