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# HOST FUNGI AND FEEDING HABITS OF CIIDAE (COLEOPTERA) IN A SUBTROPICAL RAINFOREST IN SOUTHERN BRAZIL, WITH AN OVERVIEW OF HOST FUNGI OF NEOTROPICAL CIIDS

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ABSTRACT

Ciids or minute tree-fungus beetles (Coleoptera: Ciidae) are amongst the most abundant and speciose fungivorous beetles. They spend most of their lives in or around polypore basidiomes, which are used as a food resource and shelter by larvae and adults. The study of Neotropical ciids is incipient and there is no comprehensive work on their host fungi. The present work provides a descriptive analysis of the Ciidae fauna, its feeding habits and polypore hosts at a subtropical rainforest in São Francisco de Paula, southern Brazil. A discussion on the current knowledge of host fungi of Neotropical Ciidae is also provided. Polypore basidiomes were collected in field trips carried out monthly from Aug 2006 to Mar 2007 and kept in the laboratory for up to 3 mo, while adult beetles were continuously captured from them. Basidiomes of 376 individual fungi were collected, comprising a total of 40 species. Among these, 152 individual fungi of 33 species had ciid beetles. Twenty-one species of ciids were recognized among 233 emergent adults. Only 1 ciid species was considered monophagous, 6 were considered oligophagous, and 6 polyphagous. Eight ciid species had less than 5 occurrences, and thus could not be included in any category. There is empirical evidence, from data provided or compiled herein, indicating that some morphologically similar Ciidae species, usually comprising a species group, frequently use the same or closely related species of fungi as the host. This is the first faunistic study on Ciidae and their host fungi in the Neotropical region.

Key Words: fungivory, mycetobionts, Tenebrionoidea, polypores, Basidiomycota

RESUMEN

Los ciidos, conocidos como escarabajos diminutos de hongos de árboles (Coleoptera: Ciidae), se encuentran entre los escarabajos fungívoros más abundantes y con un gran número de especies. Pasan la mayor parte de su vida en o alrededor de un basidioma de clase poliporo, que es utilizado como fuente de alimento y refugio por larvas y adultos. El estudio de los ciidos neotropicales es incipiente y no hay un trabajo exhaustivo sobre los hongos hospederos. El presente trabajo presenta un análisis descriptivo de la fauna de Ciidae, sus hábitos alimenticios y los hospederos poliporos en una selva subtropical en São Francisco de Paula, en el sur de Brasil. También, se provee una discusión sobre el conocimiento actual sobre los hongos hospederos de las especies de los Ciidae neotropicales. Los basidiomas poliporos fueron recolectados mensualmente en salidas de campo realizadas desde agosto del 2006 hasta marzo del 2007 y mantenidos en el laboratorio durante un máximo de tres meses, mientras que los escarabajos adultos fueron capturados de forma continua. Se recolectaron basidiomas de 376 hongos individuales, comprendiendo un total de 40 especies. Entre estos, habían escarabajos presentes en 152 de los hongos individuales que representan 33 especies de hongos. Veintiún especies de ciidos fueron reconocidas, con 233 datos de ocurrencia. Sólo una especie de ciido se con-

sideró monófaga, seis se consideraron oligófagas y seis polífagas. Hubo menos de cinco apariciones en ocho de las especies de ciidos y por lo tanto no fue posible incluirlas en ninguna categoría. Hay evidencia empírica, a partir de los datos obtenidos o compilados, indicando que algunas espécies de Ciidae que son morfológicamente similares y que usualmente son del mismo grupo de especies, con frecuencia usan la misma especie de hongo o especies de hongos estrechamente relacionados como hospedero. Este es el primer estudio faunístico de Ciidae y sus hongos hospederos en la región Neotropical.

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Insects, particularly dipterans and coleopterans, are the animals that most frequently utilize resources from fungi (Hanski 1989; Komonen 2003; Amat-García et al. 2004). The consumption of mycelium, basidiomes, or spores of fungi is called either fungivory or mycophagy, and may be one of the oldest feeding habits of beetles (Gillott 1982; Lawrence 1989). The specialization in using 1 or few parts of fungi has led to special adaptations of the mouthparts, ovipositor, feeding habits, and life cycle of fungivorous organisms (Lawrence 1989).

Fungi are not homogeneous resources, and nutrients may be concentrated 10 times more in the basidiomes than in the substrate on which they grow (Hsu et al. 2002). Besides being rich in proteins and carbohydrates (Gooday 1995; Hsu et al. 2002), basidiomes have large amounts of biologically important elements, such as phosphorous and nitrogen (Watkinson et al. 2006), which, for example, may accelerate the development of the larvae of beetles (Martin 1979). However, basidiomes may also contain high concentrations of toxins, such as phenols, pyrones, and heterocyclic nitrogen complexes. Therefore, there is great selective pressure for beetles to develop mechanisms to avoid intoxication against these substances while using them as food or habitat (Martin 1979).

Feeding on basidiomes may be facultative or obligatory for fungivorous beetles (Robertson et al. 2004; Grimaldi & Engel 2005). Insects that depend on fungi as food and shelter in all their developmental stages are called mycetobionts (Hammond & Lawrence 1989). Among insects, minute tree-fungus beetles in the family Ciidae are included among the most abundant and speciose mycetobionts, and currently comprise around 650 described species grouped in 42 genera (Lopes-Andrade 2008b; Lawrence & Lopes-Andrade 2010). They are usually gregarious, and sometimes thousands of individuals may live inside a single basidiome (Lawrence & Britton 1991). As true mycetobionts, ciids spend most of their lives in or around a basidiome, leaving it only for dispersal. Both adults and larvae build galleries inside the basidiome, and pupation also occurs there (Lawrence 1973; Costa et al. 1988). As females usually oviposit continuously for a long period, overlapping generations are usually observed (Lawrence 1973).

In the Neotropical region (sensu Morrone 2002), the study of Ciidae is incipient. There are about 150 described species in 13 genera reported in the region, and dozens of undescribed forms known from museum and institutional collections (Lawrence & Lopes-Andrade 2008; Lopes-Andrade 2008b). The present work provides a descriptive analysis of the Ciidae and their feeding habits and their polypore hosts at a subtropical rainforest in São Francisco de Paula, southern Brazil. A compilation and brief discussion on the current knowledge of host fungi of Neotropical Ciidae is also provided. This is the first faunistic study of Ciidae and their host fungi in the Neotropical region.

## MATERIALS AND METHODS

### Study Area

This study was carried out at the National Forest of São Francisco de Paula (FLONA/SFP, 29°23'-29°27'S, 50°23'-50°27'W), located in the municipality of São Francisco de Paula, in the state of Rio Grande do Sul, southern Brazil. FLONA/SFP has remnants of subtropical rainforest (Diverio et al. 2001), which occupies 40% of its area, in addition to plantation areas of *Araucaria angustifolia* (Bertol.) Kuntze, *Pinus* spp., and *Eucalyptus* spp. (Dobrovolski et al. 2006). The whole area covers 1,606 ha and reaches a maximum altitude of 923 m (Diverio et al. 2001). The climate is temperate, without a dry season, and with a hot summer ("Cfa" in the Koeppen-Geiger climate classification, sensu Peel et al. 2007). All mo are rainy, with an average annual precipitation of 2,252 mm (Backes et al. 2005).

### Field Collection

Field trips were carried out monthly from Aug 2006 to Mar 2007. During arbitrary walks along tracks in forest areas of FLONA/SFP, polypore basidiomes, which usually develop on dead tree trunks, were collected with a knife. Sampling of the same individual fungi in subsequent field trips was avoided by following different tracks during each field trip. Young basidiomes, which usually do not have ciids, were not collected. An individual fungus was defined as the basidiome(s) occurring on a single trunk, because it is not possible to know where an individual fungus begins and ends in the field. Therefore, the number of basidiomes sampled from different individual fungi

varied. Sampling effort was quite constant, with an average of 40 individual fungi collected per field trip. After removing the basidiomes from the trunks, they were separately packed in paper towels and plastic bags to prevent escape of beetle larvae and adults.

Laboratory Work

Samples were sorted for beetles within 3 days after of field collection to avoid fungal rotting and beetle death. After the first beetle sorting, the basidiome(s) of each individual fungus was kept individually to allow newly emerged beetles to breed. Basidiomes were stored in plastic containers covered with a fine mesh cloth to keep beetles inside (Komonen 2001). Moist tissue paper was put inside the containers to prevent fungi from drying out, and the containers were partially closed (Jonsell et al. 2001; Schigle 2008).

As it was difficult to observe beetles outside the woody fungi, their containers were wrapped in aluminum foil and a glass vial was attached to each 1 to attract beetles to light (Jonsell et al. 2001). However, not all beetle species were attracted to light, so all fungi were dissected 3 mo later to observe whether or not there were live beetles inside them. Before being dissected, all fungi were submitted to humidity monitoring and extraction of adult beetles twice a week. For individual fungi hosting a large number of adult beetles, at least 50 beetles were collected to guarantee capture of all species. According to Schigle (2008), direct collecting on the fungus and rearing adult beetles from their basidiomes remain reliable and sensible methods of the field research. Due to the methodology used here, all host fungi records were treated as breeding records.

All fungi that had associated Ciidae were identified following the pertinent works on their taxonomy (Ryvarden & Johansen 1980; Gilbertson & Ryvarden 1986, 1987; Ryvarden 1991; Silveira & Guerrero 1991; Ryvarden & Iturriaga 2003; Ryvarden 2004). A key to the pileate polypores found in FLONA/SFP was provided by Silveira et al. (2008) based on the fungi collected for the present study, including all species except for *Mycobonia flava* (Sw.) Fr. (Polyporales: Boreostereaceae). Voucher specimens of the fungi were deposited at the ICN herbarium (Instituto de Biociências - UFRGS). Adult ciids were identified by comparison to named specimens and literature data (Lawrence 1967, 1971; Lopes-Andrade et al. 2002; Lopes-Andrade & Lawrence 2005; Lopes-Andrade 2008b). Voucher specimens of the adult ciids were deposited at the collection of the Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul (MCNZ, Porto Alegre, RS, Brazil), and at the Lopes-Andrade Collection housed in the Universidade Federal de Viçosa (LAPC, Viçosa, MG, Brazil).

Classification of Feeding Habits

The classification of insects as specialists and generalists is based on the number of hosts utilized by each species. However, such classification is a matter of convention, because species of a major taxonomic group may show a continuum in the number of host species (Thompson 1998; Begon et al. 2006). In the case of fungivorous insects, there are divergent opinions on how many records are necessary for a given fungus species to be considered as a host (Lawrence 1973; Orledge & Reynolds 2005). Consequently, studies on feeding habits of fungivorous insects are based on different concepts of feeding specificity, and there is no single or most correct classification (Jonsell et al. 1999; Jonsell & Nordlander 2004). Here, we considered monophagous species as strict specialists (who feed in only 1 host species). When a ciid species exclusively or preferably used 1 fungus family as its host (according to Kirk et al. 2001), it was defined as oligophagous, otherwise as polyphagous (Gess & Gess 2004; Schoonhoven et al. 2005; Blüthgen & Metzner 2007). Therefore, we called oligophagous species the specialists with at least 90% of occurrence in the same fungus family. When the percentage of occurrences in a single fungus family was less than 90%, the ciid species was considered polyphagous (generalist). Here, an occurrence refers to the collection of 1 to several specimens of a ciid species in a single individual fungus. Classification of feeding habits was applied only to ciid species with at least 5 records of occurrence.

RESULTS

Basidiomes of 376 individual fungi were collected, comprising a total of 40 species. Among these, 152 individual fungi of 33 species (see Figs. 1-8 for a few examples) had ciid beetles. The ciid host fungi belonged to 7 families, 6 in the order Polyporales and 1 in Hymenochaetales (Table 1). Basidiomes of the following 7 fungi species were devoid of Ciidae: *Abundisporus subflexibilis* (Berk. & M. A. Curtis) Parmasto, *Antrodiella liebmanii* (Fr.) Ryvarden, *Antrodiella reflexa* Ryvarden & Núñez, *Inonotus fulvomelleus* Murrill, *Junghuhnia* sp. (probably *J. minuta* I. Lindblad & Ryvarden), *Laetiporus sulphureus* (Bull.) Murrill, and *Polyporus ciliatus* Fr. These non-host species are not listed in Tables 1 and 3. The occurrence of ciids in *Mycobonia* Pat., *Amauroderma* Murrill, *Flaviporus* Murrill, and *Junghuhnia* Corda are the first records of ciids feeding on fungi of these genera.

Twenty-one species of ciids (Table 2) were recognized, with 233 occurrence data. In several cases there was more than 1 ciid species in an individual fungus. Ten ciid species were identified to species level, 9 were determined to genus level
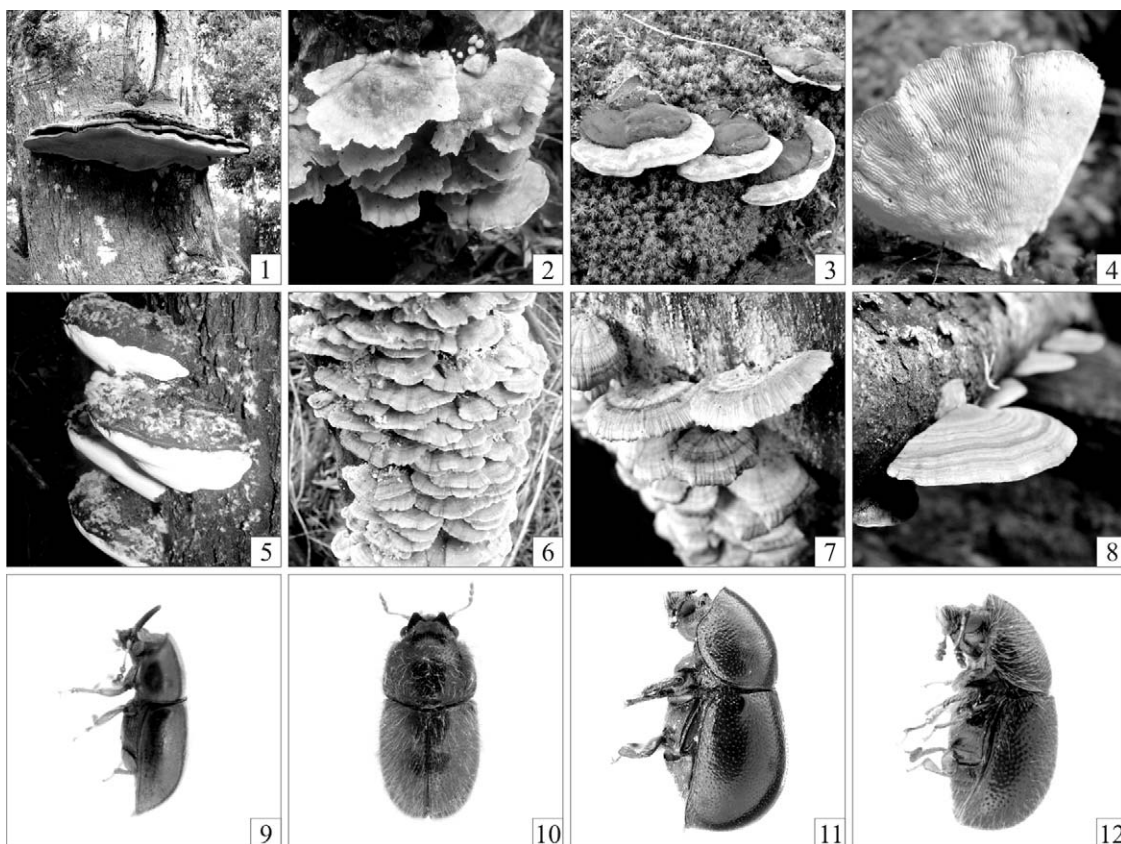
Figs. 1-12. Some host fungi (1-8) and Ciidae (9-12) collected in a subtropical rainforest in São Francisco de Paula (Rio Grande do Sul, southern Brazil): 1, *Ganoderma australe*; 2, *Rigidoporus concrescens*; 3, *Fomitella supina*; 4, *Lenzites betulina*; 5, *Perenniporia martii*; 6, *Trametes membranacea*; 7, *Trichaptum sector*; 8, *Flaviporus subhydrophilus*; 9, male of *Ceracis simplicicornis*, lateral view; 10, male of *Cis melliei*, dorsal view; 11, male of *Xylographus corpulentus*, lateral view; 12, male of *Xylographus gibbus*, lateral view.

only, and 2 species belong to 2 undescribed genera (Table 2). The following 4 ciid species (Figs. 9-12) are new country records for Brazil: *Ceracis simplicicornis* (Pic), *Cis melliei* Coquerel, *Xylographus corpulentus* Mellié, and *X. gibbus* Mellié. These 4 species were previously known only from their original descriptions. Three species-groups of *Cis* Latreille (named *fagi*, *melliei* and *vitulus* by Lawrence 1971), each with 1 species from FLONA/SFP (see Table 2), are new country records of the groups from Brazil.

The sampled ciid species had variable host ranges (Table 3). *Scolytocis fritzplaumanni* Lopes-Andrade was the only monophagous species, with all 19 occurrences in *Ganoderma australe* (Fr.) Pat. Six ciid species were considered oligophagous (Table 3). Among these oligophagous species, *Ceracis limai* Lopes-Andrade, Madureira & Zacaro and Gen.1 sp. were exclusively or mostly frequently associated with Hymenochaetaceae. The remaining oligophagous species were exclusively or mostly frequently associated

with Polyporaceae. Six ciids were considered polyphagous (Table 3). Eight ciid species had less than 5 occurrences, and thus could not be included in any category (Table 3).

Among the 8 ciid species without an attributed feeding habit, 3 showed a tendency to oligophagy: *Cis* sp.3 (*comptus* group) and *Cis diadematus* Mellié, each with 3 occurrences only in Polyporaceae species; and *Cis kawanabei* Lopes-Andrade, with 4 occurrences in *Rigidoporus* spp. (Meripilaceae). Three non-categorized ciid species showed a tendency to polyphagy: *Cis* sp. 5 (*fagi* group) with 3 occurrences, each in a fungus of a different host family; *Cis melliei* with 3 occurrences in hosts of 2 families; and *Ceracis* sp.3 with 2 occurrences, each in a host from different families. No tendency could be traced for *X. gibbus* because it was captured only once. The last non-categorized ciid species, Gen.2 sp., occurred in only 1 host fungus, *Perenniporia martii* (Berk.) Ryvarden (with 4 occurrences).

TABLE 1. HOST FUNGI OF CIIDAE COLLECTED AT A SUBTROPICAL RAINFOREST IN SÃO FRANCISCO DE PAULA (RIO GRANDE DO SUL, SOUTHERN BRAZIL).

| Order | Family | Fungus species |
|---|---|---|
| Hymenochaetales | Hymenochaetaceae | *Cyclomyces tabacinus* (Mont.) Pat. |
| | | *Inonotus* sp. |
| | | *Phellinus apiahynus* (Speg.) Rajchenb. and J.E. Wright |
| | | *Phellinus fastuosus* (Lév.) S. Ahmad |
| | | *Phellinus gilvus* (Schwein.) Pat. |
| | | *Phellinus grenadensis* (Murrill) Ryvarden |
| | | *Phellinus wahlbergii* (Fr.) D.A. Reid |
| | | *Phellinus* sp.1 |
| | | *Phellinus* sp.2 |
| | | *Phellinus* sp.3 |
| Polyporales | Boreostereaceae | *Mycobonia flava* (Sw.) Fr. |
| | Ganodermataceae | *Amauroderma coltricioides* T.W. Henkel, Aime and Ryvarden |
| | | *Ganoderma australe* (Fr.) Pat. |
| | Grammotheleaceae | *Bjerkandera adusta* (Willd.) P. Karst. |
| | Meripilaceae | *Rigidoporus concrescens* (Mont.) Rajchenb. |
| | | *Rigidoporus microporus* (Sowerby) Imazeki |
| | | *Rigidoporus ulmarius* (Sowerby) Imazeki |
| | | *Rigidoporus* sp.1 |
| | | *Rigidoporus* sp.2 |
| | Polyporaceae | *Coriolopsis rigida* (Berk. and Mont.) Murrill |
| | | *Datronia mollis* (Sommerf.) Donk |
| | | *Fomitella supina* (Sw.) Murrill |
| | | *Lenzites betulina* (L.) Fr. |
| | | *Perenniporia martii* (Berk.) Ryvarden |
| | | *Perenniporia* sp. |
| | | *Polyporus dictyopus* Mont. |
| | | *Pycnoporus sanguineus* (L.) Murrill |
| | | *Trametes cubensis* (Sw.) Kreisel |
| | | *Trametes membranacea* (Sw.) Kreisel |
| | | *Trametes villosa* (Sw.) Kreisel |
| | | *Trichaptum sector* (Ehrenb.) Kreisel |
| | Steccherinaceae | *Flaviporus subhydrophilus* (Speg.) Rajchenb. and J.E. Wright |
| | | *Junghuhnia undigera* (Berk. and M.A. Curtis) Ryvarden |

TABLE 2. SPECIES OF CIIDAE COLLECTED IN BASIDIOMES OF HYMENOCHAETALES AND POLYPORALES IN A SUBTROPICAL RAINFOREST IN SÃO FRANCISCO DE PAULA (RIO GRANDE DO SUL, SOUTHERN BRAZIL). THE SUPERSCRIPT "A" BEFORE A NAME INDICATES THAT IT IS THE FIRST RECORD OF THE SPECIES OR SPECIES-GROUP FROM BRAZIL.

| Tribe | Ciidae species | Species-group |
|---|---|---|
| Ciini | | |
| | *Ceracis bicornis* (Mellié) | *cucullatus* |
| | *Ceracis limai* Lopes-Andrade et al. | *singularis* |
| | [a]*Ceracis simplicicornis* (Pic) | *furcifer* |
| | *Ceracis* sp.1 (aff. *multipunctatus*) | |
| | *Ceracis* sp.2 (aff. *powelli*) | |
| | *Ceracis* sp.3 | *furcatus?* |
| | *Cis diadematus* Mellié | |
| | *Cis kawanabei* Lopes-Andrade | *taurus* |
| | [a]*Cis melliei* Coquerel | [a]*melliei* |
| | *Cis testaceimembris* (Pic) | *taurus* |
| | *Cis* sp.1 | *taurus* |
| | *Cis* sp.2 (aff. *fasciatus*) | [a]*vitulus* |
| | *Cis* sp.3 | *comptus* |
| | *Cis* sp.4 | *tricornis* |
| | *Cis* sp.5 | [a]*fagi* |
| | Gen.1 sp. | |
| | Gen.2 sp. | |
| | *Strigocis* sp. | |
| Orophiini | | |
| | [a]*Xylographus corpulentus* Mellié | |
| | [a]*Xylographus gibbus* Mellié | |
| Xylographellini | | |
| | *Scolytocis fritzplaumanni* Lopes-Andrade | *fritzplaumanni* |

DISCUSSION

Ciidae of FLONA/SFP

The Ciidae found at FLONA/SFP are characteristic of a Neotropical fauna, and the species, species-groups, and most genera are, for instance, quite distinct from those of the Andean region (see Lopes-Andrade 2010 for a brief discussion on the composition of the Andean Ciidae fauna). Among the new records from Brazil, *C. simplicicornis* belongs to the *furcifer* species-group, together with the common Neotropical species *Ceracis cornifer* (Mellié) and *Ceracis furcifer* Mellié. It was previously known only from the type locality in Buenos Aires, Argentina (Pic 1916). *Cis melliei* belongs to the *melliei* species-group, which comprises also *Cis crinitus* Lawrence, *Cis rotundulus* Lawrence, *Cis ursulinus* Casey, *Cis hirsutus* Casey, and *Cis hirtellus* Jacquelin-Duval, the latter 2 being possible synonyms (Lawrence 1971). All species of the *melliei* species-group are rarely collected, and few specimens are available in collections for most of them. *Xylographus corpulentus* and *X. gibbus* were formerly known only from Peru and Colombia, respectively. However, both have been collected in several localities in southeast-ern, northeastern, and northern Brazil, but the specimens from São Francisco de Paula are the first collected in southern Brazil (C.L.A., unpublished data). Each of these 2 species of *Xylographus* Mellié may indeed constitute a species-complex, rather than a single species.

*Ceracis bicornis* Mellié, *Cis testaceimembris* (Pic), and *Cis kawanabei* Lopes-Andrade are species frequently collected in Brazil (C.L.A., unpublished data). The former belongs to the *cucullatus* species-group, and the latter 2 belong to the *taurus* species-group together with *Cis* sp.1. However, all these species are widespread and polymorphic, and each may constitute a species-complex, instead of a single species.

*Cis diadematus* was previously known only from its original description, from Bahia, Brazil (Mellié 1849). In fact, it does not fit the generic limits of *Cis* and will be transferred to a new genus in a work already in preparation (C.L.A., unpublished data). *Cis* sp.3 possibly belongs to the *comptus* species-group, which comprises species of broad geographic distribution in the Neotropics (Lopes-Andrade et al. 2003; de Almeida & Lopes Andrade 2004) and several Nearctic and Palearctic species (Lawrence 1971; Królik 2002). *Cis* sp.4 belongs to the *tricornis* species-group, which is mostly Neotropical (Lawrence 1971).

TABLE 3. CIIDAE AND THEIR RESPECTIVE HOST FUNGI OF THE ORDERS HYMENOCHAETALES AND POLYPORALES IN A SUBTROPICAL RAINFOREST IN SÃO FRANCISCO DE PAULA (RIO GRANDE DO SUL, SOUTHERN BRAZIL) SHOWING THE NUMBER OF OCCURRENCES (N) FOR EACH CIID SPECIES, THE NUMBER OF INDIVIDUAL FUNGI BEARING CIIDS (N IND. FUNGI) AND THE NUMBER OF CIID SPECIES (N CIIDAE SPP.) FOR EACH FUNGUS SPECIES. CLASSIFICATION OF FEEDING HABIT WAS NOT POSSIBLE FOR THE LESS FREQUENT BEETLE SPECIES (SEE TEXT).

| | *Ceracis bicornis* | *Ceracis limai* | *Ceracis simplicicornis* | *Ceracis* sp.1 | *Ceracis* sp.2 | *Ceracis* sp.3 | *Cis diadematus* | *Cis kawanabei* | *Cis melliei* | *Cis testaceimembris* | *Cis* sp.1 | *Cis* sp.2 | *Cis* sp.3 | *Cis* sp.4 | *Cis* sp.5 | Gen. 1 sp. | Gen. 2 sp. | *Strigocis* sp. | *Xylographus corpulentus* | *Xylographus gibbus* | *Scolytocis fritzplaumanni* | N ind. fungi | N Ciidae spp. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Polyphagous | Oligophagous | Oligophagous | Polyphagous | Polyphagous | — | — | — | — | Polyphagous | Polyphagous | Oligophagous | — | Oligophagous | — | Oligophagous | — | Oligophagous | Polyphagous | — | Monophagous | | |
| **Hymenochaetales** | | | | | | | | | | | | | | | | | | | | | | | |
| *Cyc. tabacinus* | | | | | 1 | | | | 1 | | 4 | | | | | 3 | | | | | | 6 | 4 |
| *Inonotus* sp. | | | | | 1 | | | | 1 | | | | | | | | | | | | | 3 | 3 |
| *P. apiahynus* | | 4 | | | | | | | | | | | | | | | | | 2 | | | 6 | 2 |
| *P. fastuosus* | | | | | | | | | | | | | | | | | | | 1 | | | 1 | 1 |
| *P. gilvus* | | | | | | | | | | | 9 | 1 | | 1 | | 4 | | | 1 | 1 | | 12 | 5 |
| *P. grenadensis* | | 3 | | | | | | | | | | | | | | | | | 1 | | | 5 | 3 |
| *P. wahlbergii* | | 6 | | | | | | | | | | | | | | | | | | | | 6 | 1 |
| *Phellinus* sp.1 | | | | | | | | | | | | | | | | | | | 1 | | | 1 | 1 |
| *Phellinus* sp.2 | | | | | | | | | | | 1 | | | | | 1 | | | | | | 1 | 2 |
| *Phellinus* sp.3 | | 1 | | | | | | | | | 1 | | | | | | | | | | | 2 | 2 |
| **Polyporales** | | | | | | | | | | | | | | | | | | | | | | | |
| *M. flava* | | | | | | 1 | | | | | | | | | 1 | | | | | | | 2 | 2 |
| *A. coltricioides* | | | | 5 | | | | | | 14 | 1 | | | | | | | | | | | 6 | 2 |
| *G. australe* | | | | 20 | | | | | | | 2 | | | | | | | | 4 | | 19 | 59 | 5 |
| *B. adusta* | | | | | | | | | | | 1 | | | | | | | | | | | 1 | 1 |
| *R. concrescens* | | | | | | | | 1 | | | | | | | | | | | | | | 1 | 1 |
| *R. microporus* | 1 | | | | | | | 2 | | | 1 | | | | | | | | | | | 4 | 3 |

TABLE 3. (CONTINUED) CIIDAE AND THEIR RESPECTIVE HOST FUNGI OF THE ORDERS HYMENOCHAETALES AND POLYPORALES IN A SUBTROPICAL RAINFOREST IN SÃO FRANCISCO DE PAULA (RIO GRANDE DO SUL, SOUTHERN BRAZIL) SHOWING THE NUMBER OF OCCURRENCES (N) FOR EACH CIID SPECIES, THE NUMBER OF INDIVIDUAL FUNGI BEARING CIIDS (N IND. FUNGI) AND THE NUMBER OF CIID SPECIES (N CIIDAE SPP.) FOR EACH FUNGUS SPECIES. CLASSIFICATION OF FEEDING HABIT WAS NOT POSSIBLE FOR THE LESS FREQUENT BEETLE SPECIES (SEE TEXT).

| Fungus species | *Ceracis bicornis* | *Ceracis limai* | *Ceracis simplicicornis* | *Ceracis* sp.1 | *Ceracis* sp.2 | *Ceracis* sp.3 | *Cis diadematus* | *Cis kawanabei* | *Cis melliei* | *Cis testaceimembris* | *Cis* sp.1 | *Cis* sp.2 | *Cis* sp.3 | *Cis* sp.4 | *Cis* sp.5 | Gen. 1 sp. | Gen. 2 sp. | *Strigocis* sp. | *Xylographus corpulentus* | *Xylographus gibbus* | *Scolytocis fritzplaumanni* | N ind. fungi | N Ciidae spp. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Feeding habit | Polyphagous | Oligophagous | Oligophagous | Polyphagous | Polyphagous | — | — | — | — | Polyphagous | Polyphagous | Oligophagous | — | Oligophagous | — | Oligophagous | — | Oligophagous | Polyphagous | — | Monophagous | | |
| *R. ulmarius* | 2 | 1 | | 5 | 3 | | | | | | | | | | | | | | | | | 11 | 4 |
| *Rigidoporus* sp.1 | | | | | | | | | | | 1 | | | | | | | | | | | 1 | 1 |
| *Rigidoporus* sp.2 | | | | | | | | 1 | | | | | | | | | | | | | | 1 | 1 |
| *Cor. rigida* | 6 | | | | 1 | 1 | | | | | | | | | | | | | | | | 8 | 3 |
| *D. mollis* | | | | | | | | | | | 1 | | | | | | | | | | | 1 | 1 |
| *F. supina* | 4 | | | 1 | 2 | | | | | | 2 | | | | | | | 1 | | | | 10 | 5 |
| *L. betulina* | | | 1 | | | | | | | | 1 | | 1 | | | | | | | | | 3 | 3 |
| *Per. martii* | | | | | | | | | | 1 | | | 1 | | | | 4 | | | | | 2 | 3 |
| *Perenniporia* sp. | | | | | | | | | | | 2 | | | | | | | | | | | 2 | 1 |
| *Pol. dictyopus* | | | | | | | | | | | | | | | | | | 1 | | | | 1 | 1 |
| *Pyc. sanguineus* | | | 9 | | | | 1 | | | | 1 | | 1 | | | | | 3 | | | | 15 | 5 |
| *T. cubensis* | | | | | | | | | | | | | | 1 | | | | | | | | 1 | 1 |
| *T. membranacea* | 1 | | | | | | 1 | | | | 1 | 8 | 1 | 16 | | | | 3 | | | | 31 | 7 |
| *T. villosa* | | | | | | | 1 | | | | 1 | 1 | 1 | 1 | | | | 3 | | | | 8 | 6 |
| *Tri. sector* | | | | | 1 | | | | 1 | | 5 | | | | | | | | | | | 7 | 3 |
| *Fl. subhydrophilus* | | | | | | | | | | | | | | | 1 | | | | | | | 1 | 1 |
| *J. undigera* | | | | | | | | | | | | | | | | | | | | | | 2 | 2 |
| **N occurrences** | **14** | **15** | **10** | **31** | **10** | **2** | **3** | **4** | **3** | **16** | **36** | **10** | **3** | **20** | **3** | **8** | **4** | **11** | **10** | **1** | **19** | | |

*Ceracis* sp.1 is morphologically similar to *Ceracis multipunctatus* (Mellié), a northern Neotropical species that also occurs in Alabama and Florida (USA). *Ceracis* sp.2 is morphologically similar to *Ceracis powelli* Lawrence, a species from southern Arizona (USA) and northern Mexico (Lawrence 1967). *Ceracis limai* is not frequently collected, and specimens found in FLONA/SFP are the first known from southern Brazil. *Ceracis* sp.3 is a small species without secondary sexual characters in males, and of unknown morphological affinities in the Neotropical region. It somewhat resembles females of species of the *furcatus* species-group, such as *Ceracis variabilis* Mellié.

*Scolytocis fritzplaumanni* was described during the elaboration of this work, based partially on the specimens collected at FLONA/SFP (Lopes-Andrade 2008b). The species seems to be restricted to southern Brazil and is 1 of 3 species of Xylographellini found in the country (Lopes-Andrade 2008b).

The genus assignment of the *Strigocis* sp. from FLONA/SFP is a matter of discussion. The specimens have a sutural flange diverging near the elytral apex and the apex of each protibia bears a row of spines, a combination of features regarded as diagnostic for *Strigocis* Dury (Lawrence 1971; Lopes-Andrade 2011). The species named Gen.1 sp. and Gen.2 sp. belong to 2 undescribed Neotropical genera, each with a small number of species previously collected in northern and southeastern Brazil (C.L.A., unpublished data). It will certainly take several years to adequately describe the species of FLONA/SFP. The high proportion of undescribed forms, in relation to the described species, had been expected, because Neotropical species of the family have not been studied well until recently.

Host Fungi and Feeding Habits

Among the fungi recorded as ciid hosts for the first time, *Amauroderma* is a pantropical genus (Ryvarden 1991) and *Mycobonia* is distributed only in the Neotropical region (Corner 1984). *Junghuhnia* and *Flaviporus* may also be found in temperate regions (Ginns 1980; Gilbertson & Ryvarden 1986), but currently there is no available information on their use as hosts by ciids. The records of 5 ciid species in *Pycnoporus sanguineus* (L.) Murrill, a common species throughout the Neotropical region, is worth mentioning. This fungus belongs to the trametoid group and, as the other species of the genus, their basidiomes have a high concentration of cinnabarins, a group of toxic substances with antibiotic action (Smânia et al. 1998; Oliveira et al. 2007). The high toxicity of these fungi would be expected to function as a barrier for their consumption by insects, and therefore it would be expected that few beetle spe-

cies could use them as a food resource; which is supported by documented reports. So far, only species of the *Ceracis furcifer* species-group have been collected in *Pycnoporus* P. Karst. fungi (Lawrence 1973; Gumier-Costa et al. 2003). However, some insects are known to be resistant to the chemicals of their hosts (see Schoonhoven et al. 2005 for plant examples). The use of *Pyc. sanguineus* by 5 ciid species (see Table 3) suggests that insect resistance may also be possible against antibiotic constituents in fungi. Both *Ganoderma australe* (Fr.) Pat. and *Pyc. sanguineus* hosted the same number of ciid species at FLONA/SFP, although 59 occurrences of ciids were recorded from the former species, 1 of the commonest bracket fungi in the study area, and only 15 occurrences were recorded from *Pyc. sanguineus*.

Among the oligophagous species, only 2, *C. limai* and Gen.1 sp., were found mostly or exclusively in Hymenochaetaceae. The other oligophagous species were mostly associated with Polyporaceae. It is interesting to note that none of the oligophagous ciids were mostly associated with the other 5 Polyporales families, which means that fungi of these families were most frequently explored by polyphagous and monophagous species. Gen.2 sp. had all of its 4 occurrences in *Perenniporia martii* and future records may confirm that the species is monophagous.

Considering the patchy distribution of the hosts of Ciidae, the existence of strong selection against specialization, particularly monophagy, can be expected to be operating. Such a feeding habit would only be sustainable if the host were a reliably present species amenable to be used efficiently as a resource. The only monophagous species found in FLONA/SFP was *S. fritzplaumanni*, and it occurred in the most frequent and perennial fungus, *G. australe*. The specialization in closely related hosts (oligophagy), rather than in a single host species, would be the most advantageous strategy, because these hosts would be more efficiently located, and variations in population dynamics of a single fungus species would not affect the availability of resources to such ciid species. Several studies suggest that oligophagous insects tend to use closely related hosts as resources (Jonsell & Nordlander 2004; Schoonhoven et al. 2005; Bangert et al. 2006; Blüthgen & Metzner 2007). This pattern may be applied to oligophagous ciids, as in the case of *C. limai*, which occurred only in species of *Phellinus* Quél, except for 1 occurrence in *R. ulmarius*. In such cases, the oligophagous species should have the capability of detecting volatiles common to closely related host fungi, and a physiological mechanism to allow breeding in these hosts. However, the factors determining host use by ciids are not clearly elucidated (Guevara et al. 2000). It has already been suggested that host fungi have vola-

tile compounds that attract insects (Jonsson et al. 1997; Jonsell et al. 2003; Orledge & Reynolds 2005), and it has already been shown that ciid species have distinct responses to several fungal volatiles (Thakeow et al. 2008). Graf (2008) also showed that the consistency of the basidiome is important for host selection.

The available surveys or compilations on the host fungi of Ciidae are for the Nearctic and Palearctic faunas (e.g. Paviour-Smith 1960; Lawrence 1973; Reibnitz 1999). In these works, most of the ciid species were shown to be polyphagous, several were oligophagous, and a few species were truly monophagous. Lawrence (1973) suggested that the degree of host specificity would be greater in tropical forests than in temperate and subtropical regions, but he did not suggest possible explanations for this pattern. Future studies should concentrate on tropical and subtropical climate areas in order to evaluate the degree of specialization of Ciidae and its correlation to latitude and/or climate.

Host Fungi of Neotropical Ciidae

The oldest information available was provided by Mellié (1849) who cited *Pyc. sanguineus* as the host for *C. furcifer* in Izabal, Guatemala, and by Coquerel (1849) who cited *Rigidoporus lineatus* (Pers.) Ryvarden (Meripilaceae) as the host for *Cis melliei* at Fort-de-France, Martinique. Interestingly, *Cis melliei* was found in FLONA/SFP and had 3 occurrences, each from a different host fungus, 2 Hymenochaetaceae and 1 Steccherinaceae (Table 3). Future records from both locations may show that the species is polyphagous, or that there are regional differences in host-use for this species.

Lawrence (1971) listed the host fungi for Nearctic populations of several Neotropical-Nearctic *Cis* species, as follows: *Cis castlei* (Dury) mainly in *Bjerkandera adusta* (Willd.) P. Karst. and *Trichaptum biforme* (Fr.) Ryvarden; *Cis cayensis* Lawrence mainly in *Inonotus porrectus* Murrill (doubtful identification, see Lawrence 1971), *Phellinus robiniae* (Murrill) A. Ames, and *Hexagonia hydnoides* (Sw.) M. Fidalgo; *Cis creberrimus* Mellié in several hosts, which indicates polyphagous feeding habits; *Cis crinitus* Lawrence, with few records but occurring mainly in *H. hydnoides*, *Coriolopsis caperata* (Berk.) Murrill, and *Lopharia papyrina* (Mont.) Boidin; *Cis hirsutus* Casey mainly in *H. hydnoides*, *Fomes fasciatus* (Sw.) Cooke, and *Ganoderma zonatum* Murrill; *Cis subfuscus* Gorham in *Trametes hirsuta* (Wulfen) Pilát, *Panellus stipticus* (Bull.) P. Karst., *Lenzites elegans* (Spreng.) Pat., and *Pyc. sanguineus*. *Cis delicatulus* (Jacquelin-Duval), of the *tricornis* species-group, was originally found in *Trametes membranaceae* (Sw.) Kreisel (Jacquelin-Duval 1857) and has 1 record in *Trametes villosa* (Sw.) Kreisel (Navarrete-Heredia & Burgos-Solorio 2000). Interestingly, the *Cis* sp.4 from FLONA/SFP, which also belongs to the *tricornis* species-group, had 80% of its occurrences in the former fungus and 1 occurrence in the latter. Jacquelin-Duval (1857) also cited that *Cis hirtellus* Jacquelin-Duval was collected in "*boletus ungulatus*", which possibly corresponds to *Fomitopsis pinicola* (Sw.) P. Karst. *Cis fiuzai* de Almeida & Lopes-Andrade was originally found in *Pyc. sanguineus* (de Almeida & Lopes-Andrade 2004), where occasionally species of the *comptus* species-group, such as *Cis subfuscus*, are found. Notably, the only species of the *comptus* species-group found in FLONA/SFP, *Cis* sp.3, had 1 record in *Pyc. sanguineus* and the other 2 occurrences were on different species of the same fungus family. *Cis chinensis* Lawrence, an Asian species introduced in Brazil (Lopes-Andrade 2008a), was observed breeding in *Schizophyllum commune* Fr. and other unidentified fungi together with *Ennearthron victori* Lopes-Andrade & Zacaro. Finally, it is worth mentioning that although these previous host records for *Cis* species seem to be numerous, the data is scanty considering that *Cis* is the most speciose genus of the Neotropical region, with about 70 described species.

*Falsocis brasiliensis* Lopes-Andrade was collected only in *Hymenochaete luteobadia* (Fr.) Höhn. & Litsch., wrongly identified as *Phellinus* sp. by Lopes-Andrade (2007) but belonging to the same fungus family, Hymenochaetaceae. *Porculus grossus* Lawrence was most frequently found in *Rigidoporus* Murrill basidiomes (*R. concrescens* (Mont.) Rajchenb., *R. lignosus* (Klotzsch) Imazeki, and unidentified *Rigidoporus* spp.); the other 2 host records for the species, *Trametes corrugata* (Pers.) Bres. and *Ganoderma* sp., were possibly incidental (Lawrence 1987; Navarrete-Heredia & Burgos-Solorio 2000). *Porculus grossus* is a common species in the Neotropical region, and several host fungi suitable for it were collected in the present survey. However, this beetle was not found in FLONA/SFP. Few species occupied *Rigidoporus* basidiomes in FLONA/SFP, 5 of them were polyphagous (*C. bicornis*, *C. limai*, *Ceracis* sp.1, *Ceracis* sp.2, and *Cis* sp.1), whereas *Cis kawanabei* was the only beetle that occurred exclusively in *Rigidoporus*.

Species of *Phellinocis* Lopes-Andrade & Lawrence are usually found in *Phellinus* (Lopes-Andrade & Lawrence 2005). *Phellinocis erwini* Lopes-Andrade & Lawrence was collected mainly in basidiomes of *Phellinus gilvus* (Schwein.) Pat. in Panama, whereas *Phellinocis thayerae* Lopes-Andrade & Lawrence was most frequently found in *Phellinus nilgheriensis* (Mont.) G. Cunn. in the same country. However, both ciid species were also less frequently collected in unidentified *Phellinus* spp., and *Phellinocis thayerae* had 2 records in *P. gilvus* and a single record in *Phyl-*

*loporia pectinata* (Klotzsch) Ryvarden. There are no published data on the host fungi of *Phellinocis romualdoi* Lopes-Andrade & Lawrence, but the species is usually collected in basidiomes of unidentified Hymenochaetaceae in southeastern, northeastern, and northern Brazil (C.L.A., unpublished data). It is worth mentioning that no *Phellinocis* were found in FLONA/SFP, although several suitable host fungi for them were collected. The genus has 2 described species from the northern Neotropical region, and only 1 species, *Phellinocis romualdoi*, from the southern Neotropics. The southernmost record of *Phellinocis romualdoi* is from Lavras, Minas Gerais (21º14'S) (Lopes-Andrade & Lawrence 2005), about 1,000 km north of FLONA/SFP.

Data on host fungi of the New World *Ceracis* Mellié are based mainly on records for Nearctic populations of Neotropical-Nearctic species (Lawrence 1967), as follows (in part): *Ceracis curtus* (Mellié) in *Fomes fasciatus* and *H. hydnoides*; *Ceracis nigropunctatus* Lawrence mainly in *H. hydnoides* and *Trametes hirsuta*; *Ceracis pullulus* mainly in *P. gilvus*, *H. hydnoides*, and *G. zonatum*; *Ceracis punctulatus* Casey in *P. gilvus* and less frequently in several other fungi; and *Ceracis quadricornis* Gorham mainly in *Coriolopsis occidentalis* (Klotzsch) Murrill, *Trametes* spp. and *H. hydnoides*. *Ceracis similis* Horn was collected in *Ganoderma lobatum* (Schwein.) G.F. Atk. in Mexico (Navarrete-Heredia 1987). *Ceracis castaneipennis* Mellié was found in *Trichaptum sector* (Ehrenb.) Kreisel in Cuba, and the enigmatic *Ceracis taurulus* Jacquelin-Duval was taken in *Trametes membranaceae* (Jacquelin-Duval 1857). The Nearctic *Ceracis monocerus* Lawrence, a member of the *furcifer* species-group, is usually collected in *Pyc. sanguineus* (Lawrence 1967), as well as morphologically similar Neotropical species of the same species-group, such as *C. cornifer* and *C. furcifer* (Lawrence 1973; Gumier-Costa et al. 2003). *Ceracis simplicicornis* in FLONA/SFP had 90% of its occurrences in *Pyc. sanguineus*, confirming the general pattern of host-use by the species in the group. *Ceracis multipunctatus* (Mellié) was mostly found in *G. zonatum* and *Fomitella supina* (Sw.) Murrill (Lawrence 1967). A morphologically similar species from FLONA/SFP, *Ceracis* sp.1, was observed mostly in *G. australe* (64.5%). Specimens included in the type series of *C. limai* (*singularis* species-group) were collected in unidentified *Phellinus* and *Ganoderma* in southern Brazil (Lopes-Andrade et al. 2002). However, the species is most frequently collected in basidiomes of *Phellinus* spp. (C.L.A., unpublished data), in a similar pattern as found in FLONA/SFP (more than 93% of the occurrences in *Phellinus* spp.). The closely related *Ceracis singularis* (Dury), from North America, is also found in *Phellinus* spp., mainly in *P. gilvus* (Lawrence 1967). It is worth mentioning that no

other species of *Ceracis* from FLONA/SFP was found in *Phellinus*.

The Neotropical species of *Scolytocis* Blair (Xylographellini) are most frequently found in *Ganoderma* spp., *Rigidoporus* spp., and *Phellinus* spp. basidiomes (Lopes-Andrade 2008b). However, a few records provide identification of hosts to species level, as follows: *Scolytocis kiskeyensis* Lopes-Andrade in *Fomes fasciatus* (but also in an unidentified *Ganoderma*); *Scolytocis lawrencei* Lopes-Andrade in *R. lineatus*, *R. microporus* (Fr.), and *Earliella scabrosa* (Pers.) Gilb. & Ryvarden (and in *Rigidoporus* sp.); and *Scolytocis panamensis* Lopes-Andrade in *Fomes pseudosenex* (Murrill) Sacc. & Trotter (and in *Phellinus* sp.). The identified host fungus of *Scolytocis fritzplaumanni*, *G. australe*, observed in São Francisco de Paula and cited by Lopes-Andrade (2008b) corresponds exactly to the host records provided for the species in the present work. Lopes-Andrade (2008b) also cited an unidentified *Ganoderma* from Guaratuba as host for the species, which could possibly be *G. australe* in a very advanced decaying stage.

## CONCLUSION

The present work shows that most of the data previously available on host fungi of Neotropical Ciidae were scattered, provided by different authors during more than a century and a half. The data provided here on the host fungi of the Ciidae of FLONA/SFP are based on the first comprehensive survey of host fungi of a Neotropical Ciidae fauna, and a first step in elucidating the patterns of host-use and host-specialization of Neotropical Ciidae.

Furthermore, there is empirical evidence, from the present work and data compiled herein, indicating that some morphologically similar ciids, usually comprising a species-group, frequently use the same fungus species or closely related species as host. Evolutionary and ecological processes certainly determine host-use by ciids. Further studies should analyze the co-occurrence of ciid species in a host to evaluate the possibility of competitive exclusion and to explain regional patterns of host-use by ciids. Also, future work should focus on the phylogenetic analyses of ciids to make possible a comparison to phylogenetic hypotheses of their host fungi.

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