

MYCOPHAGOUS PHLAEOTHRIPIDAE (THYSANOPTERA: TUBULIFERA) IN THE INDIAN SUBCONTINENT#

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ABSTRACT

Mycophagous Phlaeothripidae (Thysanoptera: Tubulifera:) are recognizable as (a) fungal-hyphae-feeding mycetophagous Phlaeothripinae, living on fungi that infest dry twigs and (b) fungal-spore-feeding sporophagous Idolothripinae, usually present on leaf litter. In the Indian subcontinent, out of 765 species of known Thysanoptera, nearly 152 species in 66 genera fall within the mycophagous group of the Phlaeothripidae with 54 idolothripine and 98 phlaeothripine species. Taxonomic diversity of these species in bamboo- and oak-leaf litter and pine forests in the sub-Himalayan ecosystems of North-Eastern India are discussed in this article, along with the diversity that is apparent in their developmental patterns, thrips-plant-fungus association, and phenotypic plasticity, supplemented with a note on their ecological implications.

Key words: Phlaeothripidae, bamboo, pine, plant fungus, association, development, ecological implications, fungal spores and mycelia, taxonomic diversity, leaf litter, phenotypic plasticity, oak leaf litter

Thrips (Thysanoptera) are relatively small insects with asymmetrical mouthparts bearing fringed wings and protractible, adhesive pre-tarsal bladders. The term thrips denotes both singular and plural forms. meaning 'woodworm' in ancient Greek, besides other commonly used terms, such as the thunderflies, storm flies, thunderblights, storm bugs, thunderbugs, corn fleas, corn flies, corn lice, freckle bugs, harvest bugs and physopods (Kirk, 1996; Marren and Mabey, 2010; Kobro, 2011). Most of them feed on plant sap (e.g., Ananthakrishnana euphorbiae (Priesner), and some of them on floral nectar and pollen (e.g., Dichromothrips nakahari Mound, Thripidae), fungal spores (e.g., Holurothrips manipurensis Varatharajan and Chochong) and mycelia (e.g., Adraneothrips okajimai (Muraleedharan and Sen)), further to a few species being predatory (e.g., Androthrips ramachandrai Karny (all Phlaeothripidae except D. nakahari) feeding on other smaller soft-bodied insects and mites. Feeding niches of the Phaleothripidae vary highly, most feed on plants, and many others feed on pollen, fungal filaments and spores, and some of them feed on other arthropods. Thysanoptera comprises two suborders, the Terebrantia and Tubulifera, of which the body length of those belonging to Terebrantia are always < 1 mm, while those of the Tubulifera can be from 1.1 to 15 mm, such as the spore-feeding taxa of the Phlaeothripidae, viz., Bactrothrips Karny, Elaphrothrips

Buffa, *Mecynothrips* Bagnall, *Meiothrips* Priesner, *Oidanothrips* Moulton, and *Tiarothrips* Priesner (Ananthakrishnan, 1973; Eow et al. 2011; Mound and Tree, 2011) with the exception of the smallest leaf-litter inhabiting *Preeriella* Hood (Phlaeothripinae) being <1 mm (Okajima, 1998). Although considerable volume of information on fungus-feeding Thysanoptera has been documented, the present article refers to the diversity and dynamics of mycophagous Phlaeothripidae of the Indian subcontinent, drawing examples from the North-Eastern Himalayan parts of India.

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A. Diversity of the mycophagous Thysanoptera

ThripsWiki (2021) lists 6312 extant taxa under 785 genera and 175 extinct taxa under 65 genera (Mound and Vesmanis, 2021), of which a little >50% utilize fungi as their source of food (Morse and Hoddle, 2006; Mound, 2005). Among the mycophagous Thysanoptera, >700 spore-feeding idolothripines are known worldwide (Eow et al., 2011). In the Neotropics, mycophagous Thysanoptera occupy 50% of the total numbers of thrips known (Mound, 2002). The Uzelothripidae, Merothripidae, and Idolothripinae are primarily fungal-spore feeders, whereas half of the world's known Phlaeothripidae are mycelial feeders. In the Indian subcontinent out of 765 known taxa (Tyagi and Kumar, 2016; Rachana and Varatharajan, 2017), 152 are mycophagous including 54 species of spore-

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feeding idolothripines and 98 species of mycetophagous phlaeothripines (Table 1, 2). On extrapolating this statistic, we can assume that close to 1400 species of mycetophagous Thysanoptera occur in the world, since c. 700 Idolothripinae are known (Mound et al., 2013). Although the Paraneoptera (Thysanoptera) has been categorized into 15 families including that of the fossil-spore feeding Uzelothripidae (Mound, 2013), members of Phaleothripidae include c. 3500 species (ThripsWiki, 2021), of which approximately 2100 belong to fungusfeeding *Phlaeothrips* lineage (Dang et al., 2014).

In oak-leaf litter

The Sub-Himalayan region stretching from Jammu and Kashmir to Manipur (24°-34°N, 93°-95°E) is the Quercus (Fagaceae)-belt of the Indian subcontinent (Negi and Naithani, 1995). Quercus-leaf litter harbours at least 14 species of mycophagous Phlaeothripidae, of which five are idolothripines and the remainder are phlaeothripines, which dominate both in density and taxonomic diversity (Chochong and Varatharajan, 2004). The species composition and mean percentage of their occurrence in Chochong and Varatharajan's (2004) study indicates the following sequence: Urothrips tarai (Stannard) - 20%, Apelaunothrips madrasensis (Ananthakrishnan) - 18%, Adraneothrips okajimai (Muraleedharan and Sen) - 12%, Apelaunothrips consimilis (Ananthakrishnan) and Mecvnothrips simplex Bagnall - 10% each, Elaphrothrips spiniceps Bagnall, Xylaplothrips debilis Ananthakrishnan and Jagadish, and Holurothrips manipurensis Varatharajan and Chochong - 5% each, Meiothrips menoni Ananthakrishnan, Bradythrips hesperus Hood and Williams, and Tylothrips indicus Sen and Muraleedharan - 3% each, Adraneothrips disjunctus Ananthakrishnan, Preeriella formosana Okajima, and Bactrothrips idolomorphus Karny - 2% each (all Phlaeothripidae). Although the above information pertains to the Quercus forests of Manipur (24°44'N, 93°58'E), *U. tarai* (Phlaeothripidae) was first collected and described by Lewis Judson Stannard of the University of Illinois-Champaign, Illinois, in 1970, from the Quercus regions of the Tarai (29°22'N, 79°27'E). But the distribution of U. tarai from 24°44'N, 93°58'E to 28°2'N, 96°E of the north-eastern region of India confirms their occurrence throughout the Quercus belt of the Sub-Himalayan region. Similarly, species such as T. indicus and H. manipurensis are known only from Manipur, but the remaining 10 mycophagous Phlaeothripidae known earlier from the biodiversity-rich Western Ghats (Ananthakrishnan, 1973) are presently known to be occurring in north-eastern India as well. Further, the

minute leaf-litter inhabiting *P. formosana* (\sim 950 μ m) is a new record for India, which was previously known only from Taiwan (23°41'N, 120°57E) (http://anic.ento.csiro.au/thrips/resources/ Taiwan.htm). The presence of these 14 species especially in the *Quercus* belt reiterates that the thrips composition in the north-eastern India is a 'mixed bag' with species known previously from the Western Ghats, some from the Sub-Himalayan region, and some from the Indo-Myanmar bioregion (Varatharajan et al., 2010).

In bamboo forests

Nearly 125 native and 11 exotic species of bamboos (Poaceae) belonging to 23 genera are known from India, of which more than 50% occur in north-eastern India (fsi.nic.in/isfr2017/isfr-bambooresource). The overall bamboo-growing area in the Indian subcontinent has been estimated at c. 9.6 m ha. Thysanoptera are key inhabitants of bamboo litter (Ananthakrishnan, 1973; Varatharajan, 2005). The litter-inhabiting Thysanoptera of the Western Ghats and north-eastern India include five species of idolothripines and 10 of phlaeothripines. The species recorded thus far include Acallurothrips amplus (Faure), Allothrips bicolor Ananthakrishnan, A. montanus Ananthakrishnan, Elaphrothrips curvipes Priesner and Nesothrips brevicollis (Bagnall) (all Idolothripinae). On the other hand, members of the Phlaeothripinae include species such as Ablemothrips maxillatus Ananthakrishnan, Adraneothrips bambusae (Ananthakrishnan), A. limpidus Ananthakrishnan, Apelaunothrips madrasensis (Ananthakrishnan), Karnyothrips melaleucus (Bagnall), Margaritothrips flavus Bhatti, M. sumatrensis Priesner, Mystrothrips dammermani (Priesner), Ocythrips rarus Ananthakrishnan, and Stephanothrips occidentalis Hood and Williams (Ananthakrishnan and Sen, 1980; Sen et al. 1988; Varatharajan, 2005).

In pine forests

A dozen mycophagous Phlaeothripidae occurs in association with the dry needle litter of *Pinus kesiya* Royle ex Gordon (Pinales: Pinaceae), of which *Apelaunothrips consimilis* (Ananthakrishnan), *Ecacanthothrips tibialis* (Ashmead), *Karnyothrips melaleucus* (Bagnall), *Hoplandrothrips corticis* Ananthakrishnan, *Hoplothrips fungosus* Moulton, *Hoplothrips orientalis* (Ananthakrishnan), *Macrophthalmothrips splendidus* Ananthakrishnan, *Streptothrips orientalis* (Ananthakrishnan) (Phlaeothripinae) are more dominant than the sporefeeding thrips such as *Ethirothrips longisetis* (Ananthakrishnan and Jagdish), *Holothrips minor*

Table 1. List of Idolothripinae recorded in India

1. Acallurothrips amplus	16. Ethirothrips anacardii	30. Elaphrothrips	43. Meiothrips
(Faure)	(Ananth.)	notabilis	menoni
2. Aesthesiothrips	17. Ethirothrips beesoni	Ananthakrishnan	Ananthakrishnan
jatrophae	(Moulton)	31. Elaphrothrips procer	44. Meiothrips
Ananthakrishnan	18. Ethirothrips brevisetosus	(Schmutz)	nepalensis
3. Allothrips bicolour	(Ananthakrishnan &	32. Elaphrothrips	Kudo &
Ananthakrishnan	Jagadish)	spiniceps Bagnall.	Ananthakrishnan
4. Allothrips indicus	19. Ethirothrips brevis	33. Gastrothrips	45. Neosmerinthothrips
Ananthakrishnan	(Bagnall)	acuticornis (Hood)	fructuum Schmutz
5. Allothrips montanus	20. Ethirothrips indicus	34. Gastrothrips falcatus	46. Neosmerinthothrips
Ananthakrishnan	(Bagnall)	(Ananthakrishnan)	inquilinus
6. Allothrips watsoni	21. Ethirothrips longisetis	35. Gastrothrips	Ananthakrishnan
Hood	(Ananthakrishnan &	turbinatus	47. Neosmerinthothrips
7. Bactrothrips	Jagadish)	(Ananthakrishnan)	robustus
idolomorphus (Karny).	22. Ethirothrips obscurus	36. Holurothrips	(Ananthakrishnan)
8. Bactrothrips luteus	(Schmutz)	manipurensis	48. Nesidiothrips alius
Ananthakrishnan	23. Ethirothrips uredinis	Varatharajan &	(Ananthakrishnan)
9. Compsothrips	(Ananthakrishnan &	Chochong	49. Nesothrips brevicollis
congoensis (Hood).	Jagadish)	37. Ischyrothrips crassus	(Bagnall)
10. Compsothrips	24. Ethirothrips	Schmutz	50. Nesothrips lativentris
ramamurthii	vitreipennis (Priesner)	38. Loyolaia indica	(Karny)
(Ananthakrishnan)	25. Ethirothrips	Ananthakrishnan	51. Ophthalmothrips
11. Diaphorothrips	tirumalaiensis	39. Machatothrips	breviceps
unguipes Karny	(Ananthakrishnan)	corticosus	(Bagnall)
12. Dinothrips juglandis	26. Elaphrothrips	Ananthakrishnan	52. Ophthalmothrips
Moulton	curvipes Priesner	40. Machatothrips indicus	faurei
13. Dinothrips	27. Elaphrothrips	Ananthakrishnan and	(Ananthakrishnan)
longicauda	denticollis (Bagnall)	Jagadish	53. Priesneriana
(Ananthakrishnan)	28. Elaphrothrips	41. Machatothrips	kabandha
14. Dinothrips spinosus	greeni (Bagnall)	silvaticus	(Ramakrishna)
(Schmutz)	29. Elaphrothrips	Ananthakrishnan	54. Tiarothrips
15. Dinothrips	insignis	42. Mecynothrips simplex	subramanii
sumatrensis Bagnall	Ananthakrishnan	Bagnall	(Ramakrishna)

(Hood), *Machatothrips indicus* Ananthakrishnan, and *Mecynothrips simplex* Bagnall (Idolothripinae). Among these, the bark-dwelling *Hoplandrothrips corticis* were apparently restricted to dry fallen bark pieces of *P. kesiya* that grow above 1500 masl, whereas the other species such as *H. fungosus* and *H. orientalis* inhabit the dry, fungus-infested needle litter. The density and diversity of Thysanoptera collected from the needle litter of *P. kesiya* was lesser than the other plantation sectors such as bamboo and oak (Table 3).

B. Thrips-plant-fungus association

Mycophagous Thysanoptera feed on fungal spores and hyphae and use dry leaves and twigs for egg laying and colony establishment. The mycophagous Phlaeothripidae mostly show a pattern in their colonization behaviour and feeding on fungal spores. For instance, the spore feeder *Tiarothrips subramanii*

(Idolothripinae) occurs closely associated with three species of Anthostomella (Ascomycota: Xylariales: Xylariaceae), that usually grows on dry fronds of Borassus flabellifer L. (Arecaceae). Similarly, Mecynothrips hardyi (Phlaeothripidae) feeds on the spores of Dothiorella thripsita Shivas and Tree (Ascomycota: Botryosphaeriales: Botryosphaeriaceae) (Shivas et al., 2009). Species of *Pestalotia* (47.44%) (Ascomycota: Xylariales: Amphisphaeriaceae) have been found in the dissected gut of B. idolomorphus indicate the preference between B. idolomorphus and the species of Pestalotia. Further, B. idolomorphus also appear to prefer spores of the Coelomycetes, Ascomycetes, and Hyphomycetes, but not those of the Basidomycetes (Ananthakrishnan and Dhileepan, 1984). Such a pattern is evident in sporo- and mycetophagous species (Table 4), based on field observations and laboratory evaluation of spores of the gut contents.

Table 2. List of fungal-hyphae feeding Phlaeothripinae in India

1.	Ablemothrips maxillatus Ananthakrishnan	52.	Hoplothrips orientalis (Ananthakrishnan)
2.	Adraneothrips bambusae (Ananthakrishnan)	53.	Hoplothrips transvaalensis (Hood)
3.	Adraneothrips disjunctus Ananthakrishnan	54.	Idiothrips bellus Faure
4.	Adraneothrips elegans Ananthakrishnan	55.	Karnyothrips melaleucus (Bagnall)*
5.	Adraneothrips infirmus (Ananthakrishnan)	56.	Karnyothrips mucidus (Ananthakrishnan &
6.	Adraneothrips limpidus (Ananthakrishnan)		Jagadish)*
7.	Adraneothrips madrasensis Ananthakrishnan	57.	Macrophthalmothrips splendidus
8.	Adraneothrips nilgiriensis (Ananthakrishnan)		Ananthakrishnan
9.	Adraneothrips okajimai (Muraleedharan & Sen)	58.	Malacothrips natalensis (Trybom)
10.	Adraneothrips pteris (Ananthakrishnan)	59.	Margaritothrips flavus Bhatti
11.	Adraneothrips stannardi Ananthakrishnan	60.	Margaritothrips longus Bhatti
12.	Apelaunothrips bhowalii (Ananthakrishnan)	61.	Margaritothrips sumatrensis Priesner
13.	Apelaunothrips consimilis (Ananthakrishnan)	62.	Mesandrothrips emineus (Ananthakrishnan &
14.	Apelaunothrips indicus (Ananthakrishnan)		Jagdish)**
15.	Apelaunothrips lucidus (Ananthakrishnan)	63.	Mesandrothrips pictipes (Bagnall)**
16.	Apelaunothrips madrasensis (Ananthakrishnan)	64.	Mesandrothrips pusillus (Ananthakrishnan &
17.	Apterygothrips fungosus (Ananthakrishnan &	04.	Jagdish)**
- / .	Jagadish)*	65.	Mesandrothrips tener (Ananthakrishnan &
18.	Apterygothrips jogensis (Ananthakrishnan&	05.	Jagdish)**
10.	Jagadish)*	66.	Mystrothrips dammermani (Priesner)
19.	Apterygothrips rubiginosus (Ananthakrishnan &	67.	• • • • • • • • • • • • • • • • • • • •
1).	Jagadish)*	68.	Neothrips lepidus Ananthakrishnan
20.	Azaleothrips amabilis Ananthakrishnan	69.	Ocythrips rarus Ananthakrishnan
20. 21.	Azaleothrips amaonis Anantiakrisinian Azaleothrips aspersus Bhatti	69. 70.	Oidanothrips enormis (Ananthakrishnan)
22.	Azaleothrips dispersus Bhatti Azaleothrips bhattii Vijay Veer & Chauhan		Oidanothrips megacephalus (Ananthakrishnan)
23.	Azaleothrips lineus Bhatti	71.	Opidnothrips corticulus Ananthakrishnan
23. 24.	*	72.	Phiarothrips reperticus Ananthakrishnan
2 4 . 25.	Baenothrips asper (Bournier)	73.	Phlaeothrips nilgiricus Ananthakrishnan
	Baenothrips indicus (Ananthakrishnan)	74.	Phylladothrips karnyi Priesner
26. 27.	Baenothrips minutus (Ananthakrishnan)	75.	Plectrothrips corticinus Priesner
	Bradythrips hesperus Hood & Williams	76.	Plectrothrips eximius Ananthakrishnan
28.	Bunothrips cruralis Ananthakrishnan.	77.	Plectrothrips pallipes Hood
29.	Ecacanthothrips tibialis (Ashmead)	78.	Preeriella formosana Okajima
30.	Glubothrips mucidus Ananthakrishnan	79.	Priesneria insolitus (Ananthakrishnan)
31.	Habrothrips curiosus Ananthakrishnan	80.	Psalidothrips ascitus (Ananthakrishnan)
32.	Holothrips andamanensis (Sen)	81.	Pygmaeothrips angusticeps (Hood)
33.	Holothrips ananthakrishnani Okajima	82.	Socothrips verrucosus Ananthakrishnan
34.	Holothrips cracens (Ananthakrishnan)	83.	Sophiothrips nigrus Ananthakrishnan
35.	Holothrips fumidus (Ananthakrishnan)	84.	Sophiothrips typicus (Ananthakrishnan)
36.	Holothrips indicus (Ananthakrishnan)	85.	Stannardothrips longirostris Ananthakrishnan
37.	Holothrips minor (Hood)	86.	Stephanothrips adnatus Ananthakrishnan
38.	Holothrips mirandus (Ananthakrishnan)	87.	Stephanothrips occidentalis Hood & Williams
39.	Holothrips nepalensis (Pelikán)	88.	Strepterothrips orientalis Ananthakrishnan
40.	Holothrips quadrisetis Okajima	89.	Symphyothrips aberrans Ananthakrishnan
41.	Holothrips ruidus (Ananthakrishnan)	90.	Tamilthrips pini (Ananthakrishnan)*
42.	Holothrips stannardi (Ananthakrishnan)	91.	Trichinothrips breviceps (Bagnall)
43.	Holothrips subtilis (Ananthakrishnan)	92.	Tylothrips indicus Sen & Muraleedharan
44.	Holothrips typicus (Ananthakrishnan)	93.	Tylothrips samirseni Varatharajan, Singh & Bala
45.	Hoplandrothrips corticis Ananthakrishnan	94.	Urothrips tarai (Stannard)
46.	Hoplandrothrips flavipes Bagnall	95.	Veerabahuthrips bambusae Ramakrishna
47.	Hoplandrothrips kudoi Muraleedharan	96.	Xylaplothrips debilis Ananthakrishnan &
48.	Hoplandrothrips nobilis Priesner		Jagadish*
49.	Hoplothrips dubius (Bagnall)	97.	Xylaplothrips ligs Ananthakrishnan & Jagdish*
50.	Hoplothrips fungosus Moulton	98.	Xylaplothrips micans Ananthakrishnan &
51.	Hoplothrips nemorius Ananthakrishnan		Jagdish*

^{*}Species under Haplothripini and the rest come under Phlaeothrips lineage; ** Mesandrothrips (= Xylaplothrips)

Table 3. Thrips diversity and density in the leaf litters of natural and human-made forests of Manipur (24°44'N, 93°58'E)

Plantation type	Number of thrips species			Mean
with altitude	collected		No.*	
	Idolo-	Phlaeo-	Total	
	thripinae	thripinae		
Pine forest	4	8	12	9.3ª
(1500-2100 m)				
Bamboo forest	5	10	15	17.4^{b}
(900 - 1600 m)				
Oak forest	5	9	14	27.0°
(900-1300 m)				
Polyculture forest	12	30	42	33.0^{d}
(900-1800 m)				
CD at $p=0.01=4.6$				

Each value mean of seven replications*; Alphabets followed by each figure in the last vertical column different from each other at 1% level (ANOVA p=0.01); *No. collected using Tullgren funnel method

But, in Nature, a chance of more than one fungal taxon co-occurring at the same feeding site is highly likely. If this were proved right, then the spore-feeding thrips show no specificity to any particular fungal taxon.

Morphotaxonomy distinguishes members of the Phlaeothripidae into spore-feeding Idolothripinae and the fungal-hyphae-feeding Phlaeothripinae, based on the width of maxillary stylets: 2-3 μ m in the fungal-hypha feeders and 5-10 μ m in spore feeders (Mound

and Palmer, 1983). This classification gains in validity by the correlation of the width of maxillary stylets of *Mecynothrips hardyi* (Priesner) (Phlaeothripidae) and fungal spore size of *Dothiorella thripsita* (Ascomycota: Botryosphaeriales: Botryosphariaceae). For example, the mean width of the maxillary stylet of *M. hardyi* (body length - 15 mm) is $13.9\pm0.2~\mu m$ and the mean width of the ingested spore of *D. thripsita* is $10.9\pm0.3~\mu m$. This observation along with the spores extracted from the gut confirmed the spore feeding habit of *M. hardyi* (Tree et al., 2010; Eow et al., 2011). This example serves well to illustrate mycophagous habit of the other Idolothripinae.

The mutualistic relations between insects and fungi in terms of dispersal, nutrition, mechanical protection and antimicrobial defence has been elaborately explained (Bidermann and Vega, 2019). Considering that in the context of Phlaeothripidae and fungi, the mutualism between them can be described in terms of dispersal and nutrition of the involved thrips. Nearly 2100 species of the Phlaeothripidae feed on fungal hyphae and spores (Dang et al., 2014; Eow et al., 2011). Some evidences also exist to indicate that the Thysanoptera act as mechanical vectors and disseminate fungal spores on plants (Ananthakrishnan, 1980; 1993). Mechanical dispersal of fungal spores is a strong possibility because of their numerous body setae that facilitate the attachment of fungal spores to their body surfaces similar to that of pollen grains transmitted mechanically

Table 4. Thrips, plants and fungi

Thrips (Tubulifera: Idolothripinae)	Plant	Fungus
Loyolaia indica	Dry leaves and leaf sheaths of	Lojkania cynodontifolii ⁺⁺
(Ananthakrishnan)	Cynodon dactylon (L.) Pers. (Poaceae)	(Fenestellaceae)
Tiarothrips subramanii	Dry leaves of <i>Borassus flabellifer</i> L.	Anthostomella consanguinea,
(Ramakrishna)	(Arecaceae)	A. phoenicicola, A. sepelibili ⁺⁺
		(Xylariaceae)
Mecynothrips simplex	Dry leaves of Areca catechu L.	Pestalotia sp. ⁺⁺
Bagnall	(Arecaceae)	(Amphisphaeriaceae)
Mecynothrips hardyi	Acacia harpophylla F. Muell. ex Benth.	Dothiorella thripsita**
(Priesner)	(Fabaceae)	(Botryosphaeriaceae).
Priesneriana kabandha	Eucalyptus globulus Labill. (Myrtaceae)	Rhytidhysterium rufula*
(Ramakrishna)		(Patellariaceae) and
		Cytospora* (Phyllostictaceae)
Elaphrothrips	Tectona grandis L. f. (Lamiaceae)	Pestalotia sp.*
denticollis (Bagnall)		(Amphisphaeriaceae)
		Phomopsis tectonae
		(Diaporthaceae)
Nesothrips indicus	Decaying scape of Agave americana L.	Anthostomella sphaeroidea*
Ananthakrishnan	(Asparagaceae)	(Xylariaceae)
Dinothrips sumatrensis	Dry bark of <i>Piper nigrum</i> L.	Lasiodiplodia theobromae*
Bagnall	(Piperaceae)	(Botryosphaericeae)

Source: **Ananthakrishnan and James, 1983; **Tree et al. (2010) *Ananthakrishnan et al. (1984)

by certain species of the Thysanoptera, such as *Thrips hawaiiensis* (Morgan), *Frankliniella schultzei* (Trybom), and *Microcephalothrips abdominalis* (Crawford) (Thripidae) (Varatharajan et al., 2016).

C. Developmental pattern

A comparison of breeding behaviours and developmental durations of different life stages of five species each of the mycetophagous and sporophagous thrips is available (Ananthakrishnan et al., 1984) (Table 5). The duration of development from egg to adult for the above 10 species was between 15 and 28 d, but the type of reproduction varied between the mycetophagous and sporophagous thrips (Ananthakrishnan et al., 1983; 1984). For instance, the mycetophagous Phlaeothripinae were oviparous and oviposited in greater numbers during moist months (July-December) when fresh fungi were abundantly available, whereas the sporophagous Idolothripinae reproduced by either oviparous or ovoviviparous or viviparous mode influenced by fungal density and environmental factors such as temperature, rainfall, and humidity. Field observations of the idolothripines such as T. subramanii and B. idolomorphus indicated viviparous mode of reproduction especially when the fungal density was less due to seasonal dryness. This has been confirmed by rearing B. idolomorphus at 30°C and 80% RH, wherein they reproduced either ovoviparously or viviparously (Ananthakrishnan and Dhileepan, 1984). In Ethirothrips, another idolothripine, Ananthakrishnan et al. (1984) have observed that among the females of a natural population inhabiting the dry, fungusinfested leaves of a species of Zizyphus (Rhamnaceae), oviparous females formed 60% of that population, followed by viviparous and ovoviparous females, 20% each. Similar to B. idolomorphus, Bactrothrips (= Caudothrips) buffai (Karny) (Idolothrpinae) also reproduces ovoviviparously (Bournier, 1957). This behaviour has been interpreted as an adaptation wherein

Table 5. Mycophagous Phlaeothripidae

Mycetophagous	Sporophagous		
(Phlaeothripinae)	(Idolothripinae)		
Adraneothrips limpidus	Bactrothrips idolomorphus		
Ananthakrishnan	(Karny)		
Azaleothrips amabilis	Elaphrothrips denticollis		
Ananthakrishnan	(Bagnall)		
Ecacanthothrips tibialis	Elaphrothrips procer		
(Ashmead)	(Schmutz)		
Holothrips cracens	Meiothrips menoni		
(Ananthakrishnan)	Ananthakrishnan		
Hoplandrothrips flavipes	Tiarothrips subramanii		
Bagnall	(Ramakrishna)		

few larvae and eggs are laid in different batches possibly to make use of available fungal material for the development of the juveniles (Bournier, 1957; 1966). But a comparison between oviparous and viviparous females in terms of eggs-larvae output revealed that the fecundity was less during the viviparous phase (7-11 larvae/ female) compared with the oviparous phase (25-33 eggs/ female) of T. subramanii. Whatever is the type of reproduction, from the perspective of their breeding behaviour, the mycophagous Phlaeothripidae inhabit fungus-rich parts of the litter and lay eggs in such a way that the fungal spores are accessible to the emergent larvae. In species such as T. subramanii, both adult males and females exhibit parental care by guarding rows of eggs until hatching (Ananthakrishnan et al., 1983; Ananthakrishnan and Suresh, 1983).

Populations of mycophagous Phlaeothripidae are regulated by the richness of fungi. The density of litterinhabiting Phlaeothripidae is a useful, although indirect, measure to estimate fungal density: i.e., larger the thrips colony, greater is the diversity and density of the fungal flora, and the vice versa (Mound, 1974; 1977). In the mycophagous Phlaeithripidae, more apterous individuals than alates occur in the first 4-5 wk. With the dwindling of the availability of fungal spores, the situation reverses with more of alates, as shown in Priesneriana kabandha (Ramakrishna) (Idolothripinae) feeding on the spores of a species of Cytospora (Ascomycota: Sordariomycetes: Valsaceae). Thus, the abundance and depletion of fungal spores not only reveal the high and less abundance of the Phlaeothripidae, but also reflect the proportions of apterous and alate individuals within a colony (Ananthakrishnan et al., 1983). Between the two extremes, brachypterous individuals occur in many bark-dwelling Phlaeothrpidae. Brachypterae (apterous) arise when the fresh fungi are available, whereas the macropterae (alates) occur more in numbers when fungal density declines (Hood, 1940; Bournier, 1961). Influence of food in alary polymorphism can be understood with Hoplothrips fungi Zetterstedt (Phlaeothripidae) feeding on a species of Stereum (Agaricomycetes: Russulales: Stereaceae) on dead wood. Apterous individuals were abundant as long as Stereum populations were high and when Stereum was replaced by a species of *Mucor* (Mucoromycota: Mucorales: Mucoraceae), a large number of winged males and females of *Hoplothrips fungi* arose (Mound, 2005). This example highlights not only the significance of fungi as food in the production and maintenance of apterous individuals, but indirectly highlights the specificity of *H. fungi* to a species of *Stereum*.

Although alary polymorphism occurs among the mycophagous Phlaeothripidae (Figs. 1a, b), the development of apterous individuals seems to be an adaptation in the leaf-litter habitat for the following reasons:

- (a) Abundance of fungi enables the Phaleothripidae to feed and breed. For instance, *Loyolaia indica* consumes 47,600 spores of *Fusarium oxysporum* f. sp. *cubense* Smith, Snyder and Hansen (Sordariomycetes: Hypocreales: Nectriaceae) per adult and lays 4-6 eggs/ female on clumps of *Cynodon dactylon* Pers. (Poaceae). The total development time is 13-18 d when reared at 30± 2°C and 72% RH (Ananthakrishnan et al., 1984).
- (b) In the fungus-feeding *Suocerathrips linguis* Mound and Marullo (1994) in Germany, occurrence of either partial or completely de-alate adult females was common in the colony and the process of wing shedding occurred immediately after mating (Moritz, 2002; Mound, 2005). This feature was explained as *S. linguis*'s commitment to establish the colony and parental care.
- (c) The mycophagous Phlaeothripidae utilize the conducive semi-permanent niche endowed with abundant fungi to their advantage and produce more apterous adults as in *H. fungi* on the fungus-infested dead wood (Mound, 2005).
- (d) The juvenile hormone (JH) titre will be higher in apterous insects than the alates in general (Roff, 1991). Higher JH titre would mean that the duration on insect development will be longer in apterous than alates. For example, the total duration of development in Lovolaia indica was reported to be 13-18 d when reared at 30± 2°C and 72% RH, but the study did not mention it for alate or apterus individuals (Ananthakrishnan et al., 1984). Although the bioassay on thrips's hormone levels has not been attempted so far, considering the role of JH, it is presumed that the extended duration of 5 d of development may refer to the duration of apterous and the short duration of 13 d may reflect the developmental period of winged individuals, since all the rearing conditions stated above were the same.
- (e) Periodical collection and enumeration of field populations of litter-inhabiting thrips also reflected the presence of alates, apterous, normal males and females, besides large and small males reflecting morphological variation (Ananthakrishnan, 1969; 1979; Mound and Palmer, 1983; Tree et al., 2010). As a result, in a colony, it is possible to observe

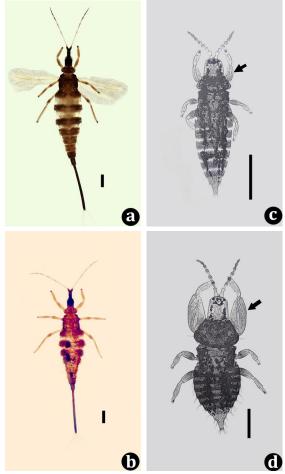


Fig. 1. a, b: Alate and Apterous *Holurothrips manipurensis*; c, d: small and large individuals of *Hoplothrips fungosus* (Scale bar = $500 \mu m$). Arrows indicate size variation of fore-femora. (Source: c, d. Ananthakrishnan, 1973).

a small proportion of large and small males, in addition to dominant population of normal-size males and females of the same species. Size variation among them is distinct as in *T. subramanii*, in which the length of third antennal segment of the small, normal, and large individuals of T. subramanii were 80, 160 and 240 µm, respectively (Ananthakrishnan, 1973; 1979). Similar variations on the size of forefemora of H. fungosus (Fig. 1c and 1d) (Ananthakrishnan, 1973), two fold long preocular projection on the heads of large males of T. subramanii, three-fold increased width of the fore-femora of large males of E. tibialis (Ananthakrishnan, 2005) and thorn-like cheek setae of large males of Mecynothrips kraussi Palmer and Mound, (Mound, 2005) are a few notable examples of intraspecific variation in comparison with the respective species of their smaller males. Based on the available data pertaining to representative examples of mycophagous Thysanoptera mentioned here, a general pattern of their development has been reconstructed (Fig. 2).

D. Phenotypic plasticity

Phenotypic plasticity is a kind of intraspecific variation among individuals belonging to same species, in which, some members of a population exhibit considerable morphological variations (Ananthakrishnan, 2005). Such a plasticity is common among the mycophagous Phlaeothripidae. As of the present, only observational evidences exist in support of the prevalence of phenotypic plasticity among the Thysanoptera, and experimental verifications are necessary to strengthen the phenotypic-plasticity theory (Mound, 2005). The literature abounds with many observational reports that many species of mycophagous Phlaeothripidae exhibit wide-ranging morphological traits, such as alary polymorphism, sexual dimorphism, and intra-specific variation of body organs. Ananthakrishnan (1979; 1984; 2005) and Mound (2005) have elaborately discussed this aspect based on morpho-taxonomy. The following remarks highlight some of the prominent features noticed among selected mycophagous Phlaeothripidae:

Alary polymorphism refers to either apterous or

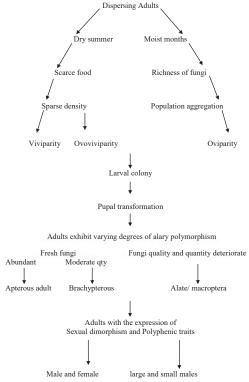


Fig 2. Developmental pattern in certain fungal spore feeding thrips

brachypterous or alate individuals. As evident in *H. manipurensis*, populations from *Quercus*-leaf litter in summer months (April-June) included more of alates, whereas in winter and spring months (November-March), *H. manipurensis* populations included more of apterous individuals in Manipur (24°44'N, 93°58'E). *Quercus griffithii* Hook f. et Thomson ex. Miq., and *Q. serrata* Murray (Fagaceae) being deciduous, accumulation of leaf litter is appreciably more in late autumn and winter compared with summer. Dense leaf litter coupled with low temperature, dampness, and short photoperiods facilitates the growth of fungus, which highly likely lead to the production of apterous individuals (Fig. 1a, b).

- In Loyolaia indica, reproductive diapause occurs in June-September on dry grass clusters, and the dispersal of alates take place later leading to the production of apterous individuals through oviparous mode of reproduction in Chennai (13°4'N,80°14'E) climate. Variation in climatic conditions along with food scarcity results in the production of alates and with the arrival of northeast monsoon in October-November, fungal growth is activated, which in turn, facilitates the population build-up of apterous individuals (Ananthakrishnan, 1984).
- The large and small individuals within the male populations of Ecacanthothrips tibialis, Elaphrothrips denticolis, M. simplex, T. subramanii, are a few examples showing striking intraspecific structural variations within one population. Their allometric data show considerable differences between the large and small individuals. For instance, in E. tibialis, the width of fore-femora in large males is (1600-1800 μ m) three times more than that of small male (400-600 μ m). Similarly, the presence of fore-femora inner tooth (400-550 μm) can be observed in large males of E. tibialis and that will be almost invisible in small males of the same species (Ananthakrishnan, 1971). Although Ananthakrishnan (1971) has elaborately described this phenomenon in many a thrips species from a taxonomic perspective, Bernard Crespi (1986) conceptualized their functional dynamics and has explained such variations within the same colony. According to Crespi (1986), in a large congregation of fungus-feeding male Hoplothrips pedicularius Haliday (Phlaeothripinae) competitive infighting occurs resulting in the death of the weaker individuals. The successful males of H.

pedicularius feed voraciously and breed to protect their eggs and siblings (Crespi, 1988). Similar to other subsocial insects such as termites (Isoptera) and fig wasps (Hymenoptera) with traits to achieve the maximum level of inclusive fitness (Hamilton, 1978; 1979), spore-feeding thrips as well, display a range of features such as parental care, sexual dimorphism and other allometric variations among the individuals of a colony, possibly with the purpose to enhance their survival fitness.

E. Ecological implications

The taxonomic diversity of litter-inhabiting Thysanoptera is c. 2100 species feeding solely on fungal spores and hyphae (Dang et al., 2014; Eow et al., 2011). Not only their diversity, but their density are high, similar to populations of Preeriella jacotia Hartwig (Phlaeothripinae) with 2500 individuals collected from forest litter in South Africa (Hartwig, 1978). Such a diversity of species coupled with dense population possibly contributes to the overall ecological services to the concerned ecosystem. By virtue of occupying the litter habitat, the mycophagous Phlaeothripidae involve themselves in the decomposition and recycling of leaf litter, either directly or indirectly. Among the litter-inhabiting arthropods, the Phlaeothripidae occupy at least a third of the soil fauna. Although the Acarina are the most abundant (55.7%) soil arthropods, the Collembola and Thysanoptera standing second (14.7%) and third (6.5%), respectively, and the remainder including species of the Coleoptera, Hymenoptera, and the Lepidoptera (Wang and Tang, 2012). The role of litter-inhabiting thrips in forest floor is known to some extent (Mound, 1974; 1977; Ananthakrishnan, 1996), but, not many studies have been attempted to know the abundance and vertical distribution of insects in general and thrips in particular and such studies will certainly contribute substantially in understanding the role of litter-inhabiting Thysanoptera.

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