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An Overview of Indian Dacine Fruit Flies (Diptera: Tephritidae: Dacinae: Dacini)

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Abstract

Fruit flies belonging to tribe Dacini are pertinent pests of horticultural crops in Southeast Asia, Sub-Saharan Africa and Australasian Oceanian region. They pose enormous threats to fruit and vegetable production throughout the world, causing both quantitative and qualitative losses. Ninety two species of dacine fruit flies (28 endemic, 30.43% endemism) belonging to three genera, viz. *Bactrocera* Macquart (51 species, 17 endemic, 33.33% endemism), *Dacus* Fabricius (10 species, 3 endemic, 30.0% endemism), and *Zeugodacus* Hendel (31 species, 8 endemic, 25.80% endemism), and 19 subgenera have been listed from India. Of these, nine endemic species, viz. *Bactrocera* (*Bactrocera*) *andamanensis*, *B.* (*B.*) *blairiae*, *B.* (*B.*) *curtivitta*, *B.* (*B.*) *patula*, *B.* (*B.*) *ranganathi*, *B.* (*Calodacus*) *harrietensis*, *Dacus* (*Mellesis*) *insulosus*, *Zeugodacus* (*Zeugodacus*) *fuscoalatus*, *Z.* (*Z.*) *havelockiae* are known only from Andaman & Nicobar Islands. The current understanding of the morphology of the tribe, together with data on their biology, habitat associations, and distribution combine presents a picture of the phylogenetic relationships within the group. Besides, the knowledge of biology and behaviour of dacine species suggests that there is a close relationship between the fly species and their host plants which involves adult's feeding, host recognition, courtship and mating, oviposition, larval feeding and bacteria associations. In the present paper notes on subgeneric classification of Dacini, their distribution, endemism, relative occurrence of different taxa, phylogeny, host associations, pest status, male lures and bacterial associations have been added.

Keywords: Dacini, phylogeny, distribution, host associations, male lures, bacterial associations

1. Introduction

Fruit flies are distributed in all biogeographic regions except in extreme desert and polar areas, where their hosts are scarce or absent (Foote et al., 1993). They have highly diverse biology and larvae of many species develop in fruits, vegetables, flower heads, buds, seeds, stems, etc. Fruit flies belonging to tribe Dacini are of greatest horticultural relevance and its most species are phytophagous and many pertinent pest species have been studied extensively, due to damage they cause in plants of economic interest (Norrbom et al., 1999). Many invasive dacine flies are pests of horticultural crops worldwide, due to their wide climatic tolerance, polyphagous nature, high reproduction potential, multivoltine nature and high capacity for dispersal (Prokopy, 1977). Tribe Dacini contains around a fifth of all known species in the family Tephritidae (Schutze et al., 2017).

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These flies are frugivorous or florivorous and about 10 per cent of the recognized species are pests of commercial fruits and vegetables (Vargas et al., 2015). They use host's tissues for larval development causing severe economic impact and liable to quarantine restrictions imposed by many countries (Foote, 1967; Aluja and Mangan, 2008). In India, fruit flies have been identified as one of the ten most serious problems of horticulture because of their polyphagous nature and cause a huge economic loss which varies from 2.5-100% depending upon the crop and season (Verghese et al., 2004; Dhillon et al., 2005). With respect to the larval host plants, most species are polyphagous; a few are oligophagous, while the remaining <1% are monophagous (Drew, 1989). Besides this, global invasion of fruit flies attracts a great deal of attention in the field of plant quarantine and invasion biology (Qin et al., 2015). India is a major producer of fruits and vegetables and with increasing globalization; it has become a challenge for this country not only to feed its own population but also to export fruits and vegetables to developed countries.

2. Tribe Dacini

The genus *Dacus* was first described by Fabricius in 1805 by its type-species *D. armatus*. Flies of tribe Dacini are often wasp mimics, usually black to brown with yellow vittae and predominantly hyaline wing with well developed costal band and anal streak (David and Ramani, 2019). Presently four genera, viz. *Bactrocera* Macquart, *Dacus* Fabricius, *Monacrostichus* Bezzi and *Zeugodacus* Hendel and 932 species are recognized in this tribe (Virgilio et al., 2015; San Jose et al., 2018; Doorenweerd et al., 2018). Drew and Romig (2013, 2016) considered *Ichneumonopsis* to be a member of Dacini, whereas Kovac et al. (2006, 2013) and Freidberg et al. (2017) included this genus in tribe Gastrozonini. Earlier 85 species of Dacini were documented from India in 3 genera except for *Monacrostichus* (Agarwal and Sueyoshi, 2005; David and Ramani, 2011; Drew and Romig, 2013; David et al., 2017). The dacine flies are characterized by scutum black/ brown/ reddish-brown with or without yellow medial and lateral postsutural vittae; significantly reduced chaetotaxy of head and thorax. Face fulvous to black with a pair of dark spots or a band; wing with cell bm deeper/broader than bcu; extension of cell bcu longer than bcu; costal band vary in width and may expand at apex in small or large spot; males usually with pecten; ceromata present, female with 2 spermathecae.

3. Generic and Subgeneric Classification

Tribe Dacini is one of the most species rich clades within the family Tephritidae and includes 4 genera, viz. *Bactrocera*, *Dacus*, *Zeugodacus* and *Monacrostichus*. These genera are well distributed in and around Indian subcontinent and extending their range to Pacific Australasian countries, while greatest diversity of genus *Dacus* occurs in Afrotropical region. Shiraki (1933) discussed the generic classification of the Dacini and provided a key to 6 genera, viz. *Chaetodacus* Bezzi, *Zeugodacus* Hendel, *Parazeugodacus* Shiraki, *Paratridacus* Shiraki, *Tetradacus* Miyake and *Mellesis* Bezzi based on characters like presence or absence of supernumerary lobe and dense aggregation of microtrichia around vein CuA + 1A in male wing; presence or absence of bristles and a brown anal stripe in wing; presence or absence of a pecten on 3rd abdominal tergite of male and shape of basal segment of ovipositor. Munro (1947) recognized only one genus *Dacus* and divided it into a number of subgenera. Hardy (1955) arranged Dacini species in 4 genera and 24 subgenera by considering groups of characters. Drew (1972) recognized two valuable characters in showing intra-tribe relationships, i.e. (1) Abdominal sternite V of male – posterior margin with a deep concavity or a very slight concavity**.** (2) size of male surstylus - either short-at most only twice as long as anterior lobe or long-at least 6 times as long as anterior lobe**.** He divided genus *Dacus* into *Dacus* group and *Strumeta* group of subgenera on the basis of these characters.

Munro (1984) elevated subfamily Dacinae to full family status namely Dacidae for African taxa and described many new subcategories in the family; however, his classification was not accepted by most tephritid taxonomists. Drew (1989) divided Dacini into four groups, viz. *Bactrocera* group, *Zeugodacus* group, *Melanodacus* group *Queenslandacus* group, and 28 Asian and Pacific subgenera. Drew and Hancock (1999) recognized four genera in the tribe: *Bactrocera*, *Dacus*, *Ichneumonopsis*, and *Monacrostichus* and placed majority of species of the first two genera in different subgenera. Agarwal (2006) placed Indian Dacini species in two groups *Bactrocera* group and *Zeugodacus* group; and 10 subgenera, namely - *Bactrocera*, *Bulladacus*, *Daculus*, *Gymnodacus*, *Tetradacus*, *Hemigymnodacus*, *Javadacus*, *Paradacus*s, *Paratridacus* and *Zeugodacus*. Hancock and Drew (2015) listed subgenera in genus *Bactrocera* in four groups namely *Bactrocera* Group, *Melanodacus* Group, *Tetradacus* – ancestral subgenus?, and *Zeugodacus* Groups. Hancock and Drew (2018) listed subgenera in the *Zeugodacus* group as: Subgroup (1) - *Aglaodacus*, *Heminotodacus*, *Nesodacus*, *Paradacus*, *Parasinodacus*, *Perkinsidacus*, Subgroup (2) - *Asiadacus*, *Austrodacus*, *Diplodacus*, *Javadacus*, *Niuginidacus*, *Papuodacus*, *Sinodacus*, *Zeugodacus*.

4. Distribution and Relative Occurrence of Different Taxa

Most Dacini are found in Afrotropical region, Southeast Asia to Australasian Oceanian region and only a few have invaded in other areas. The Asian-Pacific Dacini, primarily consisting of *Bactrocera* and *Zeugodacus* species mainly occur in South East Asia and Papua New Guinea (Drew, 2004). The distributions of known species within the tribe Dacini in India is given in Table 1. In India, Dacini is represented by 3 genera *Bactrocera*, *Dacus* and *Zeugodacus* and 92 species (28 endemic, i.e. 30.43% endemism). The genus *Bactrocera* includes (51 species, 17 endemic – 33.33% endemism), *Dacus* (10 species, 3 endemic - 30% endemism) and *Zeugodacus* (31 species, 8 endemic –

Table 1: Indian dacine fruit flies, their attractant, species complex, pest status and distribution

Sl. No.	Category	Name of taxa	No. of species*	Attractant	Species complex	Pest status	Distribution
1	Genus	*Bactrocera* Macquart, 1835	51(17)				
I	Subgenus	(*Bactrocera*) Macquart, 1835	41(14)				
	1.	*aethriobasis* (Hardy, 1973)		ME		NP	Bhutan, China (Yunnan), S. Vietnam, Thailand, Peninsular Malaysia, India (Meghalaya)
	2.	*affinis* (Hardy, 1954)		ME		PP	India (Andhra Pradesh, Karnataka, Tamil Nadu), Pakistan
	3.	*albistrigata* (de Meijere, 1911)		CL	*frauenfeldi* complex	FP	India (Andaman & Nicobar Is.), Thailand, Malaysia, Singapore, Indonesia (Sumatra, Java, Lombok, Sulawesi, Kalimantan) Australian Territory (Christmas Is.)
	4.	*amarambalensis* Drew, 2002		ME	*dorsalis* complex	NP	India (Kerala), Sri Lanka
	5.	*andamanensis* (Kapoor, 1971)		CL	*dorsalis* complex	NP	India (AN)
	6.	*apicofuscans* White & Tsuruta, 2001		ME		NP	India (Karnataka, Kerala), Sri Lanka
	7.	*apiconigroscutella* Drew, 2002		CL	*nigrotibialis* complex	NP	India
	8.	*bhutaniae* Drew & Romig, 2013		CL		NP	Bhutan, Bangladesh, India (Andaman Is.), Thailand, Vietnam, Cambodia, Taiwan
	9.	*blairiae* Drew & Romig, 2013		ME		NP	India (AN)
	10.	*carambolae* Drew & Hancock, 1994		ME	*dorsalis* complex	PP	Thailand, Malaysia, China (Yunnan), Singapore, Brunei Darussalam, Indonesia, Myanmar, Cambodia, s. Vietnam, Bangladesh, India (Meghalaya, Andaman & Nicobar Is.). Introduced - Surinam, French Guyana, northern Brazil (Amapá), eradicated from Guyana
	11.	*caryeae* (Kapoor, 1971)		ME	*dorsalis* complex	PP	India
	12.	*correcta* (Bezzi, 1916)		ME		PP	Cambodia, India, Bhutan, Myanmar, China (Yunnan, Guizhou), Nepal, Pakistan, Thailand, Vietnam, Malaysia (Peninsular), Sri Lanka, Bangladesh. USA- Florida (not established), California (eradicated)

Table 1: Continue...

Sl. No.	Category	Name of taxa	No. of species*	Attractant	Species complex	Pest status	Distribution
	13.	*curtivitta* Drew & Romig, 2013		-		NP	India (AN)
	14.	*digressa* Radhakrishnan, 1999		CL, Zingerone		NP	India (Karnataka, Tamil Nadu, Telangana, Tripura), Bangladesh
	15.	*dorsalis* (Hendel, 1912)		ME, Zingerone	*dorsalis* complex	PP	Widespread Tropical Asia Introduced Africa and Oceania. Eradicated- Japan (Ryukyu Archipelago including Okinawa), Mauritius. USA - restricted distribution (California, Florida – eradicated), Hawaii, n. Marianas Islands (Rota, Saipan and Tinian). Europe- intercepted Belgium
	16.	*fastigata* Tsuruta & White, 2001		CL		NP	India (Karnataka, Kerala), Sri Lanka
	17.	*furcata* David and Hancock, 2017		-		NP	India
	18.	*latifrons* (Hendel, 1915)		Latilure		OP	Asia-Pakistan to Taiwan, Indonesia (Kalimantan, Java, Sulawesi). Introduced- Kenya, Tanzania, Iran; USA (Hawaii; California- eradicated); Japan (Yonaguni Is.- Okinawa Prefecture - invaded)
	19.	*limbifera* (Bezzi, 1919)		CL		NP	India (Andaman & Nicobar Is.), Indonesia (Sumatra, Java, Lombok, Sulawesi, Brunei Darussalam, Flores, Kalimantan, Sumbawa), Vietnam, Philippines, Malaysia (Sarawak), Cambodia
	20.	*melastomatos* Drew & Hancock, 1994		CL	*dorsalis* complex	NP	Peninsular Malaysia, Thailand, Singapore, India (Andaman & Nicobar Is.), Indonesia (Kalimantan, Java, Sumatra)
	21.	*merapiensis* Drew & Hancock, 1994		CL	*dorsalis* complex	NP	India (Karnataka, Kerala, Andaman Is.), Indonesia (Java, Sumatra)
	22.	*neoarecae* Drew, 2002		ME	*dorsalis* complex	NP	India
	23.	*neonigrotibialis* Drew, 2002		CL	*nigrotibialis* complex	NP	India (Andhra Pradesh, Kerala, Tamil Nadu), Bhutan, Cambodia
	24.	*nigrifacia* Zhang, Ji & Chen, 2011		CL	*nigrotibialis* complex	NP	China (Yunnan), Thailand (Chain Mai), Bangladesh, India (Tripura), Taiwan

Table 1: Continue...

Sl. No.	Category	Name of taxa	No. of species*	Attractant	Species complex	Pest status	Distribution
	25.	*nigrofemoralis* White & Tsuruta, 2001		CL	*nigrotibialis* complex	NP	India, Pakistan, Sri Lanka, Bhutan, Bangladesh
	26.	*pallescentis* (Hardy, 1955)		-		NP	India
	27.	*paraosbeckiae* Drew, 2002		CL		NP	India
	28.	*paraverbascifoliae* Drew, 2002		ME	*dorsalis* complex	NP	India (Kerala), Sri Lanka
	29.	*patula* Drew & Romig, 2013		CL		NP	India (AN)
	30.	*penecorrecta* Drew, 2002		ME		NP	India
	31.	*prabhui* David, 2019		-		NP	India
	32.	*pseudoversicolor* Drew, 2002		ME		NP	India
	33.	*ranganathi* Drew & Romig, 2013		ME	*dorsalis* complex	NP	India (AN)
	34.	*rubigina* (Wang & Zhao, 1989)		CL, Zingerone		NP	China, Bhutan, Thailand, n. Vietnam, Bangladesh, India (Tripura), Taiwan, Sri Lanka
	35.	*syzygii* White & Tsuruta, 2001		Zingerone	*dorsalis* complex	NP	Sri Lanka, Bangladesh, India (Kerala, Tamil Nadu), Vietnam
	36.	thailandica Drew & Hancock, 1994		CL	*dorsalis* complex	NP	India (Meghalaya), China (Yunnan), Bhutan, Vietnam, Brunei
	37.	*tuberculata* (Bezzi, 1916)		ME		PP	Bhutan, China (Yunnan), Myanmar, Thailand, Vietnam, Bangladesh, India (Meghalaya, Tripura)
	38.	*verbascifoliae* Drew & Hancock, 1994		ME	*dorsalis* complex	NP	India (Karnataka, Kerala, Tamil Nadu, Maharashtra), Bhutan, Myanmar, Thailand, Sri Lanka, Peninsular Malaysia, Indonesia (Java), Vietnam
	39.	*versicolor* (Bezzi, 1916)		ME		MP	Bhutan, India (Bihar, Karnataka, Kerala, Maharashtra, Tamil Nadu, Telangana), Sri Lanka
	40.	*vishnu* Drew & Hancock, 1994		CL	*dorsalis* complex	NP	India (Karnataka, Kerala, Maharashtra, Telangana, Tamil Nadu), Bhutan
	41.	*zonata* (Saunders, 1842)		ME		PP	Asia- Pakistan to Vietnam; Indonesia (Moluccas). Introduced - Mauritius, United Arab Emirates. Réunion Island, Iran Sudan, Oman, Saudi Arabia (restricted distribution); Iraq, Israel (few occurrence); Oman, Yemen, Egypt, Libya (localized). USA- Trapped (in California but not established), Florida (eradicated)

Table 1: Continue...

Sl. No.	Category	Name of taxa	No. of species*	Attractant	Species complex	Pest status	Distribution
II	Subgenus	(*Bulladacus*) Drew & Hancock, 1995	1				
	42.	*cinnabaria* Drew & Romig, 2013		-		NP	India (Car Nicobar Is.), Singapore, West Malaysia
III	Subgenus	(*Calodacus*) Hancock, 2015	3(2)				
	43.	*calophylli* (Perkins & May, 1949)		-		NP	Palau, Australia (Christmas Is., NE Queensland), Papua New Guinea (Mainland), Japan (Ryukyu Is.), western Carline Is., India (Andaman and Nicobar Is.), Peninsular Malaysia, Singapore, s. Thailand, Palau, Solomon Islands (Guadalcanal), Vanuatu (Espiritu Santo)
	44.	*chettalli* David & Ranganath, 2016		-		NP	India
	45.	*harrietensis* Ramani & David, 2016		-		NP	India (AN)
IV	Subgenus	(*Daculus*) Speiser, 1924	1				
	46.	oleae (Rossi, 1790)		-		NP	Georgia, India (Jammu & Kashmir), Iran, Israel, Jordan, Lebanon, Pakistan, Saudi Arabia, Syria, Turkey, Algeria, Angola, Egypt, Eritrea, Ethiopia, Kenya, Lesotho, Libya, Mauritius, Morocco, Namibia, Réunion, Seychelles, South Africa, Tunisia, Sudan, Albania, Croatia, Cyprus, France (restricted distribution, Corsica), Greece (mainland and Crete), Italy (including Sardinia, Sicily), Malta, Montenegro, Portugal (including Azores), Serbia, Slovenia, Spain (including Balearic Is. and Canary Is.), Switzerland. Introduced - USA (California, Florida), Mexico, Madeira Is., Maltese Is., Caucasus
V	Subgenus	(*Paratridacus*) Shiraki, 1933	1				
	47.	*garciniae* Bezzi, 1913		-		NP	Sri Lanka, India (Karnataka)
VI	Subgenus	(*Parazeugodacus*) Shiraki, 1933	2(1)				
	48.	*bipustulata* Bezzi, 1914		CL, Zingerone		NP	India (Karnataka, Tamil Nadu), Sri Lanka
	49.	*conica* David & Ramani, 2019		-		NP	India

Table 1: Continue...

Sl. No.	Category	Name of taxa	No. of species*	Attractant	Species complex	Pest status	Distribution
VII	Subgenus	(*Tetradacus*) Miyake, 1919	2				
	50.	*brachycera* (Bezzi, 1916)		-		NP	India (Uttrakhand), China (Yunnan), Bhutan
	51.	*minax* (Enderlein, 1920)		weak ME		Fruit pest	Bhutan, India (Sikkim, W. Bengal), Nepal, China
2	Genus	*Dacus* Fabricius, 1805	10(3)				
I	Subgenus	(*Callantra*) Walker, 1860	1				
	52.	*longicornis* Wiedemann, 1830		CL		Cucurbits	India (Bihar, Himachal Pradesh, Karnataka, Manipur, Mizoram, Tripura), Indonesia (Java, Bali, Lombok, Sumbawa, Sulawesi, Ambon), Brunei Darussalam, Malaysia (Peninsular & Sarawak), Bhutan, Vietnam, Myanmar, Laos, Cambodia, Thailand, China (Yunnan, Guizhou), Bhutan, Bangladesh, Sri Lanka, Philippines (Luzon)
II	Subgenus	(*Didacus*) Collart, 1935	1				
	53.	*ciliatus* Loew, 1862		-		Cucurbits	Afrotropical region, Pakistan, Bangladesh, Comoros, St. Helena, Senegal, India, Nepal, Sri Lanka, Mali
III	Subgenus	(*Leptoxyda*) Macquart, 1835	1				
	54.	*persicus* Hendel, 1927		-		NP	India, Oman, Iran, Iraq, Pakistan, Sri Lanka
IV	Subgenus	(*Mellesis*) Bezzi, 1916	6(3)				
	55.	*crabroniformis* (Bezzi, 1914)		-		NP	India
	56.	*discophorus* (Hering, 1956)		CL - weak, clove oil		NP	India (Himachal Pradesh, Karnataka, Kerala, Maharashtra), Sri Lanka
	57.	*icariiformis* (Enderlein, 1920)		-		NP	India
	58.	*insulosus* Drew & Hancock, 1998		-		NP	India (AN)
	59.	*polistiformis* (Senior-White, 1922)		-		NP	India (Bihar, Uttar Pradesh, W. Bengal), Nepal, China (Yunnan)
	60.	*ramanii* Drew & Hancock, 1998		CL		NP	India (Andhra Pradesh, Karnataka, Kerala, Tamil Nadu), Sri Lanka
V	Subgenus	(*Neodacus*) Perkins, 1937	1				

Table 1: Continue...

Sl. No.	Category	Name of taxa	No. of species*	Attractant	Species complex	Pest status	Distribution
	61.	*sphaeroidalis* (Bezzi, 1916)		CL		NP	China (Fujian, Guangxi Province), India (Himachal Pradesh, Tamil Nadu, Uttrakhand, Chandigarh), Pakistan, Thailand, Vietnam
3	Genus	*Zeugodacus* Hendel, 1927	31(8)				
I	Subgenus	(*Asiadacus*) Perkins, 1937	1				
	62.	*apicalis* (de Meijere, 1911)		CL		NP	Indonesia (Java, Kalimantan, Sulawesi, East Malaysia (Sabah, Sarawak), Peninsular Malaysia, Thailand, Vietnam, China (Yunnan, Hainan), Brunei, Bangladesh, India (Tripura)
II	Subgenus	*Capparidacus* Hancock & Drew, 2018	1				
	63.	*gavisus* (Munro, 1935)		-		NP	India (Karnataka, Maharashtra, Telangana, Kerala, Odisha, Tamil Nadu), Sri Lanka
III	Subgenus	(*Hemigymnodacus*) Hardy, 1973	1				
	64.	*diversus* (Coquillett, 1904)		weak ME	*scutellaris* complex	Cucurbits	India, Bhutan, Southern Vietnam, Bangladesh, Sri Lanka, Nepal, Pakistan, Thailand, China (Sichuan, Guizhou, Yunnan)
IV	Subgenus	(*Javadacus*) Hardy, 1983	2(1)				
	65.	*scutellarius* (Bezzi, 1916)		CL		NP	India
	66.	*trilineatus* (Hardy, 1955)		CL	*arisanica* complex	NP	India (Karnataka, Kerala, Tamil Nadu), Sri Lanka, Thailand, Pakistan, Vietnam
V	Subgenus	(*Paradacus*) Perkins, 1938	1				
	67.	*duplicatus* (Bezzi, 1916)		-		NP	India (Andhra Pradesh, Karnataka, Madhya Pradesh, Maharashtra), Pakistan, Sri Lanka
VI	Subgenus	(*Parasinodacus*) Drew & Romig, 2013	3(1)				
	68.	*binoyi* Drew, 2002		CL		NP	India
	69.	*cilifer* (Hendel, 1912)		CL		NP	Taiwan, India (Tripura), Peninsular Malaysia, Thailand, Vietnam, China (Yunnan), Laos, Indonesia (Sumatra, Pasaman), Bangladesh

Table 1: Continue...

Sl. No.	Category	Name of taxa	No. of species*	Attractant	Species complex	Pest status	Distribution
	70.	*incisus* (Walker, 1861)		CL		NP	India (Andaman Is., Tripura), Bangladesh, Myanmar, Thailand, Peninsular Malaysia, Vietnam, China (Yunnan)
VII	Subgenus	(*Sinodacus*) Zia, 1936	2(1)				
	71.	*brevipunctatus* (David and Hancock, 2017)		CL	*hochii* complex	NP	India
	72.	*hochii* (Zia, 1936)		CL, Zingerone	*hochii* complex	Cucurbits	China (Yunnan, Guangxi, Hainan, Guizhou), Vietnam, India (Tripura), Indonesia (Nusa Tenggara, Java, Sumatra, Sumba), Bangladesh, Peninsular Malaysia, Thailand
VIII	Subgenus	(*Zeugodacus*) Hendel, 1927	20(5)				
	73.	*assamensis* (White, 1999)		CL	*scutellaris* complex	NP	India (Arunachal Pradesh, Himachal Pradesh), Bhutan, n. Vietnam, China (Gansu Province, Wenxian County)
	74.	*atrifacies* (Perkins, 1938)		CL	*scutellaris* complex	NP	India (Arunachal Pradesh), Bangladesh, Bhutan, Malaysia (Selangor, Sarawak), Thailand, China (Guanxi), Vietnam
	75.	*biguttatus* (Bezzi, 1916)		CL	*scutellaris* complex	NP	India (W. Bengal), Bhutan, China (Sichuan)
	76.	*bogorensis* (Hardy, 1983)		CL	*tau* complex	NP	Indonesia (Java, Sumatra, North Sulawesi), India (Tripura)
	77.	*caudatus* (Fabricius, 1805)		CL	*scutellaris* complex	Cucurbits	India, Myanmar, Cambodia, Nepal, China (Hainan), Bangladesh, Malaysia (East and Peninsular), Brunei Darussalam, Sri Lanka, Taiwan, Thailand, Vietnam, Indonesia
	78.	*cucurbitae* (Coquillett, 1899)		CL	*cucurbitae* complex	PP	Tropical Asia (widespread). Introduced - Afrotropical region and Oceania. Eradicated Japan (Ryukyu Islands), Kiribati, Nauru, USA (California - eradicated), Hawaii, N. Mariana Islands (restricted distribution)
	79.	*diaphorus* (Hendel, 1915)		CL	*scutellaris* complex	NP	India (Bihar, Meghalaya), Bangladesh, Bhutan, Peninsular Malaysia, Taiwan, Thailand, Sri Lanka, Vietnam, China (Hainan, Sichuan, Yunnan), Indonesia (Sumatra, Java)
	80.	*freidbergi* (White, 1999)		-	*scutellaris* complex	NP	India

Table 1: Continue...

Sl. No.	Category	Name of taxa	No. of species*	Attrac-tant	Species complex	Pest status	Distribution
	81.	*fuscoalatus* (Drew & Romig, 2013)		-	*watersi* complex	NP	India (AN)
	82.	*havelockiae* (Drew & Romig, 2013)		CL	*tau* complex	NP	India (AN)
	83.	*hoabinhiae* (Drew & Romig, 2013)		CL	*scutellaris* complex	NP	India (Assam), n. Vietnam, Thailand
	84.	*scutellaris* (Bezzi, 1913)		CL	*scutellaris* complex	Cucur-bits	India, Bhutan, Nepal, Myan-mar, Thailand, Pakistan, s. China, Peninsular Malaysia, Vietnam, Japan (Wakayama Prefecture)
	85.	*semongokensis* (Drew & Romig, 2013)		CL	*scutellaris* complex	NP	East Malaysia (Sarawak and Sabah), India (Andaman and Nicobar Is.)
	86.	*signatus* (Hering, 1941)		CL	*tau* complex	NP	India (Sikkim, Karnataka), Bhu-tan, Pakistan, Thailand
	87.	*tau* (Walker, 1849)		CL	*tau* complex	PP	Asia - Pakistan to Philippines; south to Sumatra and Sulawesi. Trapped Japan (Ishigaki Island)
	88.	*trivandrumensis* (Drew & Romig, 2013)		-	*tau* complex	NP	India
	89.	*vultus* (Hardy, 1973)		CL	*scutellaris* complex	NP	Thailand, China, Laos, Bhu-tan, East Malaysia (Sarawak, Sabah), Peninsular Malaysia, Indonesia (Java, Bali, Lombok), Philippines (Luzon Is.), Vietnam
	90.	*watersi* (Hardy, 1954)		-	*watersi* complex	NP	India
	91.	*yoshimotoi* (Hardy, 1973)		CL	*scutellaris* complex	NP	Bhutan, Thailand, India (Meghalaya), Nepal, Vietnam
	92.	*zahadi* (Mahmood, 1999)		CL	*tau* complex	NP	India (Karnataka, Kerala, Tamil Nadu, Tripura, Uttar Pradesh), Sri Lanka, Pakistan, Bhutan, Nepal, Myanmar, Vietnam

CL: Cue-lure; ME: Methyl eugenol; NP: Non pest; FP: Fruit pest; PP: Polyphagous pest; OP: Oligophagous pest; MP: Monophagous pest; India (AN): Species recorded from India (Andaman & Nicobar Islands) only; *Figures in parentheses indicate number of endemic species

25.80% endemism) (Figure 1, Table 1). The relative occurrence of species in each genus and subgenus is depicted in Figure 2. Nine species of Indian dacine flies (9.78%) are described only from Andaman and Nicobar Islands (Table 1). *Dacus* and *Zeugodacus* species namely, *D. longicornis, Z. caudatus, Z. diversus, Z. scutellaris* and *Z. tau* and are well distributed in most countries of Southeast Asia. Indian dacine species also show relationship with the corresponding fauna of other regions. *B*. (*Daculus*) *oleae*, an African species spread to Mediterranean region and northwest India and Pakistan. The genus *Dacus* is known by 10 species in 5 subgenera, of which, *D. craboniformis, D. icariiformis* and *D. insulosus* are endemic. Two subgenera of African origin, *Didacus* and *Leptoxyda,* have radiated back to Asia with the occurrence of *D.* (*Didacus*) *ciliatus* (cucurbit feeders) and *D.* (*Leptoxyda*) *persicus* (in asclepiads) (Drew et al., 1998). *B. carambolae* has introduced into Neotropical region. Species namely, *B. albistrigata*, *B. correcta*, *B. carambolae*, *B. dorsalis*, *B. latifrons*, *B. oleae*, *B. zonata*, *B. calophylli*, *D. ciliatus*, *D. persicus*, and *Z. cucurbitae* have also been recorded/ intercepted/ eradicated (not established) from other zoogeographical areas (Agarwal, 2006).

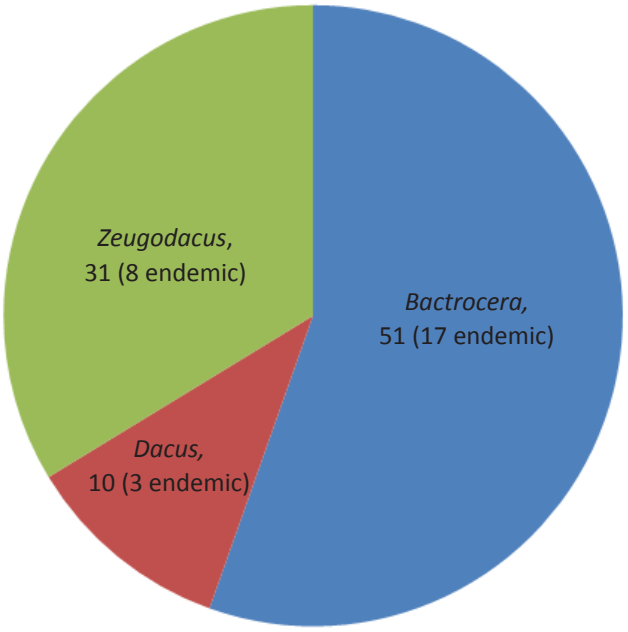

Figure 1: Relative occurrence of species in different genera of tribe Dacini in India

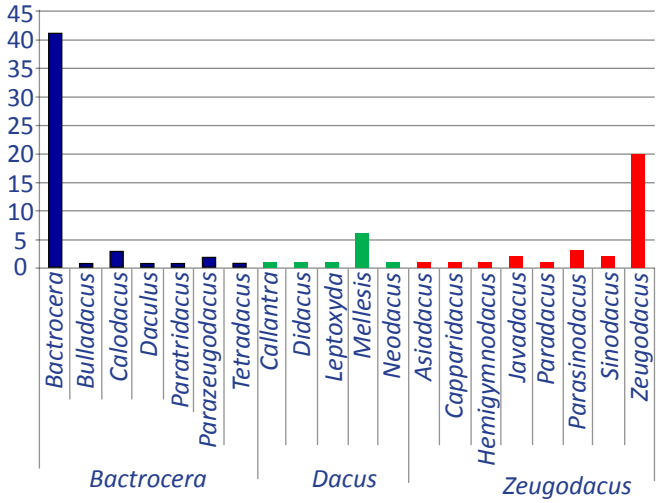

Figure 2: Relative occurrence of different taxa in tribe Dacini in India

5. Host Associations

Agarwal (2019) listed 296 species of fruit flies belonging to 90 genera from India. Species belonging to the genera *Bactrocera* and *Zeugodacus* are most economically significant with at least 50 polyphagous species considered to be important pests in tropical and subtropical areas of the world (White and Elson-Harris, 1992). The adults of polyphagous species have high mobility, relatively long life span (often more than 3 months) and high fecundity (> 1000 eggs/female) (Vargas et al., 1984), scramble type competition in the larval stage, several generations per year and the ability to pass unfavourable periods in a facultative reproductive diapause (Fletcher, 1987). Adult dacines mostly feed on plant secretions, nectar, sap, honey dew, bird dropping and microorganisms (Christenson and Foote, 1960) and direct damage begins with female puncturing the host's skin and ovipositing underneath it. During oviposition, fruit-rottening bacteria from the intestinal flora of the fly are introduced into the host which multiply and cause its tissues to rot (Vayssières et al., 2009). The larvae make feeding galleries resulting in conversion of host's tissues in a spongy mess. The second and especially third instar stages are voracious feeders and generally, the fruit falls to the ground as, or just before the maggots pupate (Ekesi and Billah, 2006). The larvae feeding forms a "non-interactive grazing system" while other major class of food substrates constitute plant parts, e.g. shoots, flowers, roots and species utilizing such food operate in an "interactive grazing system" (Zwolfer, 1983).

Host utilization by fruit fly species, whether mono-, oligo-, or polyphagous, must depend on adult's choice in terms of attraction to the host for oviposition. Female uses visual cues such as plant colour and odours emitted by a host (mainly but not exclusively host's specific). Light and Jang (1996) noted that there are 3 types of volatiles that can draw females (or males) to a particular habitat, "green leaf volatiles" such as aliphatic aldehydes and alcohols emitted by leaves and unripe fruit; (b) volatiles, mainly esters, emitted by ripening fruit; and (c) volatiles emanating from rotting fruit, bacteria, and other food sources, and species-specific volatiles emitted by the hosts of specialized fruit fly species. After alighting on a host, the female assesses its surface texture and chemical properties with tarsi and decide to bore or not. Finally, sensors at the tip of the aculeus send the last series of signals, allowing the female to reject the fruit or to accept it and lay eggs (Rice, 1989).

6. Phylogeny

Dacini is a tropical and subtropical evolutionary radiation of flies with centers of diversity in Southeast Asia and Sub-Saharan Africa. Early molecular phylogenetic studies focussed on pest species, often of a particular region, leading to biased results on the relationships between species that may not precisely reflect monophyletic origins or sister-group assignments (Smith et al., 2003; Nakahara and Muraji, 2008). Further phylogenetic studies molecular data resulted into splitting of large genus *Bactrocera* into *Bactrocera* and *Zeugodacus* (Krosch et al., 2012; Virgilio et al., 2015; San Jose et al., 2018). Besides, the Dacini taxa have been variably assigned to species complexes, species groups, subgenera and species-complex groups (Clarke et al., 2005; White, 2006; Drew and Romig, 2013). The largest and most intensively studied is the *Bactrocera dorsalis* complex with 88 species includes the largest number of pest species (Doorenweerd et al., 2018). This complex, like most others, is not monophyletic (Leblanc et al., 2015; Virgilio et al., 2015; San Jose et al., 2018). For Southeast Asian Dacini recent two-part work including a revision (Drew and Romig, 2013) and the accompanying keys

(Drew and Romig, 2016) are pertinent. For other regions, all treatments are older and with perplexity.

Phylogenetic studies on Dacini using morphological characters are few except for the work by White (1999), wherein 51 pest species were analysed using 38 morphological characters. His studies revealed *Monacrostichus* as a sister group to *Bactrocera* and *Dacus* as that of Drew and Hancock (1999). A subgeneric phylogeny of genus *Dacus* using morphological characters was provided by Hancock and Drew (2006). Phylogenetic studies on Dacini using molecular markers were explored by several researchers: Smith et al. (2002) confirmed the monophyly of *Dacus* and *Bactrocera*. Smith et al. (2003) also reported monophyly of *Bactrocera* and noted the paraphyletic status of *Zeugodacus* in their analysis. White (2006) also indicated a sister group relationship between *Zeugodacus* group and genus *Dacus*. Han and Ro (2009) reconfirmed monophyly of subfamily Dacinae using 12s, 16s and COII gene fragments. Asokan et al. (2011) and Yong et al. (2015) revealed monophyly of *Bactrocera* using COI and 13 protein coding genes, respectively.

Krosch et al. (2012) concluded that genus *Bactrocera* consists of 2 clades, *Bactrocera* s.s. and *Zeugodacus* group of subgenus. They considered *Zeugodacus* clade, a sister group of *Dacus* and recommended to raise subgenus *Zeugodacus* to genus level. Virgilio et al. (2015) raised the subgenus *Bactrocera* (*Zeugodacus*) to generic rank (*Zeugodacus* Hendel, stat. nov.) and placed all species of subgenus (*Zeugodacus*) in the genus *Zeugodacus*; however, they concluded that exact relationship between *Zeugodacus, Dacus and Bactrocera* still needs to be resolved. San Jose et al. (2018) also confirmed the monophyly of genera *Bactrocera*, *Dacus* and *Zeugodacus* based on 7 genes in 167 species of the tribe Dacini. David and Ramani (2019) analysed phylogenetic relationships between *Bactrocera*, *Dacus* and *Zeugodacus* from India based on morphological characters. Cladistic analysis revealed the monophyly of Dacini, *Bactrocera* and *Dacus* with supporting non-homplasious synapomorphies. *Zeugodacus* was retrieved as a monophyletic sister-group to *Dacus*.

7. Male Lures

Chemical cues and signals influence the behavior, physiology, and ecology of fruit flies and lures are used for surveillance, suppression, and ecological studies. Males of many dacine fruit flies are attracted to plant-derived secondary compounds termed male lures (Sivinski and Calkins, 1986). Howlett (1912) reported existence of fruit fly male lures in citronella (*Cymbopogon nardus*, Fam. Poaceae) oil. Howlett (1915) reported that the attractive component was phenyl proponoid methyl eugenol (ME) or 3-4 dimethoxy-1 allylbenzene and its effectiveness was rediscovered by Steiner (1952). Barthel et al. (1957) observed anisyl acetone or 4(p-methoxyphenyl)-2-butanone as an effective attractant for the melon fly. A derivative cue-lure (CL) or 4(p-acetoxyphenyl)-2-butanone was found to be more attractive to some dacine species (Beroza et al., 1960). Drew and Hooper (1981) reported that each dacine species responded only to one of these attractants and some species did not respond to either. However, several studies (Tan and Nishida, 1996; Tan et al., 2011) have demonstrated that certain male lures (e.g., methyl eugenol, raspberry ketone, and zingerone) are used in synthesizing male sex pheromones. ME is a widely distributed natural plant product that occurs in >450 plant species in 80 families found mainly in the tropics (Tan and Nishida, 2012). CL has not been isolated as a natural product but is rapidly hydrolyzed to form 4-(p-hydroxyphenyl)-2-butanone, rheosimin, or raspberry ketone (RK), a constituent of raspberries (*Rubus idaeus* and *R. strigosus*, Fam. Rosaceae) with a raspberry-like odour (Metcalf and Metcalf, 1992). RK was originally isolated from an orchid, *Dendrobium superbum* (Nishida et al., 1993).

Of the 86 Dacini species that are horticultural pests, 41 respond to CL/RK and 18 to ME (Dacine Fruit Flies of the Asia-Pacific website, 2012). Based on this attraction, detection and monitoring traps and the suppression/eradication technique called male annihilation technique (MAT) was developed using these chemicals. Vargas et al. (2014) summarized future trends for use of male lures (Figure 3), such as the use of reduced risk insecticides, new lures, lure mixtures, and new dispenser formulations.

Among Indian Dacini males of 47 species respond to cue-lure, 20 species to methyl eugenol, 6 species to zingerone while *B. latifrons* males to latilure (Table 1). These attractants are

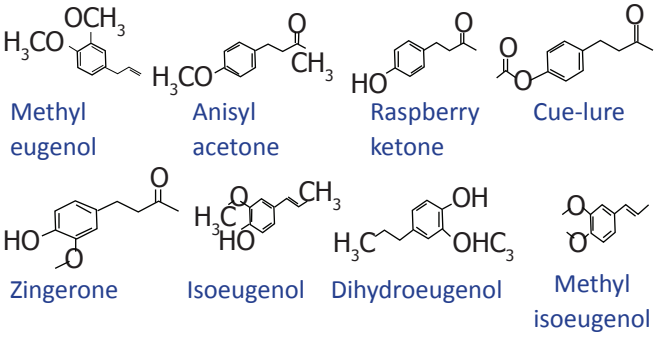

Figure 3: Male lures of fruit flies

also used in the surveillance system targeting more than one species at a time and are a powerful monitoring tool for the early detection of a species and population monitoring. Stringer et al. (2019) reported that in fruit fly management using various lure combinations reduces the cost of operation. Recently in Oceania and Asia, more attractive male lures (isoeugenol, methylisoeugenol, dihydroeugenol, and zingerone) were identified for several weakly CL- and methyl eugenol (ME) responsive species (Royer et al., 2019).

8. Bacterial Associations

Tephritid flies harbour communities of bacteria dominated by species of Enterobacteriaceae. These microbes are involved in

nitrogen fixation, reproductive success, temporal host range expansion, protection from pathogens and detoxification (Akami et al., 2019). Petri (1909) first observed symbiotic association with bacteria in olive fly, *B. oleae*. The attractancy of protein solutions containing bacteria to fruit flies was first reported by Gow (1954). Cultures of fruit fly type bacteria growing on peptone yeast extract agar (Drew et al., 1983) and hydrolyzed protein solutions inoculated with these bacteria are strong attractants for dacine species (Drew and Fay 1988). These bacteria provide nutrients for adult females and possibly larvae as a food substrate, olfactory cue to attract flies to the host plant, lure flies to the plant to ensure courtship and mating, and may play a role in the fly defense mechanisms against bacterial pathogens such as *Serratia* species. Krischik and Jones (1991) defined the bacteria associated with dacine fruit flies as insect mutualists, not symbionts and stated that the bacteria beneficially affect the capacity of the fly to explore the plant, and in turn the microorganism is affected by the insect-plant interaction.

In dacine flies bacterial mediation is hypothesized as being integral to the larval host plant being the 'centre of activity' of the fly (Raghu et al., 2002). The role of bacteria as a food source for adult fruit flies and how they affect their behaviour and fitness have been studied extensively by Drew et al., 1983; Drew and Lloyd, 1987, 1989, 1990; Drew, 1987 and by Fitt and O'Brien (1985), who reported that some bacteria found on ripening fruits also exist in the digestive tract of flies and that females transmit these bacteria to their offspring during oviposition. Gujjar et al. (2017) attempted to decipher the gender specificity of gut bacterial communities of two major fruit fly species of India and based on molecular identification, *B. dorsalis* females were found to predominantly harbor the bacterial species *Enterobacter cloacae, E. asburiae* and *Citrobacter freundii*, while *B. dorsalis* males were found to harbor *Providencia rettgerii, Klebsiella oxytoca, Enterococcus faecalis* and *Pseudomonas aeruginosa*. The cultivable diversity from females of *Z. cucurbitae* comprised mainly of *Morganella morganii* and *Bacillus pumilis* while *Z. cucurbitae* males were predominantly colonized by aerobic endospore formers, viz. *Bacillus cereus, B. licheniformis* and *B. subtilis*.

9. Conclusion

The Indian Dacini fauna comprises of 92 species belonging to 3 genera and 19 subgenera. Efforts are in vogue to manage dacine fruit flies by using male lures which have been found of profound significance in monitoring, suppression and population eradication programmes. However, there is ample scope for further researches to study the molecular characterization of Indian dacine flies and to discover new attractants, particularly for females. Efforts should also be made by quarantine authorities to remain aware so that invasive pest species may not enter in India.

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