

Phylogenetic relationships of native and introduced *Bemisia tabaci* (Homoptera: Aleyrodidae) from China and India based on mtCOI DNA sequencing and host plant comparisons*

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Abstract Phylogenetic relationships for *Bemisia tabaci* were reconstructed by analysis of a ~780 bp fragment of the mitochondrial cytochrome oxidase I (mtCOI) gene with an emphasis on geographic range and distribution among eight eudicot plant families that are common hosts of *B. tabaci* worldwide to elucidate key phylogeographic linkages between populations extant in China ($n=31$) and India ($n=34$). Bootstrap values for the Maximum Parsimony tree were highly robust for all major nodes involving the major Asian clade, subgroups and sister groups within, at 92%–100%. Between-clade distances for the Southeast Asia and three other major clades, e.g. from sub-Saharan Africa, North Africa-Mediterranean, and the Americas, were approximately > 16% divergent. Two major Asian subgroups (I, II) were resolved, which represented populations indigenous to the region, comprising two (Ia, Ib) and five (IIa–e) sister groups, respectively, which diverged by 11%. Two distinct populations from sunflower in Hyderabad grouped separately within the two Asian subgroups. All other populations grouped uniquely within Asian subgroup II or I. The “B” biotype was identified in 23 collections from China at 97.3%–99.5% nucleotide identity with “B” biotype reference sequences; it was not identified in collections from India. The majority of haplotypes were associated with 3–4 plant families, with one exception that for sister group II d (sesame, India), it might be monophagous. Thus, *B. tabaci* from the southeast and near eastern regions of the Asian continent comprise of a large number of ancestral, richly divergent, mostly polyphagous populations. This region is therefore hypothesized to constitute an important Old World center of diversification for the *B. tabaci* complex, together with sub-Saharan Africa.

Keywords: *Bemisia tabaci* complex, cytochrome oxidase I, host range, phylogenetic relationship.

The whitefly *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) complex^[1] represents a collection of biotic and genetically diverse variants that are agricultural pests and plant virus vectors in tropical and mild temperate regions^[1–6]. Certain populations are polyphagous, with some known to colonize up to several hundreds species^[2,7]. Other variants or biotypes are known that are host-specific or have a moderate to narrow host range^[1,6,8,9]. Although *B. tabaci* has been recognized as a pest and vector of plant viruses in the subtropics since the late 1800s, it has only recently become highly problematic, world widely^[2,6,9,10]. One reason for such increased importance has been the widespread practice of transporting whitefly-infested plants internationally. As pervasive a problem is the propensity of *B. tabaci* to develop resistance to insecticides^[11–13]. And, the increased practice of growing crops in

monoculture under irrigation to extend the growing season is likewise conducive to the development of large *B. tabaci* populations that cannot be controlled. Such outbreaks often lead to the emergence of new or previously unimportant plant viruses transmitted by *B. tabaci*, resulting in epidemics in a large number of cultivated species^[6,9,10].

B. tabaci is best described as a complex of morphologically indistinguishable variants that differ genetically and biologically, while retaining identical morphological characters, e.g. cryptic species^[1,9,12,14–31]. Thus, outbreaks caused by new or introduced variants are often not immediately recognized until populations have reached uncontrollable levels. Further, not all populations have the same propensity to achieve pest or vector status, nor has the biological basis for biotype variation been attributable to a defined population's genetic structure. As well, very little is known

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about the evolutionary origin or evolutionary history of biotypes of the *B. tabaci* complex.

Owing to its cryptic nature, molecular sequence analysis of the mitochondrial cytochrome oxidase I gene (mtCOI) has become recognized as one of the most useful molecular markers for differentiating *B. tabaci* populations and for identifying biotypes^[1, 9, 12, 22, 24, 25, 28, 31, 32].

A number of biotypes have now been characterized with respect to geographic distribution, host range or preferences, life history traits, virus transmission competency, and/or insecticide resistance^[1, 8, 9, 11, 12, 14–16, 19, 20, 22, 23, 25, 32, 33]. Among the best studied are the “A”, “B”^[32], *Jatropha*, *Sida*^[8], and “Q” biotypes^[22]. The B and Q biotypes have been transported by humans from their indigenous habitats and introduced into naive agroecosystems in which they have proven difficult to control^[12, 23, 25, 28]. They also both are polyphagous and highly fecund^[19, 22, 32, 34], and exhibit insecticide resistance^[11–13, 26, 34–36]. However, there remains a plethora of unstudied or poorly characterized variants worldwide and most have received little attention owing to their benign nature and an only recent interest in the population genetics of this insect.

Although *B. tabaci* indigenous to the Asian continent have not been well studied at the biotype level, population genetics data are beginning to suggest that *B. tabaci* populations can exhibit broad genetic variability^[25, 27–29, 37]. In China, *B. tabaci* was first identified in 1949^[38]. In the mid 1990s *B. tabaci* became a serious pest in the southern region of China. Shortly thereafter, outbreaks occurred in the middle, north, and northwest regions of the country that have been attributed to the invasion of the “B” biotype^[29, 39]. Likewise, in India, *B. tabaci* has been recognized since the 1940s as a pest and virus vector affecting cucurbits, composites, legumes (pulses), and cotton^[6, 10]. Although several *B. tabaci* variants from India have been studied in some detail^[19, 25, 40–42], little is known about the genetic structure or host-associations for the majority of indigenous populations there. However, the “B” biotype is known to occur in at least certain parts of India as a result of its introduction in 1999–2000^[43].

The aim of this study was to investigate the genetic diversity of *B. tabaci* throughout the Southeast Asian continent, with an emphasis on the region occupied collectively by China and India, and an emphasis on geographic range and distribution among eight eudicot plant families that are common hosts of *B. tabaci* worldwide^[2, 7]. The long-term goal is to elucidate key phylogeographic linkages both between populations extant to the Asian continent, and within major *B. tabaci* clades worldwide.

1 Materials and methods

1.1 Whitefly collections

Sixty-five populations of *B. tabaci* from China ($n=31$) and India ($n=34$) were examined. Populations from China were collected from 22 provinces during 2001–2004, and the populations of *B. tabaci* from India were collected from all the major regions of the country where *B. tabaci* occurred, representing diverse and distinctive climatic and flora characteristics. In India, whitefly collections were made during 1993–1994 by placing adult and immature instars separately into a vial containing 95% ethanol. The locations and host plants from which Chinese and Indian populations were collected are shown in Tables 1 and 2. Whiteflies collections from China were identified at Department of Entomology, South China Agricultural University, based on key morphological characteristics of pupae stage^[3]. Collections from India were identified at California State Department of Food and Agriculture, USA.

1.2 Analysis of mtCOI sequences from *B. tabaci*

Adult *B. tabaci* individuals were prepared, from which DNA was extracted and the PCR was carried out as described previously^[24, 44, 45]. PCR products were visualized under an ultraviolet light and samples that yielded a PCR product of the expected size of 820–850 bp.

The amplified DNA fragments were bi-directionally sequenced using an ABI Model 377 DNA sequencer, the mtCOI sequences were aligned manually using an overlap of 500–600 bases. A consensus sequence with at least >98%–100% identity was obtained among populations.

Table 1. Geographic origin (city, province), host plant, and GenBank accession numbers for *Bemisia tabaci* populations from China.

Geographic location	Host plant	Acronym	Accession No.
Danzhou, Hainan	Tomato	Danzhou tomato *	AY611642
Fuzhou, Fujian	Collard	Fuzhou collard *	AY686062
Guangzhou-1, Guangdong	Tomato	Guangzhou tomato *	AY686063
Guangzhou-2, Guangdong	Ornamental <i>Codiaeum variegatum</i>	Guangzhou ornamental	AY686064
Haidian, Beijing	Tomato	Haidian tomato *	AY686065
Hangzhou, Zhejiang	Eggplant	Hangzhou eggplant *	AY686066
Hefei, Anhui	Tomato	Hefei tomato *	AY686067
Heshan, Guangdong	Hibiscus	Heshan hibiscus *	AY686068
HongKong	Cucumber	Hong Kong cucumber *	AY686069
Kunming, Yunnan	Tomato	Kunming tomato *	AY686070
Macau	Hibiscus	Macau hibiscus *	AY686071
Meizhou, Guangdong	Tomato	Meizhou tomato	AY686072
Nanchang, Jiangxi	Eggplant	Nanchang eggplant *	AY686073
Nanning, Guangxi	Tomato	Nanning tomato *	AY686074
Nantou, Taiwan	Poinsettia	Nantou poinsettia	AY686075
Putuo, Shanghai	Hibiscus	Putuo hibiscus *	AY686076
Shixing, Guangdong	Weed, <i>Chenopodium album</i>	Shixing weed *	AY686077
Simao, Yunnan	Pumpkin	Simao pumpkin *	AY686078
Taifan, Shandong	Tomato	Taifan tomato *	AY686079
Tainan, Taiwan	Tomato	Tainan tomato *	AY686080
Taiyuan, Shanxi	Eggplant	Taiyuan eggplant *	AY686081
Urumchi, Xinjiang	Tomato	Urumchi tomato *	AY686082
Wengyuan, Guangdong	Pumpkin	Wengyuan pumpkin	AY686083
Xifan, Shaanxi	Tomato	Xifan tomato *	AY686084
Xiangtan, Hunan	Eggplant	Xiangtan eggplant	AY686085
Xinhui, Guangdong	Hibiscus	Xinhui hibiscus *	AY686086
Yangzhou-1, Jiangsu	Collard	Yangzhou collard *	AY686087
Yangzhou-2, Jiangsu	Cotton	Yangzhou cotton	AY686088
Yichang, Hubei	Hibiscus	Yichang hibiscus	AY686089
Zhengzhou, Henan	Tomato	Zhengzhou tomato *	AY686090
Zhongxian, Chongqing	Poinsettia	Zhongxian poinsettia	AY686091

The populations marked with * were identified to be B biotypes with COI sequencing

Table 2. Geographic origin (city, state), host plant, and acronym for *Bemisia tabaci* populations from India

Geographic origin	Host plant	Acronym	Accession No.
Ahmedabad, Gujarat	Squash	Ahmedabad squash	DQ116641
Bangalore, Karnataka	Potato	Bangalore potato	DQ116642
Bangalore, Karnataka	Solanum	Bangalore solanum	DQ116643
Coimbatore, Tamil Nadu	Eggplant	Coimbatore eggplant	DQ116644
Coimbatore, Tamil Nadu	Solanum	Coimbatore solanum	DQ116645
Coimbatore, Tamil Nadu	Soybean	Coimbatore soybean	DQ116646
Coimbatore, Tamil Nadu	Sunflower1	Coimbatore sunflower1	DQ116647
Coimbatore, Tamil Nadu	Sunflower2	Coimbatore sunflower2	DQ116648
Gandhinagar, Gujarat	Eggplant	Gandhinagar eggplant	DQ116649
Hyderabad, Andhra Pradesh	Cotton	Hyderabad cotton	DQ116650
Hyderabad, Andhra Pradesh	Eggplant	Hyderabad eggplant	DQ116651
Hyderabad, Andhra Pradesh	Solanum	Hyderabad solanum	DQ116652
Hyderabad, Andhra Pradesh	Sunflower1	Hyderabad sunflower1	DQ116653
Hyderabad, Andhra Pradesh	Sunflower2	Hyderabad sunflower2	DQ116654
Hyderabad, Andhra Pradesh	Sunflower3	Hyderabad sunflower3	DQ116655
Kerala	Eggplant	Kerala eggplant	DQ116656
Kerala	Sesame	Kerala sesame	DQ116657
Madras, Tamil Nadu	Croton	Madras croton	DQ116658
Madras, Tamil Nadu	Eggplant	Madras eggplant	DQ116659
Madras, Tamil Nadu	Ipomoea	Madras ipomoea	DQ116660
Madras, Tamil Nadu	Poinsettia	Madras poinsettia	DQ116661
Marathwada	Sunflower	Marathwada sunflower	DQ116662
New Delhi, New Delhi	Eggplant	New Delhi eggplant	DQ116663
New Delhi, New Delhi	Sunflower	New Delhi sunflower	DQ116664
New Delhi, New Delhi	Tobacco1	New Delhi tobacco1	DQ116665
New Delhi, New Delhi	Tobacco2	New Delhi tobacco2	DQ116666
New Delhi, New Delhi	Tomato	New Delhi tomato	DQ116667
Padappai, Tamil Nadu	Eggplant1	Padappai eggplant1	DQ116668
Parbhani, Tamil Nadu	Eggplant2	Padappai eggplant2	DQ116669
Sulkunte, Bangalore	Eggplant	Sulkunte eggplant	DQ116670
Thackary	Lantana1	Thackary lantana1	DQ116671
Thackary	Lantana2	Thackary lantana2	DQ116672
Thuckalay	Cassava	Thuckalay cassava	DQ116673
Trivandrum	<i>Jatropha</i> spp.	Trivandrum Jat	DQ133381

1.3 Phylogenetic analysis

The identity of the sequences was determined using Clustal W software^[45]. Phylogenetic analysis was carried out using maximum likelihood (ML) and parsimony (MP) options available in Phylogenetic Analysis Using Parsimony* (PAUP*), version 4.0 beta10b^[46]. A single most parsimonious tree was constructed using the heuristic search method and the tree-bisection-reconnection and random branch swapping options, for 1000 bootstrap replicates. Bootstrap values were calculated using the > 70% majority rule. Likelihood trees were established using default parameters in the general time reversible and gamma distribution options of the heuristic search method, and the SPR branch-swapping option^[39].

Reference mtCOI sequences for well-studied *B. tabaci* biotypes or haplotypes were obtained from the NCBI GenBank database. The geographic origin, haplotype/variant or biotype, eudicot host plant, acronym and the respective GenBank Accession number for reference sequences are shown in Table 3, with many being cited previously^[19, 25, 28, 30, 31]. The genus outgroups employed was *Trialeurodes vaporariorum* (West.) (GenBank Accession number AF342774).

2 Results

The mtCOI sequences of *B. tabaci* from China and India have been deposited in the GenBank database, and the information on collection sites, hosts, and accession numbers are shown in Tables 2 and 3. The phylogenetic relationships of *B. tabaci* haplotypes from China (13 populations) and India (23 populations) are shown on the maximum likelihood (ML) tree, in relation to one another and to reference mtCOI sequences for previously studied populations of *B. tabaci* (Fig. 1). Because the basal position was occupied by the outgroup genus *T. vaporariorum*, and field collections from China and India grouped within the large (albeit, diverse) monophyletic group containing only *B. tabaci*, field populations examined here were considered to be correctly identified as *B. tabaci*.

Table 3. Geographical location, host plant and GenBank accession numbers for reference *B. tabaci* mtCOI used in the analysis

Geographical location	Host plant	Acronym	Accession No.
Africa	Cassava	KAUcassava	DQ133374
Bolivia	Tomato	Bolivia99	DQ133370
India	Cassava	India cassava	AF418670
India	<i>Euphorbia</i>	India euphorbia	AF418664
Hainan, China	Cotton	HCChina	AF342777
India	Watermelon	IWIndia	AF110702
India	brinjal	India brinjal	AJ748359
Japan	Tomato	JWBJapan	AF246644
Culiacan, Mexico	Tomato	CULMexico	AY057125
Nepal	Watermelon	NEWNepal	AF342779
Pakistan	Cotton	PC91 Pak	AF342778
Pakistan	Cotton	PC92 Pak	AY057582
Pakistan	Cotton	PC95 Pak	AY057582
Puerto Rico	<i>Jatropha gossypifolia</i>	JatPR00	AF110705
Spain	Tomato	SP92tomato	DQ133377
Sudan	Cotton	SCSudan	AF110706
Turkey	Cotton	TCTurkey	AF342776
Phoenix, Arizona, USA	Cotton	AZA04	DQ133368
Phoenix, Arizona, USA	Cotton	AZA88	AY057112
Tucson, Arizona, USA	Poinsettia	AZB00	AY057123
Brawley, California, USA	Cotton	CAL-ABrawleeCA	AY057124
Gainesville, Florida, USA	<i>Solanum nigrum</i>	FCB Florida	AF246640

Because the parsimony and ML trees exhibited an overall similar topology, the ML tree was selected for presentation in this report (Fig. 1). Four major well-resolved and geographically-based *B. tabaci* clades are represented in the ML (Fig. 1) and MP (data not shown) trees (sequences were not included for the sub-Saharan region of Africa). These include three major *B. tabaci* clades representing populations from the Mediterranean-Middle East-North Africa, and the one including the B and Q biotypes (100% bootstrap), the Americas/Caribbean region (100% bootstrap), and two sister clades in Asia (92% bootstrap) (Fig. 1, bootstrap tree not shown).

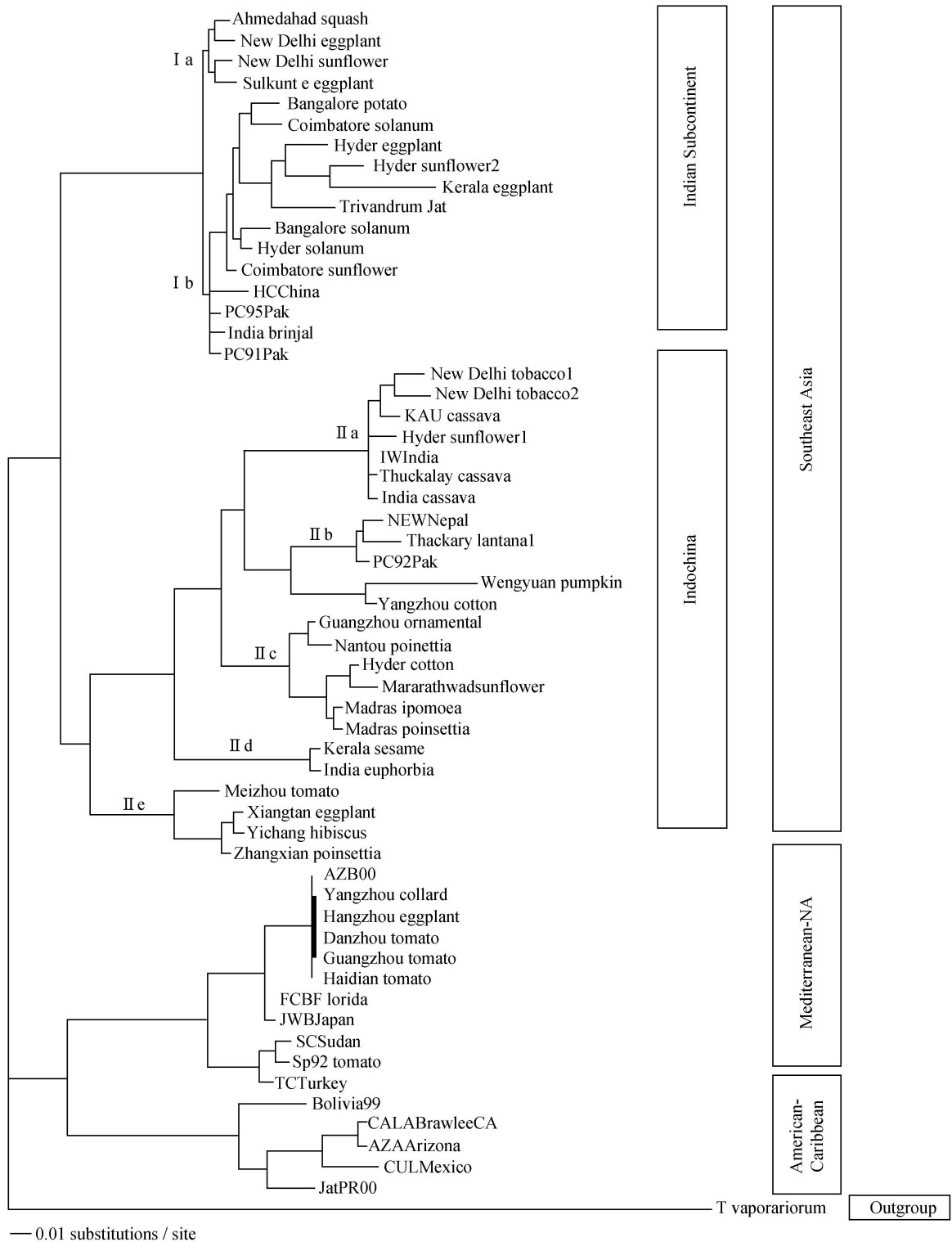


Fig. 1. Maximum likelihood tree for *Bemisia tabaci* from China and India based on the mtCOI DNA sequence and selected reference sequences for well characterized haplotypes/ biotypes are available in GenBank.

Among the Asian field populations, 23 of the 31 populations from China grouped in the “B” biotype clade (5 populations were selected for inclusion in the ML tree), at 97.3%–99.5% nucleotide identity^[24,31]. The “B” biotype was not identified in any collections from India, for they were the ones prior to the first reported introduction there.

The remainder of Asian populations from China and India clustered into two major sister clades (I, II), seven in subgroup I (Indian subcontinent) and five in subgroup II (Indochina) (Fig. 1). Both sister clades (I, II) and the subclades (Ia, b and IIa–e) were well supported by bootstraps of 99%–100%, respectively (data not shown). Thus, those populations in sister clades I and II were considered indigenous to the Asian continent. That those *B. tabaci* originating from the southern and eastern portions of the African continent were found to comprise seven discrete groups ranging from 79% to 90% shared nucleotide identity, and reflects a relatively high genetic variability (11% divergence). The Asian sister group I comprises two subgroups (a, b), the subgroup a contains populations from China, India, and Pakistan ($n=12$) with a within-clade divergence at 3%, and the subgroup b representing *B. tabaci* from India only ($n=13$) at about 6% within-clade divergence. These two groups diverged from one another at 6%–7%, roughly similar to the degree of divergence observed for the two major New World groups from North and Central America/Caribbean region and South America^[30].

Asian group Ib, which contained populations only from India, was the most genetically variable of the two, however, taxa were more narrowly distributed, compared to those in its sister group Ia, which represented populations native to both China and India. Even so, the Ia (wider distribution) and Ib (narrower distribution) subclades shared two eudicot families in common with respect to host range (Compositae, Solanaceae) (Table 4). However, members of sister group Ia also were uniquely recorded from cucurbits (Cucurbitaceae) and cotton (Malvaceae), whereas, Ib (India only) was uniquely identified from *Jatropha* spp. (Euphorbiaceae). And, one of two sunflower collections from Hyderabad, India was found to harbor a representative of each of the sister groups, revealing an example of haplotypes that are phylogenetically divergent, while also sharing with geographical and host associations.

Table 4. Asian subgroups and sister groups within-group shared nucleotide identity, and the eudicot host families colonized by *B. tabaci* field populations from China and India

Sister group (Geographic origin)	Number of populations (n)	Eudicot host family	Within-group nt identity (%)
Ia (China, India, Pakistan)	12	Asteraceae, Cucurbitaceae, Solanaceae, Malvaceae	95.5–98.5
Ib (India)	13	Asteraceae, Euphorbiaceae, Solanaceae	89.5–95.5
IIa (India)	6	Cucurbitaceae, Euphorbiaceae, Solanaceae	95.0–99.0
IIb (China, India, Nepal, Pakistan)	6	Cucurbitaceae, Malvaceae, Verbenaceae (<i>Lantana camara</i>)	94.0–97.0
IIc (China, India)	7	Compositae, Convolvulaceae, Euphorbiaceae, Malvaceae	96.0–98.5
IId (India)	1	<i>Sesamum indicum</i> (Pedaliaceae)	—
IIE (China)	4	Euphorbiaceae, Malvaceae, Solanaceae	95.5–99.0

The second main Asian sister group (II) was composed of at least five distinct subgroups, which diverged from one another by as much as 8% (nt identity 81.0%–89.0%), albeit, certain sister groups were less divergent in individual pair wise comparisons (Table 4). Within sister clade II, the subgroups IIa ($n=5$; 4% divergence) and IId ($n=1$) contained populations found only in India, while group IIE contained haplotypes only from China ($n=4$; 2%). In contrast, group IIb ($n=4$) was distributed more widely on the continent in that it was represented in India, Nepal, and Pakistan, but not in China (at 3% divergence). Group IIc was the only sister group II cluster to house representatives both from China and India. Interestingly, all of these populations were from mountainous provinces in China.

One population from sunflower 1 (Hyderabad) contained a mixture of two genotypes, with one genotype each grouping with one of the two major Asian groups.

A reference haplotype from Australia was an outlier to the Asian clade I, with which it diverged from all other *B. tabaci* from the Asian continent at 64.4%–71.8%.

3 Discussion

B. tabaci is best described as a cryptic species. Taxonomically, it is hypothesized to constitute a species complex or group, based on widespread evidence for biological and genetic variation among a number of distinctive populations, and the lack of corresponding morphological variation in fourth instar whiteflies^[4–6, 20, 25, 48–49]. Biological, biochemical, and molecular genetic analyses have distinguished a large number of polymorphic populations, or variants, presently assigned to the *B. tabaci* taxon. However, no detailed investigation has been undertaken to link diverse haplotypes to plant host range. This study focuses on *B. tabaci* populations from China and India (Southeast Asia), and is of great interest because they are poorly studied with respect to population variability, and these two regions have been implicated as possible evolutionary origins of *B. tabaci*^[2, 4, 5]. Herein, we report the first such an analysis for 65 *B. tabaci* collections (native and introduced) representing a large number of provinces and states in China and India respectively, and from plant hosts representing eight eudicot families containing plant genera and species known to serve as *B. tabaci* hosts worldwide: Asteraceae, Convolvulaceae, Cucurbitaceae, Euphorbiaceae, Malvaceae, Pedaliaceae, Solanaceae and Verbenaceae. Although the *B. tabaci* specimens were collected in China and India in 2001–2004 and 1993–1994, respectively, there might be some differences among the whitefly populations in each place, recent reports also indicated that their major divisions are still to be the native populations and exotic populations (such as B biotype), and the food habits of the whiteflies were stable since that one decade is a brevity comparing with the evolutionary history of *B. tabaci*^[9, 25, 29, 40–42].

The MP and ML trees revealed a broadly congruent topology, which was considered to be sufficiently robust based on the relatively high bootstrap values for all four major phylogeographical clades (Asia, North Africa-Mediterranean, the New World) and the large, diverse Asian clade (bootstraps at 92–100) (tree not shown) delineated here. A reference mtCOI sequence from Australia was included as the closest relative to *B. tabaci* apparently native to continental Asia.

The Australian population diverged at 64.4%–71.8% from the native Asian *B. tabaci* haplotypes,

suggesting that although it is the closest extant relative among collections available from SE Asia, the two are phylogeographically distinct. Excluding the Australian population, between-clade distances were similar for the SE Asian clade with respect to the three other major clades, e. g. sub-Sahara Africa, North Africa-Mediterranean, and Americas, each at about 16% interclade divergence^[25]. The *B. tabaci* complex extant to China and India represented minimally (2%) and moderately (11%) divergent (between-clade) groups. Certain of the haplotypes examined here were more tightly grouped with a basis in geography (e. g. India or China), whereas, other populations were distributed more widely on the continent (China, India, Nepal, Pakistan). The main groupings within the Asian clades I and II diverged at about 8%, which is approximately the same value as between subgroup differences for the two subgroups extant to the North Africa-Mediterranean region Africa^[31].

The within group divergence for the SE Asia clades (I, II) and sister-groups (I a, b and II a–e) ranged from 0.40% to 6.0%, suggesting that most groups are somewhat divergent from one another, and that owing to the moderate to high between-clade divergence estimates, it seems likely that gene flow between clades has been limited even for apparently sympatric populations. Nonetheless, it should be noted that no notable geographical or behavioral barriers have been identified for these populations that readily explain such restrictions.

It was not surprising to find that 23 of the 31 collections from China were identified as the exotic “B” biotype, given recent reports of its introduction in China. Fortunately a large number of samples appeared to represent *B. tabaci* populations that are native to China. That the “B” biotype was not identified among the collections from India can be explained by the timeframe during which collections were made e. g. 1993–1994, prior to the introduction of the “B” biotype there in about 1999–2000.

There is minimal evidence for definitive plant host-haplotype associations at the single family or genus levels (monophagy). This conclusion is based on the observation that the majority of *B. tabaci* haplotypes are associated with 3–4 plant families, with the exception of the clade II d haplotype, a single collection from sesame (*Sesamum indicum* Linn.) (Pedaliaceae) in Kerala, India. It is not known if the

sesame population from Kerala is monophagous given the small sample size. It is notable that the IIc sister group contained the colonizers of both *Ipomoea* (Convolvulaceae) and the Euphorbiaceae, albeit this sister group also colonized genera within the Compositae and Malvaceae. Whether there is a substantive link between the ability of *B. tabaci* in India to colonize *Ipomoea* and the observation that certain populations from the Americas and Africa (North Africa-Mediterranean and sub-Saharan Africa groups) also colonize sweet potato and its wild relatives is not known. Finally, the population colonizing sunflower 1 from Hyderabad, India (one of two sunflower collections from this location) were affiliated with separate subgroups (either I or II). Whether the two types are reproductively isolated even though they colonize the same host species is not known. The remaining sister groups contained haplotypes associated with some or all members of the seven families: Compositae, Cucurbitaceae, Euphorbiaceae, Malvaceae, Pedaliaceae, Solanaceae, and Verbenaceae (*Lantana camara* Linn.), which is more or less typical of *B. tabaci* in other locales. Specifically, these are common eudicot hosts of *B. tabaci* in the Americas (A biotype and close relatives), and for certain populations in northern Africa /Mediterranean region. It should be noted that the breadth of the host range for sub-Saharan African populations has not been sufficiently studied even though there is some conjecture for cassava-specific lineages.

The results of this study suggest that native *B. tabaci* extant in southeastern (China) and near-eastern (India, Nepal, Pakistan) of the Asian continent comprise a large number of richly divergent populations, particularly those aligning with subgroup II, making the region an important Old World center of diversification of the *B. tabaci* complex, together with sub-Saharan Africa^[3]. Further, despite the introduction of the B biotype in certain locations throughout the country (and later in India) did not appear to pose a serious threat to a number of native populations. This possibly suggests that they are often better adapted to the local environment than the arid land-adapted B biotype. Additional studies will be required to determine if the subcontinent does indeed harbor more variability than the southeastern section of the larger Asian continent. It is notable that data presented here indicate that at least two sister clades each contain populations exclusively from China or India/Pakistan/Nepal only, which supports

the notion that the southern and far eastern regions of the continent collectively constitute an important mainstay of genetic diversity for the Asian continent and possibly nearby smaller landmasses in the region. Extant *B. tabaci* might occur in this region owing to at least two radiations, with clade II haplotypes apparently representing the older of the two. Apparently, the Australian haplotype diverged prior to the split of clade I from II, the latter contains five divergent sister groups that are widely distributed geographically and by plant family. Thus, a substantial number of distinct haplotypes are indigenous to the Asian continent, with the variability distributed somewhat equally throughout much of the region.

The extent of indigenous diversity, together with at least one invasive haplotype/biotype (B) (Fig. 1) that may possibly be capable of genetic introgression, suggests that the *B. tabaci* complex is likely to continue to diversify in tropical and mild temperate Asia. It will likewise not be surprising to discover new biotypes in time, given rapidly changing practices in trade and agricultural production, which would be expected to select for populations more fit in these new environments. Further, these richly variable populations represent a plethora of diversity with the potential for dynamic evolutionary outcomes owing to the highly polyphagous nature of many populations in this species group. Thus, further study is expected to yield additional important insights into the origins and evolutionary history of the *B. tabaci* species complex or group.

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