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ECOLOGICAL STUDIES OF HYPOGEOUS FUNGI. I. COLEOPTERA ASSOCIATED WITH SPOROCARPS

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SUMMARY

Eight species of beetles are reported from ten previously unreported hypogeous fungus substrates. The associations include: *Catopocerus capizzii* with *Hymenogaster parksii* and *Zelleromyces gilkeyae; C. cryptophagoides* with *Elaphomyces granulatus* var. *granulatus; C. ovatus* with *Hysterangium* sp.; *C. rothi* with *Hymenogaster parksii, Barssia oregonensis, Hysterangium* sp., *Martellia ellipsospora, Rhizopogon parksii, Truncocolumella citrina* var. *citrina,* and *Z. gilkeyae; C. subterraneus* with *M. vesiculosa; Nossidium* sp. with *Hymenogaster parksii; Thalycra concolor* with *Gautieria* sp.; *Hydnobius* sp. (*matthewsi* ?) with *Gautieria* sp. and *Geopora cooperi* f. *gilkeyae;* and *Agonum* sp. probably a predator of *Hydnobius* sp. (*matthewsi* ?) in *Gautieria* sp.

Familiar animals such as squirrels, deer, and pigs are commonly recognized as consumers of mushrooms and hypogeous fungi (truffles and false-truffles). The great diversity of molluscs and arthropods that eat fungi are less well appreciated, although the literature on insect mycophagy is quite extensive (4, 5).

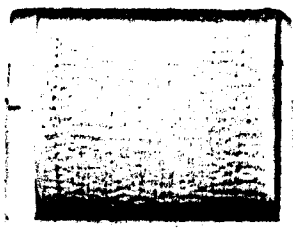
The most frequently reported insect mycophagists are Diptera, mainly Mycetophilidae or Phoridae, or Coleoptera, separable into bark beetles and other beetles. Agaricaceae and Polyporaceae encompass a large portion of the commonly reported substrates. Most of the literature contains lists of insects extracted or reared from fungal sporocarps. Such lists probably conceal complete food chains since little or no experimental verification of food habits has been done. Consequently, data on food consumption rates, chemical composition, species numbers, population dynamics, etc., have seldom been reported.

Mycophagy is presumably a major means of spore dispersal for hypogeous fungi. Most of these fungi do not forcibly discharge spores: their

TABLE I

REPORTED TRUFFICOLOUS COLEOPTERA

Insect	Insect family	Fungus	Fungus family	Reference
1. *Agaricophagus cephalotes* Schm.	Leiodidae	truffles	?	2
2. *Anisotoma ferruginea* (? author)	Leiodidae	truffles	?	9
3. *Bolboceras gallicus* (Muls.)	Scarabaeidae	*Hydnocystis arenaria* Tul.	Tuberaceae	3
= *Bolboceras gallicus* (Muls.)		*Rhizopogon* sp.	Hymenogastraceae	3
		Tuber requieni Tul.	Tuberaceae	3
4. *Bolboceras mobilicornus* Fab.	Scarabaeidae	hypogeous fungi	?	2
= *Odontaeus armiger* Scop.				
5. *B. darlingtoni* (Wallis)	Scarabaeidae	*Rhizopogon nigrescens* Coker & Couch	Hymenogastraceae	6
= *Odontaeus darlingtoni*		*R. pachyphloes* Zeller & Dodge	Hymenogastraceae	12
6. *Colenis bonnairei* Duv.	Leiodidae	truffles	?	2
= *C. immuda* Sturm.	Leiodidae	*Tuber brumale* Vitt.	Tuberaceae	2
7. *C. dentipes* Gyll.	Leiodidae	truffles	?	8
8. *Cryptophagus lycoperdi* Hbst.	Cryptophagidae	*Choiromyces maendriformis* Vitt.	Tuberaceae	2
9. *Homalota dilaticornis* Kr.	Staphylinidae	truffles	?	8
10. *Leiodes cinnamomea* Pz.	Leiodidae	truffles	?	8
= *Anisotoma cinnamomea*		*Tuber aestivum* Vitt.	Tuberaceae	2
		T. brumale	Tuberaceae	2
		T. melanosporum Vitt.	Tuberaceae	9
11. *L. furva* Er.	Leiodidae	hypogeous fungi	?	2
12. *L. picea* Pz.	Leiodidae	*Picoa juniperi* Vitt.	Terfeziaceae	9
13. *Proteinus ovalis* Stephens	Staphylinidae	truffles	?	8
14. *Thalycra carolina* (Wickham)	Nitidulidae	*Rhizopogon nigrescens*	Hymenogastraceae	7
		R. sp.	Hymenogastraceae	7
15. *T. fervida* Ol.	Nitidulidae	*R. rubescens* (Tul.) Tul.	Hymenogastraceae	2
16. *T. parsonsi* Howden	Nitidulidae	*R.* sp.	Hymenogastraceae	7
17. *T. sinuata* Howden	Nitidulidae	*R.* sp.	Hymenogastraceae	7
18. *Triarthron maerkeli* Märk	Leiodidae	hypogeous fungi	?	2



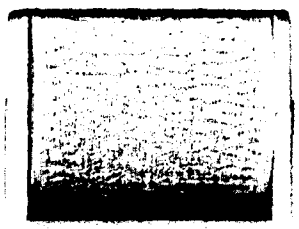


TABLE II

ADDITIONAL TRUFFICOLOUS COLEOPTERA

Insect	Insect family	Fungus	Fungus family	Location	Date (1973)
1. *Catopocerus capizzii* Hatch	Leiodidae	*Hymenogaster parksii* Zeller & Dodge	Hymenogastraceae	Benton Co., Oregon	8 March
		Hymenogaster parksii		Benton Co., Oregon	7 March**
		Hymenogaster parksii		Benton Co., Oregon	11 April
		Zelleromyces gilkeyae R. Sing. & A. H. Sm.	Russulaceae	Tillamook Co., Oregon	1 October
2. *C. cryptophagoides* Mann.	Leiodidae	*Elaphomyces granulatus* Fr. var. *granulatus*	Elaphomycetaceae	Thurston Co., Wash.	16 October
3. *C. ovatus* Hatch	Leiodidae	*Hysterangium* sp.	Hysterangiaceae	Benton Co., Oregon	10 July
4. *C. rothi* Hatch	Leiodidae	*Hymenogaster parksii*	Hymenogastraceae	Lincoln Co., Oregon	20 November*
		Hymenogaster parksii		Benton Co., Oregon	14 November
		Hymenogaster parksii		Benton Co., Oregon	7 March**
		Barssia oregonensis Gilkey	Tuberaceae	Benton Co., Oregon	10 July
		Barssia oregonensis		Benton Co., Oregon	8 April
		Hysterangium sp.	Hysterangiaceae	Benton Co., Oregon	10 July
		Martellia ellipsospora (Zeller) R. Sing. & A. H. Sm.	Russulaceae	Benton Co., Oregon	16 September
		Truncocolumella citrina Zeller var. *citrina*	Hymenogastraceae	Benton Co., Oregon	15 October
		Rhizopogon parksii A. H. Sm.	Hymenogastraceae	Benton Co., Oregon	15 October
		Zelleromyces gilkeyae	Russulaceae	Benton Co., Oregon	26 September
5. *C. subterraneus* Hatch	Leiodidae	*Martellia vesiculosa* R. Sing. & A. H. Sm.	Russulaceae	Benton Co., Oregon	11 October
6. *Nossidium* sp.	Ptiliidae	*Hymenogaster parksii*	Hymenogastraceae	Benton Co., Oregon	29 March*
7. *Thalycra concolor* Lec.	Nitidulidae	*Gautieria* sp.	Hymenogastraceae	Clear Creek Co., Colo	7 September
8. *Hydnobius* sp. (*matthewsi* ?)	Leiodidae	*Gautieria* sp.	Hymenogastraceae	Deschutes Co., Oreg.	3 October
		Geopora cooperi Harkn. f. *gilkeyae* Burdsall	Tuberaceae	Iron Co., Utah	17 August
		Gautieria sp.	Hymenogastraceae	Larimer Co., Colo.	5 September
9. *Agonum* sp. (predator of *Hydnobius* sp. (*matthewsi* ?) ?).	Carabidae	*Gautieria* sp.	Hymenogastraceae	Larimer Co., Colo.	5 September

* Collected 1972 instead of 1973. ** Collected 1974 instead of 1973.

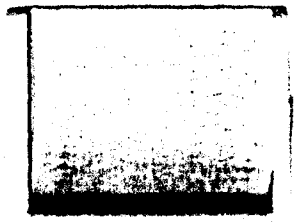


TABLE III

HOST PREFERENCE OF COLEOPTERA FOUND ASSOCIATED WITH SPOROCARPS OF HYPOGEOUS FUNGI

Fungi →	*Elaphomyces granulatus* var. *granulatus*	*Barssia oregonensis*	*Geopora cooperi* f. *gilkeyae*	*Hymenogaster parksii*	*Rhizopogon parksii*	*Truncocolumella citrina* var. *citrina*	*Gautieria* sp.	*Martellia elipsospora*	*Martellia vesiculosa*	*Zelleromyces gilkeyae*	*Hysterangium* sp.	number of fungus species	number of verified records
Beetles													
Catopocerus capizzii				4						1		2	5
C. cryptophagoides	1											1	1
C. ovatus											1	1	1
C. rothi		1		2	1	1		1		1	1	7	8
C. subterraneus									1			1	1
Thalycra concolor							1					1	1
Hydnobius (*matthewsi* ?)			1				2					2	3
Nossidium sp.				1								1	1
Agonum sp.							1					1	1
Number of beetle species	1	1	1	3	1	1	3	1	1	2	2	X	X
Number of verified records	1	1	1	7	1	1	4	1	1	2	2	X	22

sporocarps have sterile tissue completely enclosing the sporogenous tissue. If their dispersal is via mycophagy, spores of these fungi would have to be capable of germination following defecation. Leach, Orr, and Christensen (10) reported germination of *Ceratostomella ips* Rumbold ascospores isolated from the fecal pellets of *Ips pini* Say and *I. grandicollis* (Eich). Nuortera and Laine (11) have recently demonstrated that *Fomes annosus* (Fr.) Cooke diaspores can germinate following ingestion and subsequent defecation by *Hylobius abietis* L. Similar information for spores of hypogeous fungi is unavailable.

Little work has been done on the food value of hypogeous fungi other than commercial truffles. Fresh commercial truffles contain 75–79.2% water, 7.6% proteinic substances, 0.5% fats, 16.6% nitrogen-free extract, 6.4% fiber, and 1.9% ash (13). *Tuber melanosporum* Vitt., after drying, contains 24.9–25.6% protein, 1.8–2.1% fat, 38.8–45.7% carbohydrate, and 8–8.1% ash (1). The calcium (6–9.4% dry wt.) and phosphorus (as phosphoric anhydride: 18.4–30.2% dry wt.) contents are remarkably high (13).

Except for the work of Howden (6, 7) and Sim (12), essentially all of the trufficolous Coleoptera were originally reported before 1913 (2, 3, 8, 9). Laboulbène (9) provided the first comprehensive treat-

ment of trufficolous mycophagists and a refutaton of the theory that truffles are plant galls resulting from insect bites. Fabre (3) related a very interesting and entertaining account of mycophagy experiments on captive *Bolbolasmus gallicus* (Muls.).

A tentative list of trufficolous Coleoptera resulting from an extensive literature search is presented in TABLE I. Considering when many of the reports were published, absolute confidence cannot be placed in the species identifications. A similar synopsis is presented in TABLES II and III for the beetles found during the processing of hypogeous fungi by the senior author, with specific collection data presented in Appendix 1.

Voucher specimens are deposited at these institutions: *Catopocerus* and *Thalycra,* Carleton University; *Nossidium,* Field Museum of Natural History; *Hydnobius* and *Agonum,* Museum of Comparative Zoology.

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APPENDIX 1

SPECIFIC COLLECTION DATA

1. Oregon, Benton Co.: Woods Creek Road on Mary's Peak; 10 mi W of Philomath; 44° 35′ N Lat., 123° 30′ W Long.; elevation 1,500 ft (460 m); 65-yr-old *Pseudotsuga menziesii* stand:
   Catopocerus capizzii: 2 ♂, 6 ♀, from *Hymenogaster parksii;* 8 March 1973; R. Fogel 19 E; det. S. B. Peck.—1 ♂, 2 ♀, from *H. parksii;* 11 April 1973; R. Fogel 21 E; det. S. B. Peck.—1 ♂, from *H. parksii;* 7 March 1974; R. Fogel 124 E (part); det. S. B. Peck.
   C. rothi: 2 ♂, 3 ♀, from *H. parksii;* 14 Nov. 1973; R. Fogel 102 E; det. S. B. Peck.—1 ♂, from *H. parksii;* 7 March 1974; R. Fogel 124 E (part); det. S. B. Peck.— 2 ♀, from *Hysterangium* sp.; 10 July 1973; R. Fogel 106 E (part); det. S. B. Peck.— 1 ♂, 6 ♀, from *Martellia ellipsospora;* 16 Sept. 1973; R. Fogel 107 E; det. S. B. Peck.—1 ♂, from *Truncocolumella citrina* var. *citrina;* 15 Oct. 1973; R. Fogel 109 E; det. S. B. Peck.—3 ♂, 2 ♀, from *Rhizopogon parksii;* 15 Oct. 1973; R. Fogel 110 E; det. S. B. Peck.—36 individuals, 1 larva ?; from *Zelleromyces gilkeyae;* 26 Sept. 1973; R. Fogel 111 E; det. S. B. Peck.—1 ♂, 1 ♀, from *Barssia oregonensis;* 10 July 1973; R. Fogel 104 E; det. S. B. Peck.
   C. ovatus: 1 ♂, from *Hysterangium* sp.; 10 July 1973; R. Fogel 106 E (part); det. S. B. Peck.

2. Oregon, Benton Co.: Marys Peak, 12 mi W of Philomath; 44° 30′ N Lat., 123° 30′ W Long.; *Abies procera-Pseudotsuga menziesii* stand; elevation ca. 4,000 ft (1,220 m):
   Catopocerus subterraneus: 15 individuals, from *Martellia vesiculosa;* 11 Oct. 1973; R. Fogel 113 E; det. S. B. Peck.
3. Oregon, Lincoln Co.: Cascade Head Experimental Forest; 45° 07′ N Lat., 123° 56′ W Long.; *Pseudotsuga menziesii-Tsuga heterophylla* stand:
   Catopocerus capizzi: 1 ♂, from *Hymenogaster parksii;* 20 Nov. 1972; collected J. M. Trappe communicated to R. Fogel 18 E; det. S. B. Peck.
4. Oregon, Tillamook Co.: 1 mi N of Woods; 45° 15′ N Lat., 123° 57′ W Long.; *Picea engelmannii-Alnus rubra* stand on sand; elevation ca. 200 ft (61 m):
   Catopocerus capizzii: 4 ♂, 3 ♀, from *Zelleromyces gilkeyae;* 1 Oct. 1973; R. Fogel 112 E; det. S. B. Peck.
5. Colorado, Clear Creek Co.: Mt. Goliath Natural Area; 39° 38′ 37″ N Lat., 105° 35′ 34″ W Long.; *Pinus aristata-Picea engelmannii* Krummholz; elevation 11,520 ft (3,510 m):
   Thalycra concolor: 2 individuals, from *Gautieria* sp.; 7 Sept. 1973; R. Fogel 120 E; det. H. F. Howden.
6. Oregon, Benton Co.: Forest Peak, 3.25 mi E of Airlie; 44° 42′ N Lat., 123° 18′ W Long.; *Pseudotsuga menziesii* stand; elevation 500 ft (ca. 152 m):
   Nossidium sp.: 1 individual, from *Hymenogaster parksii;* 29 March 1972; R. Fogel 100 E; det. H. Dybas.
7. Colorado, Larimer Co.: Sawmill Creek, near Cameron Pass; 40° 35′ N Lat.; 105° 51′ 30″ W Long.; *Pinus contorta* stand; elevation ca. 9,700 ft (2,960 m):
   Agonom sp.: 1 individual, from *Gautieria* sp.; 5 Sept. 1973; R. Fogel 119 E (part); J. F. Lawrence (pers. comm.) felt it to be a predator.
   Hydnobius sp. (*matthewsi* ?): from *Gautieria* sp.; 5 Sept. 1973; R. Fogel 119 E (part); det. J. F. Lawrence.
8. Oregon, Deschutes Co.: West Lava Campground, vicinity McKenzie Pass; 44° 16′ N Lat., 121° 47′ W Long; *Pinus contorta-Picea engelmannii* stand; elevation 5,174 ft (ca. 1,575 m):
   Hydnobius (*matthewsi* ?): from *Gautieria* sp.; 3 Oct. 1973; R. Fogel 115 E; det. J. F. Lawrence.
9. Utah, Iron Co.: Bristlecone trail, near Cedar Breaks National Monument; 37° 35′ N Lat., 112° 50′ W Long.; *Abies lasiocarpa-Picea engelmannii* stand; elevation 9,900 ft (3,020 m):
   Hydnobius (*matthewsi* ?): from *Geopora cooperi* f. *gilkeyae;* 18 Aug. 1973; R. Fogel 117 E; det. J. F. Lawrence.
10. Washington, Thurston Co.: Meadow Creek near Mowich Lake, NW corner of Mt. Rainier National Park; ca 46° 56′ N Lat., 121° 52′ W Long., *Abies amabilis* stand; elevation ca. 4,000 ft (1,220 m):
    Catopocerus cryptophagoides: 3 ♂, 10 ♀, from *Elaphomyces granulatus* var. *granulatus;* 16 Oct. 1973; R. Fogel 121 E; det. S. B. Peck.