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Laboulbeniales on beetles: host utilization patterns and species richness of the parasites

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Fungi of the order Laboulbeniales are obligate ectoparasites that are easy to detect on the integument of their arthropod hosts. This apparency, and other characteristics that suit them for the role of 'model' group in the exploration of parasite biodiversity patterns, are discussed. Salient features of the general biology of these organisms are summarized and past patterns of species description reviewed. In recent years, much as in the fungi as a whole, roughly equal proportions of new species have been described from tropical and temperate regions. Comparison of the known Laboulbeniales mycobiotas of Europe, Asia and 'tropical Asia' reveals that most of the more significant parasite genera are more or less equally well represented in each region. Patterns of host utilization are also largely similar, with more than 50% of host species recorded from each region belonging to the two beetle families Carabidae and Staphylinidae. However, there are indications that parasite species that are not confined to a single host species have significantly broader geographical ranges than any of their hosts. The pattern of host utilization in the relatively fully-inventoried assemblage of beetles of a tropical forest in North Sulawesi is described, in terms of the taxonomic group membership, habitat affiliation and feeding biology of recorded hosts. On the basis of the Sulawesi dataset and other available data on host exploitation patterns at various spatial scales, we suggest that between 2 and 5%, i.e. between ca 40 000 and ca 100 000 of an estimated 2 million extant beetle species, are hosts of one or more species of Laboulbeniales. Known and predicted levels of host specificity imply that a global figure for Laboulbeniales species exploiting Coleoptera is likely to be between 10 000 and 50 000 species. A smaller number of Laboulbeniales species, probably no more than half the number associated with beetles, are to be found on other arthropod hosts. Ways in which these estimates might be refined are discussed.

Keywords: Arthropoda; biodiversity; Laboulbeniales; parasites; species richness.

Introduction

The significance of tropical data, including good inventory data for single sites, in assaying the global species richness of relatively poorly studied but hyper-diverse groups of organisms has been stressed by Hammond (1990, 1992, 1994, 1995). Recent detailed reviews of the possible magnitude of global fungal diversity (Hawksworth, 1991) have been largely based on the ratio between the number of vascular plants and their associated fungi in well-studied temperate localities. While these estimates provide a basis for further refinement only very few studies have since been directed towards elucidating the likely scale and patterns of species richness for any major group of fungi in the tropics (Bills and Polishook, 1994). These lacunae arise because of the difficulties involved in collecting and culturing large samples of most groups of fungi.

Hawksworth's (1991) estimate that around 1.5 million species of fungi occur globally was considered by the author to be conservative. This judgement was partially based on the knowledge that no special allowance had been made for the fungi associated with hyper-diverse hosts such as insects and other invertebrates. Clearly, if there are many, as yet undetected, fungi on these hosts as suggested by Madelin (1966) and others, their numbers could considerably inflate the global species total of fungi.

Investigations are currently in progress (Weir *et al.*, in preparation) aimed at elucidating the overall scale and major patterns of species richness in one group of parasitic fungi, the Laboulbeniales, that are associated exclusively with Arthropoda as hosts. At first glance these organisms might seem a strange choice for use as a focal group. Mycologists have rarely collected and recorded these fungi in a systematic way and there are very few contemporary workers in the field. On the other hand there are a number of advantages which make the Laboulbeniales ideal for such studies:

1. The Laboulbeniales are the only fungi known to exhibit any marked specificity that have been recorded from a wide range of and/or numerous arthropod hosts.
2. Although producing small fruit-bodies these are, for the most part, fairly easily seen on the integument of a given host, whether living or a long-dead individual in a museum collection.
3. There is no requirement to culture these fungi in order to assess patterns of species richness.
4. Large systematic collections of easily examined specimens of host groups are available for study in many of the major natural history museums of the world.
5. Extensive samples gathered specifically to assess the local species richness of arthropod groups that act as hosts are also available for a range of sites in both tropical and temperate regions.
6. Largely as a direct result of the monumental endeavours of one man, Roland Thaxter, there is a consistency and stability of classificatory concepts which can be equalled in very few other large groups of organisms and is almost unique among the fungi.

In this paper we present and discuss data on patterns of host utilization by Laboulbeniales, with particular reference to the well-inventoried beetle assemblage of a tropical forest in Sulawesi, Indonesia. To place these data and the discussion in context the most salient features of the biology of the Laboulbeniales are first summarized.

General biology of Laboulbeniales

The Laboulbeniales are a relatively large, monophyletic order of fungi which have been classified at one time or another in Zygomycota or Basidiomycota (one species was even originally described as a parasitic worm!) but are now rightly placed among the Ascomycota. They are unique due to their occurrence on, and exploitation of, the integument of living arthropods and the determinate development and reduced hyphal system of their minute thalli. Virtually all of the 2000 described species are considered to be obligate ectoparasites of arthropods, mainly insects. The only known exceptions are the handful of known species of the family Pyxidiophoraceae which have sexual stages which are mainly coprophilous. Amongst the Insecta, representatives of ten orders are known as hosts viz.: Blattodea (cockroaches and allies), Coleoptera (beetles), Dermaptera (earwigs), Diptera (true flies), Heteroptera (bugs), Hymenoptera, (bees and wasps) Formicidae (ants), Isoptera (termites), Mallophaga (bird lice), Orthoptera (crickets and allies) and Thysanoptera (thrips). In addition, both millipedes (Diplopoda) and mites (Arachnida, Acari) are known to carry infections. Although, at first glance, this might seem an extensive range of potential hosts the vast majority of known parasite species both globally (79%) and in well-studied temperate mycobiotas (ca 80%) have been recorded from beetles, with the contribution made by most other insect orders being very low (Table 1).

Ascospores are spindle-shaped and bicellular throughout the order and are often discharged in pairs. One of the two segments of the ascospore is smaller than the other, the whole enclosed by a gelatinous sheath which is significantly broader around the longer of the two segments. This segment forms the basal portion of the fungal thallus including the organelle of attachment known as the *foot* from which an internally penetrating haustorium develops. The time required for development from germinating ascospore to fully grown, mature, thallus varies in most of the species studied from 10 to 21 days and there is some evidence that ascospores are short-lived, persisting away from their hosts for only one or two weeks (Lindroth, 1948; De Kesel, 1995).

As a rule, transmission of the adhesive ascospores appears to be achieved during direct contact, often that involved in sexual encounters, between two host individuals. Opinions differ (e.g. Kaur and Mukerji, 1994; De Kesel, 1995) as to the likelihood and prevalence of indirect transmission, i.e. infection by spores shed onto a host's substrate, although this is known to occur in at least some instances. With particular reference to north temperate areas, Huldén (1983) identified seven factors (reworded here) favourable, or in some cases, essential to the existence of these parasites:

Table 1. Known hosts of Laboulbeniales and approximate numbers of parasite species recorded globally (column 1) and from relatively well-worked north temperate regions Poland (column 2) and the UK (column 3)

Arachnida	54	4	0
Acari	54	4	0
Diplopoda	6	1	1
Juloidea	5	1	1
Spirostrepoidea	1	0	0
Hexapoda	1790	179	128
Blattodea	25	2	0
Coleoptera	1470	150	102
Dermaptera	28	1	1
Diptera	180	17	12
Heteroptera	45	6	2
Hymenoptera	4	0	1
Isoptera	7	0	0
Mallophaga	11	3	0
Orthoptera	19	0	0
Thysanoptera	1	0	0

1. Hosts overwintering at least partially in the imaginal (adult) stage.
2. Overlapping generations of host adults.
3. Mating between members of different host generations.
4. Large and/or dense host populations.
5. Low isolation between host populations.
6. Stable host populations.
7. Warmth.

Hammond (1995) emphasized the significance of a further factor – moisture – and suggested that host cuticle characteristics and host defences may also have parts to play in determining the likelihood and patterns of infection. De Kesel (1995) surmised that host habitat choice might also exert an influence in transmission, if indirect, as he found that ascospores had a short life-span and that the efficiency of indirect transmission was probably related to soil characteristics which in turn affected the behaviour of hosts. In sum, if ascospores are always short-lived, the phenology and also the reproductive biology and defences of various arthropod species may rule them out as possible primary hosts for Laboulbeniales. However, in other respects, the 'suitability' of any given arthropod as a host is likely to involve an interplay between a range of factors, many of which remain to be clearly identified. These will include both phenological and demographic attributes of populations of the potential host, some of which are listed in crude form above. Host habitat choice and various aspects of host behaviour, including activity levels, are also likely to be involved. However, not all 'rules' with respect to host 'suitability' may be expected to apply with equal force in all situations as most relevant parasite attributes are likely to be variable.

Compared with most other groups of parasites that exploit arthropods, the level of host specificity displayed by Laboulbeniales is clearly generally high (Frank, 1982; Huldén, 1983; Hammond, 1995; Weir, 1996). A relatively small proportion of the parasite species have been reported from more than one host, but host association data are too fragmentary for many firm conclusions on specificity levels to be drawn. In the best-studied mycobiota for these fungi, that of Poland (Majewski, 1994a), the greatest proportion (85%) of the parasite species have been recorded from more than one host. However, the host range for any given parasite appears, with very few exceptions, to be restricted taxonomically, and generally encompasses only species that belong to the same genus or group of closely related genera. Also, although there are few good data which have been published, at any one site the number of parasite species reported from more than one host species is likely to be relatively low. To conclude this section, it is worth remembering that almost all of the data quoted have been obtained from rather few taxa, all of them temperate. These are not necessarily representative, especially perhaps of tropical mycobiotas.

Methods

A number of methods were employed to investigate the potential species richness of Laboulbeniales. Historical information on the rates of species description with time has been extracted from the literature, although synonymies or new combinations of names appearing subsequently have not been taken into account. The numbers of newly described species for the years 1975–1990 and the regions in which their type localities lie were obtained mainly from the *Index of Fungi*. Countries were defined as 'tropical' if 50% of their land area falls between latitudes 20°N and 20°S. All other countries were categorized as 'temperate'. Information on the Laboulbeniales mycotas of Europe and Asia was extracted from the works of Santamaria *et al.* (1991) and Lee (1986) respectively.

Information on the recorded Laboulbeniales mycotas of various regions and countries was assembled, making particular reference to the works of Huldén (1983) Majewski (1994a) Santamaria *et al.* (1991) and Weir (1996). Additional data on the composition of mycobiotas and on parasite-host associations were obtained from the database maintained by A. Weir (unpublished). Fresh sample data were obtained from a variety of sources. The most significant dataset was assembled using the collections of Coleoptera obtained from Northern Sulawesi in 1985 during the year-long Project Wallace expedition. Data concerning the beetle species recorded from Sulawesi and their habitat and 'feeding group' affiliations etc. were obtained from published papers (Hammond, 1990; Hammond *et al.*, 1997) and an unpublished database by Hammond. All of the material in the voucher collection, including representatives of the 4026 beetle species so far identified as occurring in the principal study area (a 500 ha tract of lowland rain forest) was screened for Laboulbeniales infections. Including some material from other locations in Northern Sulawesi, some 80 000 beetles in all were checked for infections.

Results

The broad patterns of species description of Laboulbeniales over time are documented in Fig. 1. which has been annotated to show major influences on the numbers of species described. The relative proportions of newly described Laboulbeniales taxa from tropical and temperate countries over a shorter time scale (1975–1990) vary greatly from year to year, but exhibit no very clear trends (Fig. 2). For the years 1981–1990 these figures are compared with the totals for fungi as a whole (also extracted from the Index of Fungi) in Table 2.

Comparisons of the known Laboulbeniales mycobiotas of Europe, Asia and a subset of the latter 'tropical Asia' are presented in Table 3. Most of the main components of diversity, even at the level of genus are similar, as are the patterns of host utilization, with the majority of host species recorded from each region belonging to the two beetle families Carabidae and Staphylinidae (Table 4).

Screening of some 80 000 specimens from the Sulawesi sample revealed some 500 infected individuals belonging to 158 species of beetles. This represents 0.6% of the individuals screened and 2.7% of the species likely to be present. Within the stricter confines of the lowland forest study area 127 species of beetles (3%) were infected with at least one species of Laboulbeniales fungi.

Within the lowland forest study area the patterns of host utilization by laboulbenialean fungi can be further dealt with in terms of the taxonomic group membership, feeding biology, forest stratum and habitat affiliation, and sampling methodology of recorded hosts.

Taxonomic group membership of hosts

The taxonomic distribution of the Sulawesi beetle species recorded as hosts of Laboulbeniales is, as expected, clumped. Several beetle families that are well represented in the study area contain *no* species found to be a host for Laboulbeniales. These include

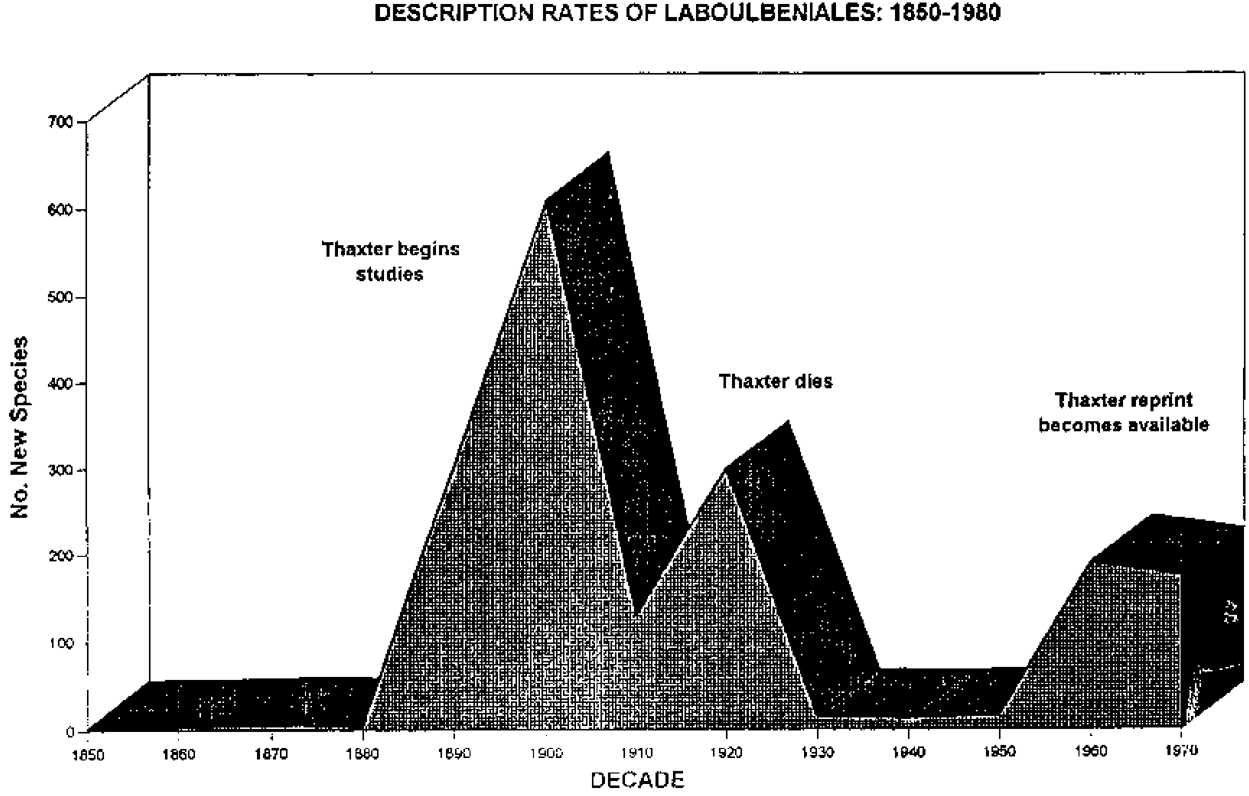

Figure 1. Broad patterns of species description of Laboulbeniales fungi over time with the major role played by Roland Thaxter on the rate of description. The first species were described in the 1850s.

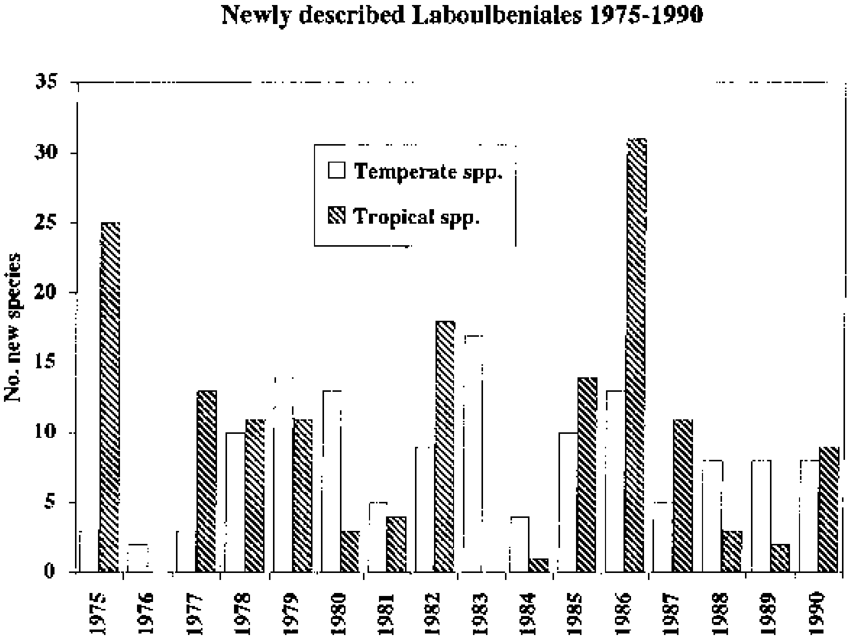

Figure 2. Numbers of newly described species of Laboulbeniales from temperate and tropical localities during the period 1975–1990.

Table 2. Numbers of new species of Laboulbeniales (A) and fungi as a whole (B) described from tropical countries and the rest of the world between 1981–1990

	A	(%)	B	(%)
Total number in tropics	93	54	7878	49
Rest of world	79	46	8135	51
World total	172	100	16013	100

Table 3. Numbers of recorded species in the more significant parasite genera from Asia (A), tropical Asia (B) and Europe (C) as a % of the total Laboulbeniales known in each region

	A	(%)	B	(%)	C	(%)
Laboulbenia	112	24	60	19	92	26
Rickia	54	12	37	12	15	4
Dimeromyces	35	8	29	9	5	1
Corethromyces	33	7	32	10	8	2
Peyritschiella	21	5	12	4	13	4
Chitonomyces	19	4	12	4	9	3
Monoicomyces	17	4	15	5	16	5
Stigmatomyces	14	3	14	4	35	10
Rhachomyces	11	2	0	0	28	8
Cantharomyces	3	< 1	0	0	11	3
Other genera	145	32	100	31	129	36

Table 4. Main beetle host families of Laboulbeniales fungi in Asia (column 1) and Europe (column 2) with the percentage of the total Laboulbeniales known which utilize them from each region

Carabidae	27	30
Staphylinidae	26	27
Hydrophilidae	3	3
Chrysomelidae	3	< 1
Tenebrionidae	3	< 1
Dytiscidae	3	3

Histeridae (89 species), Pselaphidae (91 species), Buprestidae (69), Elateridae (74), Eucnemidae (107), Lycidae (44), Mordellidae (126), Aderidae (103), Cerambycidae (160), Chrysomelidae other than Alticinae (113), Curculionidae (354) and Scolytidae (177). Considered at the level of superfamilies, no hosts for Laboulbeniales are to be found in the Elateroidea, Cantharoidea, Buprestoidea, Bostrichoidea, Dermestoidea and Lymexyloidea, and proportionally very few hosts are found in the Curculionoidea, Chrysomeloidea, Scarabaeoidea and Eucinetoidea. The most marked over-representation of hosts, proportionally speaking, is found in the Caraboidea and Dytiscoidea, followed by the Staphylinoidea, Cucujoidea and Cleroidea (Fig. 3). The families in which Laboulbeniales are best represented are the Carabidae, with 42 species (out of 169) known to be hosts of Laboulbeniales and the Staphylinidae, with 32 species (out of 579) known as hosts. Individuals of all four of the species of Gyrinidae recorded from the study area were found to be infected with Laboulbeniales. Apart from the Carabidae and Gyrinidae, the only other families in which 10% or more of the species are known to be hosts are Geotrupidae (one out of two species), Sphindidae (2 out of 14) and Languriidae (4 out of 18) (see Table 5 for further details).

Feeding groups of hosts

The feeding biology, in some measure correlated with taxonomic group membership (see above), of the subset of species recorded as hosts of Laboulbeniales also exhibits a pattern that differs markedly from that of the Sulawesi beetle dataset as a whole. Predacious beetles (63.9% of the recorded hosts but only 29% of the area's beetles overall) predominate, while species feeding on the living parts of plants (3.1%) are under-represented, and wood-feeding host species are totally lacking (See Fig. 4).

Forest stratum affiliation

The proportional representation of the beetle species from the Sulawesi study area in tree-crowns on the one hand, and the lower strata of the forest on the other, was considered by Hammond *et al.* (1997), who concluded that around 25% of the species occurred at tree-crown level on a regular basis (i.e. not just as vagrants), although less than half of these (around 10% of the species in the forest) could be considered as tree-crown specialists (i.e. not found at lower levels except as vagrants). Twenty-eight (out of 127) of the beetle species recorded as hosts of Laboulbeniales were represented in samples taken at tree-crown level, but only three of these (none of them plant-feeders) were allocated with any confidence by Hammond *et al.* (1997) to the tree-crown specialist category, and 12 of them were allocated to the category of specialists in the lower strata of the forest. Thus, only

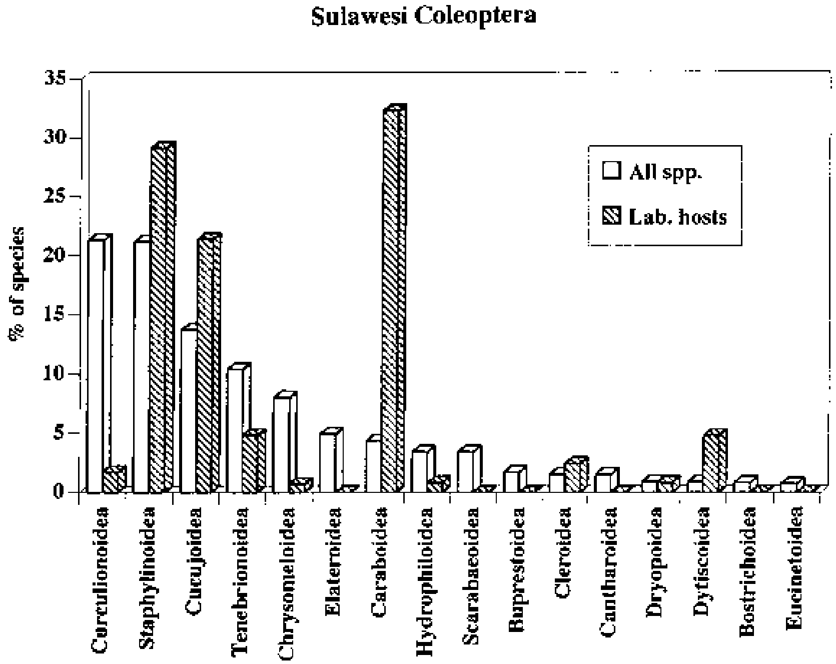

Figure 3. Proportional representation of major taxonomic groups (superfamilies) among the 4026 beetle species ['all species'] recorded from a 500-hectare area of lowland forest in Sulawesi (Hammond *et al.*, 1997) contrasted with the representation of the same groups among the 127 beetle species ['lab. hosts'] from this study area found to be hosts of Laboulbeniales (Weir, unpublished). Two additional beetle superfamilies, Dermestoidea (with 11 species) and Lymexyloidea (six species), are represented in the study area, but none of the species are recorded as hosts of the Laboulbeniales.

2.4% of the host beetle species overall are tree-crown specialists and no more than an additional 10% other tree-crown dwelling species (i.e. generalists also occurring regularly at lower levels).

Habitat affiliation

The habitat affiliation of the subset of species recorded as hosts of Laboulbeniales is also at variance with the Sulawesi beetle dataset as a whole. Species which occupy truly aquatic or riparian habitats account for a small proportion (5%) of the area's beetles overall but a much higher proportion (25%) of the infected subset of species. This is also the case for beetles associated with the fruiting bodies of larger fungi (including slime moulds) (8% and 14% respectively) and those associated with decomposing matter (including dung, carrion, decaying fruit etc.) (6 and 13%, respectively). On the other hand those beetles associated with living plants or wood habitats are under-represented in the subset of infected species (Fig. 5)

Sampling methods

A further reflection of the favoured habitats of host Coleoptera species from the Sulawesi lowland forest study area is to be found in the type of sample from which infected beetle

Table 5. Beetle 'family groups' (i.e. families or large subfamilies in the main) with species from the Sulawesi tropical forest study area (see text) found to be hosts of Laboulbeniales. Columns 1 to 4 give (1) the numbers of species of these beetle groups recorded from the study area (Hammond *et al.*, 1997), (2) the numbers of these found to be hosts of Laboulbeniales, (3) the principal habitat affiliation of each group (see Fig. 5), and (4) the principal feeding habits of each group (see also Fig. 4)

	1	2	3	4
Caraboidea				
[Carabidae]				
Paussinae	5	1	Litter	Predacious
Other Carabidae	164	41	Various	Predacious
Dytiscoidea				
Dytiscidae	28	2	Water	Predacious
Gyrinidae	4	4	Water	Predacious
Hydrophiloidea				
[Hydrophilidae]				
Sphaeridiinae	24	1	Dung*	Predacious
Staphylinoidea				
[Leiodidae]				
Leiodinae	29	3	Litter	Predacious
Scydmaenidae	46	1	Litter	Predacious
[Staphylinidae]				
Omaliinae	11	3	Various	Predacious
Oxytelinae	37	4	Dung*	Saprophagous
Megalopininae	8	1	Fungi	Predacious
Steninae	8	1	Water	Predacious
Paederinae	93	9	Various	Predacious
Staphylininae	62	6	Various	Predacious
Tachyporinae	41	4	Various	Predacious
Aleocharinae	253	2	Various	Predacious
Scaphidiidae	51	2	Fungi	Mycophagous
Scarabaeoidea				
Geotrupidae	2	1	Fungi	Mycophagous
Dryopoidea				
Limnichidae	13	1	Water	?Phytophagous
Cleroidea				
Cleridae	36	3	Wood	Predacious
Cucujoidea				
Nitidulidae	73	5	Various	Varied
Sphindidae	14	2	Fungi	Mycophagous
Laemophloeidae	28	1	Wood	Mycophagous
Silvanidae	24	1	Wood	Mycophagous
Languriidae	18	4	Various	Mycophagous
Erotylidae	32	3	Fungi	Mycophagous
Corylophidae	101	7	Various	Mycophagous
Endomychidae	46	3	Fungi	Mycophagous
Coccinellidae	66	1	Plants	Predacious

Table 5 (*Continued*)

	1	2	3	4
Tenebrionoidea				
Anthicidae	24	1	Various	?Saprophagous
Othniidae	5	1	Wood	?Mycophagous
Lagriidae	22	1	Various	Saprophagous
[Tenebrionidae]				
Leiochrini	5	2	Litter	Phytophagous
Other Tenebrionidae	84	1	Various	Varied
Chrysomeloidea				
[Chrysomelidae]				
Alticinae	52	1	Plants	Phytophagous
Curculionoidea				
Anthribidae	225	2	Wood	Varied

individuals derive. However, as the amount of sampling by various methods is not directly comparable, only limited conclusions may be drawn as to the relative success of different sampling methods in obtaining infected hosts. In the Sulawesi study area the four types of sample in which the greatest number of infected beetle species were located were flight interception traps (FIT), Malaise traps (MT), unbaited pitfull traps (PFT), and light traps (LT) (Table 6). No other sampling method obtained more than three infected beetle species that were not found infected in samples of other types.

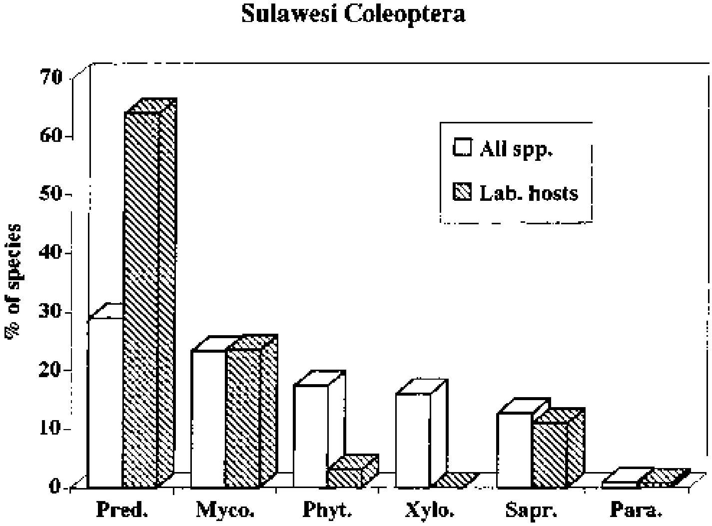

Figure 4. Proportional representation of major 'feeding groups' (or trophic guilds) among the 4026 beetle species ['all species'] recorded from a 500-hectare area of lowland forest in Sulawesi (Hammond *et al.*, 1997) contrasted with the representation of these groups among the 127 beetle species ['lab. hosts'] from this study area found to be hosts of Laboulbeniales (Weir, unpublished). **Pred.** = predacious. **Myco.** = mycophagous (including xylomycophagous and slime-mould feeding species). **Phyt.** = phytophagous. **Xylo.** = xylophagous feeding directly on living or dead wood). **Sapr.** = saprophagous. **Para.** = parasitoid.

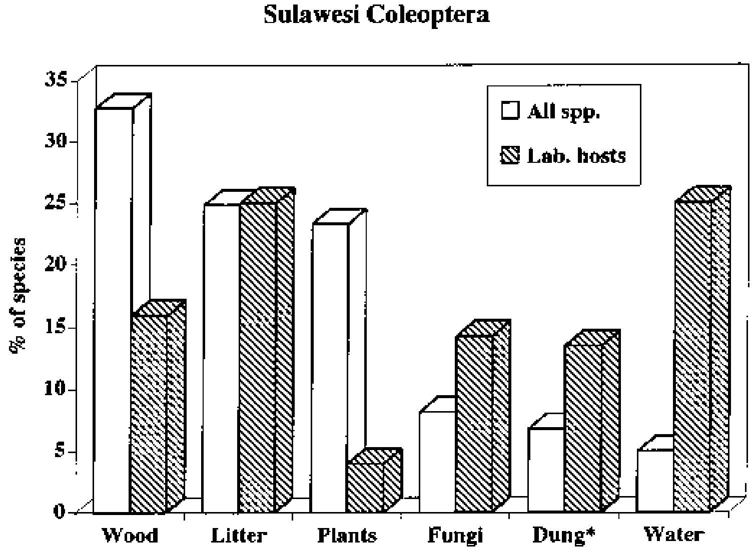

Figure 5. Proportional representation of major habitat groups among the 4026 beetle species ['all species'] recorded from a 500-hectare area of lowland forest in Sulawesi (Hammond, 1990; Hammond *et al.*, 1997) contrasted with the representation of these groups among the 127 beetle species ['lab. hosts'] from this study area found to be hosts of Laboulbeniales (Weir, unpublished). The 'dung*' habitat group includes accumulations of decaying fruit, fungi, carrion, etc., as well as dung. The 'water' group includes strictly riparian as well as aquatic species. For fuller definitions of these and other habitat groups see Hammond (1990, p. 211).

Precise totals are not available for the numbers of beetle species overall (i.e. including the several thousand species not recorded as hosts of the Laboulbeniales) taken by each of the sampling methods, or the numbers examined for Laboulbeniales for each type of sample. Nevertheless, it is clear that unbaited pitfall trap and flight interception trap catches produced the best returns of infected individuals (and species) for searching effort involved. Flight interception traps were particularly successful in trapping infected individuals of beetle species associated with litter, fungus fruiting bodies and decaying material such as dung and carrion. Pitfall traps also obtained many infected individuals of species associated with litter and decaying material. Wood and fungus associated species

Table 6. Numbers of beetle species known to be hosts of Laboulbeniales, and numbers of beetle species infected with Laboulbeniales in samples of various types from a 500-hectare area of lowland forest in Sulawesi. A = species present; B = species present only in samples of this type. 'Other' samples include those taken by fogging tree-crowns with insecticide, direct collecting from vegetation and extraction from leaf-litter, decaying wood and other substrates

Sampling method	FIT	MT	PFT	LT	Other
Known host species (A)	56	58	19	57	86
Known host species (B)	4	5	–	8	15
Infected individuals present (A)	28	16	13	12	17
Infected individuals present (B)	20	12	6	10	14

predominated among the infected individuals taken in Malaise traps, while light traps were particularly successful in obtaining infected individuals of aquatic and riparian species.

Other findings, including those in relation to British and other beetle assemblages, are dealt with in the Discussion section.

Discussion

As is the case with other 'hyperdiverse but poorly known' groups of organisms (Hammond, 1990), the pattern of species description over time in the Laboulbeniales does little more than reflect the varying taxonomic effort that has been invested (Fig. 1). As a result, the previous record is uninformative with respect to the size of the remaining descriptive task. The geographical pattern of recent description also provides little indication of how the proportion of species awaiting description might vary from region to region. Over the years 1975–1990 roughly equal numbers of Laboulbeniales were described from tropical countries on the one hand and non–tropical countries on the other (Fig. 2), although the numbers and proportions varied greatly from year to year. However, this equal split, resembling that for the fungi as a whole over a shorter time period (Table 2), is unlikely to be reflected in the actual numbers of species still undescribed in the tropics and elsewhere. None of the contemporary workers in laboulbenialean taxonomy resides in the tropics, and north temperate mycobiotas remain disproportionally the object of their attentions. Collections of host groups available for screening are also sure to be biased in favour of temperate taxa.

These same collections of arthropods are also likely to be biased in favour of larger species and those that, for one reason or another, are more apparent to, or are particular objects of interest to collectors and/or curators. Additional biases in the pattern of discovery and description of new species of Laboulbeniales may be introduced by the way in which collections are screened for parasites if, for example, host groups considered most likely to support parasites receive the most attention. Nevertheless, one feature of the record of description to date that is unlikely to be especially misleading is the broad pattern of host exploitation that it reveals. Although the true proportions of hosts of Laboulbeniales that belong to various of the major arthropod groups are likely to differ somewhat from those so far reported, new data from natural assemblages are consistent with the accepted view that most species that serve as hosts are beetles, and that a large proportion of remaining hosts are Diptera. At a finer taxonomic scale too, at least within the Coleoptera and Diptera, many currently recognized patterns, e.g. a preponderance of hosts in such groups as Carabidae and Staphylinidae, seem certain to reflect relatively faithfully the situation that actually occurs. Host lists (and knowledge of how these were assembled) for the better-known mycobiotas, as well as data drawn from representative samples of natural assemblages support this view. Of course, host species are sure to have been under–recorded (relatively speaking) to date in some groups. Various families of Diptera, some families of Coleoptera Cucujoidea, and most groups that are restricted to or are proportionally best represented in the tropics may fall into this category.

The conclusions that may be drawn from considering regional laboulbenialean species lists, incomplete as they are, are limited. However, such lists do suggest that the taxonomic composition of regional mycotas varies relatively little (see Table 3), even at the level of genus. Regional lists also reveal, given that the species-level taxonomy is reliable, that it is common for species of Laboulbeniales to have broad geographical distributions. Ranges of individual parasite species quite often encompass both tropical and cool temperate areas (Hammond, 1995; Weir and Hammond, in press), something almost unknown in species of the arthropod groups which include most of their hosts.

Data from a moist tropical site

Further insights on the pattern of host exploitation in Laboulbeniales may be derived from sample data, if these are extensive enough, on natural assemblages. The primary findings from an intensive investigation of the parasites in a tropical beetle assemblage are described above. In the main, these are consistent with the broad patterns of host exploitation already suggested by the previous record. Species serving as hosts for Laboulbeniales are highly clumped, taxonomically speaking (Fig. 3), are frequently predacious (Fig. 4), and show a preference for aquatic, riparian or otherwise 'moist' habitats (Fig. 5).

These patterns will be explained much more fully elsewhere (Weir and Hammond, unpublished data) but there is clearly an indication that habitat selection, feeding etc. are probably of great importance in determining host suitability.

Calculating true host exploitation rates from sample data

In theory there are various approaches which could be employed in attempting to calculate true host exploitation rates; however, in practice, one is more or less restricted to what can be gleaned from the best-recorded species. Taken at face value the data for Sulawesi include records for many hosts (and parasites) but do not fully represent the 'true' situation. These data are, however, sufficiently randomly gathered that they can serve as a basis for predictions of the real numbers of hosts and/or parasite species which this assemblage contains. One simple approach is to consider the proportion of species recorded as hosts and the proportion of individuals of each of these shown to be infected in the subset of species for which relatively large numbers of individuals were screened. This subset, consisting of the 100 beetle species in which 32 or more (in some instances approaching 1000) individuals were screened, contained 17 species (i.e. 17%) with which Laboulbeniales were associated. If two assumptions are made, first that the number of species found to be Laboulbeniales hosts in this subset approximates to the true number, and second that this subset is representative of the whole, a 17% exploitation rate for the beetle assemblage as a whole (i.e. ca 685 of the voucher collection species, and 1092 of the 6435 beetle species estimated to occur in the study area) would be predicted. This is very different from the rate (ca 2.7%) found by the screening. However, infection rates for the 17 host species in the subset, varying between 0.9 and 23.9% (mean 8.5%), with the modal figure being 6.1%, suggest that the second of the two assumptions made above is unreasonable. If the modal infection rate of 6.1% found in the subset of 17 species is, in fact, representative, a much smaller proportion of hosts should have been missed among the remaining species. The complex calculation required to predict the number of hosts missed at an infection rate of 6.1% with any precision has not been done, but a very simplified calculation suggests that the number of host species missed should lie in the range 120–150. Adding in the 127 species already known as hosts, this gives an overall figure of around 6% to 7% of the species screened. If this figure is, in fact, a more reasonable one, it indicates that host species are over-represented in the subset of species that are best represented in the voucher collection. If this is the case, the most obvious explanation is that this subset contains an atypically high proportion of beetle species that are in some sense common in the study area or have dense populations and, as a result are especially suitable as hosts.

The limited data available for single sites in the north temperate regions, where Laboulbeniales have been most fully investigated, suggest that beetle host exploitation patterns there resemble those of the Sulawesi beetle assemblage in most respects. However, there are some differences (Compare Figs 3, 4 and 5 with Fig. 6). The UK data (Fig. 6) used for illustration here derive from a wooded site comparable in size to the Sulawesi study area, for which a relatively complete inventory of beetle species is available (Hammond, 1996).

Do host utilization patterns in temperate and tropical areas differ?

Many features of the beetle host utilization patterns observed in the Sulawesi dataset are probably also typical of beetle assemblages the world over. Host lists for all countries and regions for which these are available indicate that adephagan (e.g. Caraboidea and Dytiscoidea) and staphylinoid beetles, predacious species and those associated with moist habitats predominate, while those belonging to several major beetle groups, most notably the Curculionoidea and species that are phytophagous or plant-associated are scarce. However, closer examination of the limited data available suggests that some differences do occur.

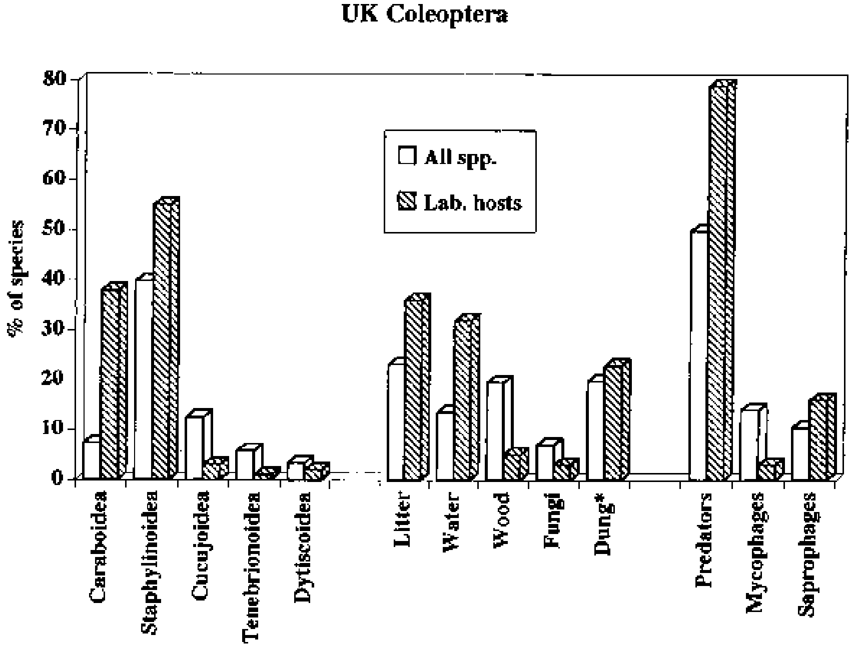

Figure 6. Proportional representation of various taxonomic, 'habitat' and 'feeding groups' among the 1058 beetle species ['all species'] recorded from Burnham Beeches National Nature Reserve, UK (Hammond, 1996) contrasted with the representation of these groups among the 100 beetle species ['lab. hosts'] recorded from the site that have been reported as hosts for Laboulbeniales in the UK (Weir, 1996).

First, there are some groups of Coleoptera (e.g. Staphylinidae Megalopininae, and Tenebrionidae Leiochrini in the Sulawesi dataset) containing species that serve as hosts in moist tropical areas that are absent from temperate regions. Also, the Sulawesi data indicate that in some beetle superfamilies a greater proportion of the species act as hosts there than is ever the case in temperate regions. The most significant of these are the Cleroidea (especially Cleridae), Cucujoidea (especially Corylophidae, Endomychidae, Languriidae and Nitidulidae), and Tenebrionidae (see Fig. 3). It is also notable that the only Curculionoidea so far known as hosts of Laboulbeniales are moist tropical forest species of Anthribidae. In addition, data from some other tropical sites suggest that chrysomeloids (principally Alticinae and Eumolpinae) are proportionally better represented as hosts there than at temperate sites.

The data presented in this paper lend support to, or are at least consistent with, the view that the greater part of laboulbenialean species richness is associated with: (1) Coleoptera as hosts; and (2) the moist tropics. Thus, a reasonably accurate idea of the number of Coleoptera species to be found in the moist tropics and the proportion of these that act as hosts for Laboulbeniales will furnish a useful basis for assessing the global species richness of these parasites. Unfortunately, data on individual sites cannot be extrapolated with any confidence to the moist tropics as a whole, as there are grounds for supposing that the proportion of species serving as hosts is scale dependent. If, as seems probable, the size of a beetle species' geographical range is positively correlated with the likelihood of its being a host of Laboulbeniales, the proportion of beetle species that serve as hosts may be expected to fall as the spatial scale under consideration increases. However, the other crucial relationship, that between the number of host species exploited and the number of parasite species occurring in any given area, is more probably subject to the reverse trend. Although nowhere well-documented, the limited data available suggest that the host species: parasite species ratio is generally relatively low at the level of a single site. In Europe, the best data are those of Majewski (1994b), who investigated the Laboulbeniales of a 154 ha sector of the Bialowieza National Park, in north-eastern Poland relatively thoroughly over a four year period (1987–1991); 50 species of Laboulbeniales on 84 species of insect hosts (78 Coleoptera and 6 Diptera) were found at this site. These data give a host: parasite ratio of 1.68:1. Similar ratios were obtained at the best-studied UK sites (Weir, unpublished). Taxonomic investigation of the parasites recorded in the Sulawesi study are still incomplete (Weir, in preparation) but the host: parasite ratio in this dataset appears to be lower, and probably between 1.1:1 and 1.3:1. At the scale of country, the best-studied Laboulbeniales mycobiotas include Finland (Huldén, 1983), Poland (Majewski, 1994a) and the UK (Weir, 1996) where the ratio consistently comes out at around 2:1 or higher. The ratio is not much higher, at around 2.2:1 at the global scale. However, many host associations are likely to remain unrecorded and, fuller data on these are, in principle, likely to push the ratio upwards. This is only so, of course, if newly established host associations (by no means always the case) involve species not previously known to be hosts. Nevertheless, a general pattern whereby 'new hosts' accumulate with an increase in geographical scale, at a faster rate than 'new parasites' is very likely.

The data considered in this paper suggest that Laboulbeniales assemblages in the moist tropics are much richer than their counterparts in temperate regions. The greater species richness of such tropical assemblages may be roughly proportional to the higher local species richness of their principal host groups, although there are some indications that parasite species richness is, in fact, proportionally somewhat higher. The principal patterns of host exploitation, in terms of host taxonomy, habitat affiliation and so on, appear to be very similar in tropical and temperate assemblages. However, some differences may prove to be significant especially if a more substantial proportion of some sizeable beetle groups, including a range of cucujoid families, and perhaps also tenebrionoids, Chrysomelidae and Anthribidae, turn out to be prone to infection in tropical settings. On the other hand, ratios of tropical to temperate species richness in some of the most favoured host groups, notably the Carabidae (and Dytiscidae), are probably low compared with the Coleoptera as a whole (Hammond, unpublished).

The high local species richness of Laboulbeniales that may be typical for moist tropical forest is unlikely to be general throughout the warmer regions of the world. As yet very few Laboulbeniales have been described from the more arid parts of the tropics and subtropics and any evidence that these support rich Laboulbeniales assemblages is lacking. In general, arid and, to a lesser extent semi-arid, areas support fewer species of 'potential' hosts, and a smaller proportion of these inhabit constantly moist environments. In addition, it is likely, where seasonality is more marked, that overlapping generations of adults, normally a pre-requisite for parasite transmission, are less frequent.

Global richness

It seems unlikely that there are vast numbers of unaccounted species of Laboulbeniales and there is certainly no evidence to suggest that each arthropod supports its own unique species of this order. In fact, there is every indication that many of the largest groups of terrestrial arthropods contain no species that serves as host to a laboulbenialean fungus.

Assuming that the moist tropics and beetles give us the main part of the answer, some speculations may be made, based on the discussion above. As with other poorly known groups, the empirical relationship between its species richness in (say) the UK and that of better-known groups (e.g. birds) may be used. However, such approaches involve many assumptions, not least that this relationship holds across spatial scales. A more productive approach may be to utilize rather than ignore patterns of host utilization and attempt to calculate potential host numbers as a stepping-stone to a figure for the parasites.

If 6% is a more or less modal figure for local beetle assemblages, but this percentage falls with increasing area to (say) 4–5% at the level of country, 3% or so at the regional level, and somewhat lower (say 3%) globally, the total number of beetle species serving as Laboulbeniales hosts, accepting a global estimate of 2 million beetle species, will be about 60 000. If the ratio of host species:parasite species is of the order 2:1 globally, this gives a global figure of 30 000 Laboulbeniales species infecting beetles and a global total for the Order overall of 40 000, if we accept that 75% of the parasites occur on beetles. Lower estimates of beetle species richness, a higher host:parasite ratio at the global level, or a higher proportion of beetle species acting as hosts at the global level will all give lower estimates. To achieve a markedly higher figure estimates of beetle species richness must be considerably inflated, or a large proportion of new parasite species must be found on proportionally fewer new hosts or on existing species of hosts (in order to decrease the host:parasite ratio), or on hosts other than beetles (reducing the proportion of beetle species acting as hosts at the global level).

From the foregoing discussion and the speculative estimates arrived at it is clear that these curious and little-studied fungi may represent a key resource capable of providing good quantitative data on patterns and levels of infection, which could provide insights into likely global species richness patterns of other groups of fungi, or other groups of parasites. In addition to more information on aspects of the general biology of these fungi, particularly from Tropical regions, critical taxonomic studies involving molecular methods to investigate those species which are considered to display extremely broad geographical and host ranges are also required. Other datasets of reasonably well inventoried beetle assemblages must also be examined and compared with the data obtained from Sulawesi. In particular, assemblages from the New World Tropics may provide contrasting data on the patterns of host utilization and species richness of the parasites.

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