

APHIDS AND THEIR HOST AFFINITY- II: *APHIS* SPP.

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Abstract: Host affinity of 608 species of *Aphis* was investigated based on information published in the literature. It was observed that 62.93% species were monophagous and out of these 40.68, 55.93, 3.15 and 0.24% species were affiliated to lignosae, herbaceae (dicotyledons), corolliferae (monocotyledon) and gymnosperms, respectively. When host affiliation was computed for all the species together a very similar picture emerged as in the case of monophagous species. Host preference in 4 *Aphis* species-groups based on molecular studies viz., *A. craccivora*, *A. fabae*, *A. gossypii* and *A. spiraecola* was compared, the different groups co-evolving with different host species within *Aphis* species-group. In general, it appears that large number of *Aphis* species is co-evolving with Rosaceae, Leguminosae, Euphorbiaceae, Asteraceae, Apiaceae, Lamiaceae and to some extent Liliaceae. Co-evolutionary linages were also evident and one or two lineages were common in all the 4 species groups.

Keywords: *Aphis* spp., Dicotyledons, Monocotyledons, Lignosae, Herbaceae, General Affiliation Index (GAI).

INTRODUCTION

Aphis is the largest aphid genus in the family Aphididae, and most of which occur in northern hemisphere [1]. Molecular study of Von Dehlen and Teulon [2] however, suggests that *Aphis* may have derived from an ancestor in the southern hemisphere. The genus is a species-rich group with 9 genera and 90% of the species are included in the subgenus *Aphis* [3, 4]. Taxonomy of the genus is highly complicated and several species grouped on the basis of morphological similarity [5, 6]. There are many notorious species of agricultural importance and has wide host range. In this section, we have tried to study host affinity of 608 species of this genus.

MATERIALS AND METHODS

The information on number of *Aphis* species and their host plants was mainly extracted from the publications of Blackman and Eastop [1, 4, 7]. Families of host plants were aligned in

Received Mar 21, 2017 * Published Apr 2, 2017 * www.ijset.net

different taxonomic groups following classification of Hutchinson [8] and other details are given in the Part I of the publication on Host Affinity in Aphids-I *Acyrtosiphon* spp.

RESULTS AND DISCUSSION

A general scanning of the results presented in Table 1 revealed that 413 species out of 608 were monophagous i.e. 62.93%. Out of these 168 (40.68%), 231 (55.93%), 13 (3.15%) and 1 (0.24%) were in lignosae, herbaceae in dicotyledons, corolliferae in monocotyledons and gymnosperms, respectively (Table 1). The maximum number of monophagous species harboured host species in the family Rosaceae (41), followed by Fabaceae (26), Euphorbiaceae (20), Verbenaceae (7), etc in lignosae, whereas the order of preference was Asteraceae (100), Apiaceae (27), Scrophulariaceae (18) and Lamiaceae (15) in herbaceae. In monocotyledons host species belonging to Corolliferae (13) were infested. Monophagous species encompassed host plants in 25 orders (32 families) in lignosae, 23 orders (31 families) in herbaceae, 5 orders (6 families) in Corolliferae and 1 order and family in Equisetaceae in gymnosperms. In all the divisions, host plants from primitive orders were exploited. This shows each *Aphis* species has special affinity with a taxonomic group of plants and co-evolving accordingly. Most of the monophagous species has GAI value around 1.000.

Table 1. Monophagous species of *Aphis* associated with different plant families and orders

Sl. No.	Order	Family	Name of <i>Aphis</i> species	Total no. of species
1.	Annonales (2)	Annonaceae	<i>A. sassceri</i>	1
2.	Rosales (6)	Rosaceae	<i>A. acaenaevora</i> , <i>A. acaenovinae</i> , <i>A. agrimoniae</i> , <i>A. agrimoniae</i> ssp. <i>ucrainica</i> , <i>A. alchemillae</i> , <i>A. cercocarpi</i> , <i>A. comari</i> , <i>A. dasiphorae</i> , <i>A. feminea</i> , <i>A. filipendulae</i> , <i>A. forbesi</i> , <i>A. grandis</i> , <i>A. grata</i> , <i>A. holodisci</i> , <i>A. ichigicola</i> , <i>A. ichigocola</i> , <i>A. kamtchatica</i> , <i>A. kogomecola</i> , <i>A. longicauda</i> , <i>A. marthae</i> , <i>A. minima</i> , <i>A. mongolica</i> , <i>A. mutini</i> , <i>A. neilliae</i> , <i>A. neospiraeae</i> , <i>A. naudicoda</i> , <i>A. potentillae</i> , <i>A. proffti</i> , <i>A. roepkei</i> , <i>A. rubicola</i> , <i>A. rubiradicis</i> , <i>A. sanguisorbae</i> , <i>A. sanguisorbicola</i> , <i>A. schuhi</i> , <i>A. soon</i> , <i>A. spiraephila</i> , <i>A. subviridis</i> , <i>A. tianschanica</i> , <i>A. tormentillae</i> , <i>A. ucrainensis</i> , <i>A. whiteshellensis</i> .	41
3.	Leguminales (7)	Fabaceae	<i>A. alhagii</i> , <i>A. astragalicola</i> , <i>A. astragalina</i> , <i>A. cicero</i> , <i>A. coronillae</i> ssp. <i>arenaria</i> , <i>A. craccivora</i> ssp. <i>canavaliae</i> , <i>A. craccivora</i> / <i>cyttisorum</i> group, <i>A. gallowayi</i> , <i>A. healyi</i> , <i>A. hedgsari</i> , <i>A. indigofera</i> , <i>A. klimeschi</i> , <i>A. laburni</i> , <i>A. lhasaensis</i> , <i>A. lotiradicis</i> , <i>A. lupinehansonii</i> , <i>A. lupine</i> , <i>A. oxytropiradicis</i> , <i>A. pawneepae</i> , <i>A. oxytropis</i> , <i>A. platylobii</i> , <i>A. pseudocomis</i> , <i>A. tacita</i> , <i>A. ulicis</i> , <i>A. vineti</i> , <i>A. yanbayaingana</i>	26
4.	Cunoniales (8)	Escalloniaceae Grossulariaceae Hydrangeaceae	<i>A. iteae</i> <i>A. atromaculata</i> , <i>A. manitobensis</i> , <i>A. popovi</i> , <i>A. schneideri</i> <i>A. philadelphia</i> , <i>A. philadelphicola</i> , <i>A. usigicola</i>	1 4 3
5.	Araliales (10)	Araliaceae Caprifoliaceae Cornaceae	<i>A. araliaeradicis</i> , <i>A. hederiphaga</i> , <i>A. kalopanacis</i> , <i>A. ponomarenkoi</i> <i>A. crassicauda</i> , <i>A. lantanae</i> ssp. <i>coriaria</i> , <i>A. viburniphila</i> , <i>A. xylostei</i> <i>A. callignosa</i> , <i>A. maculatae</i> , <i>A. neogillettei</i> , <i>A. nigratibialis</i>	4 4 4
6.	Urticales (19)	Cannabaceae Moraceae	<i>A. humuli</i> , <i>A. lupuli</i> , <i>A. sativae</i> <i>A. ficicola</i> , <i>A. kachkouli</i> , <i>A. mori</i>	3 3
7.	Salicales (12)	Salicaceae	<i>A. farinosa</i> , <i>A. farinosa</i> ssp. <i>yanagicola</i> , <i>A. maculata</i> , <i>A. roumanica</i>	4
8.	Bixales (20)	Cistaceae	<i>A. cliftonensis</i> , <i>A. fumanae</i> , <i>A. helianthemii</i> , <i>A. helianthemii</i> ssp. <i>thermophile</i> , <i>A. lupoi</i>	5
9.	Tamaricales (25)	Tamaricaceae	<i>A. ishkovi</i> , <i>A. viridissima</i>	2
10.	Violales (26)	Violaceae	<i>A. sumire</i> , <i>A. violae</i> , <i>A. violaeradicis</i>	3
11.	Cucurbitales	Cucurbitaceae	<i>A. ecaballii</i> , <i>A. roborum</i> ssp. <i>longisetosus</i>	2

	(30)			
12.	Malvales (33)	Malvaceae	<i>A. rostella</i>	1
13.	Malpighiales (34)	Linaceae	<i>A. lini</i> , <i>A. linorum</i>	2
14.	Euphorbiales (35)	Euphorbiaceae	<i>A. agrariae</i> , <i>A. brotericola</i> , <i>A. esulae</i> , <i>A. euphorbicola</i> , <i>A. gerardiana</i> , <i>A. glareosae</i> , <i>A. hillerislamberti</i> , <i>A. hispanica</i> , <i>A. myrsini</i> , <i>A. myrsinitidis</i> , <i>A. paludicola</i> , <i>A. propinqua</i> , <i>A. pseudeuphorbiae</i> , <i>A. pseudoeuphorbiae</i> , <i>A. pseudopaludicola</i> , <i>A. pseudopulchella</i> , <i>A. pulchella</i> , <i>A. sensoriata-euphorbiae</i> , <i>A. vallei</i>	20
15.	Ericales (38)	Ericaceae	<i>A. callunae</i> , <i>A. madronae</i> , <i>A. ramaudieri</i> , <i>A. uvaeursi</i>	4
16.	Guttiferales (39)	Clusiaceae	<i>A. hyperici</i> , <i>A. hypericiphaga</i> , <i>A. hypericiradicus</i> , <i>A. pavlovskii</i>	4
17.	Celastrales (41)	Cyrtillaceae	<i>A. nigra</i>	1
18.	Santalales (43)	Santalaceae	<i>A. neothesii</i> , <i>A. thesii</i>	2
19.	Rhamnales (44)	Rhamnaceae Vitaceae	<i>A. commensalis</i> , <i>A. exploratus</i> , <i>A. mammulata</i> , <i>A. utitis</i> <i>A. ripariae</i> , <i>A. vitis</i>	4 2
20.	Sapindales (49)	Aceraceae	<i>A. aceriella</i>	1
21.	Loganiales (50)	Oleaceae	<i>A. excelsioris</i>	1
22.	Apocynales (51)	Apocynaceae	<i>A. apocynicola</i> , <i>A. sycoangi</i>	2
23.	Lamiales (82)	Lamiaceae Myoporaceae	<i>A. agastachyos</i> , <i>A. incerta</i> , <i>A. lamiorum</i> , <i>A. lycopicola</i> , <i>A. mastichinae</i> , <i>A. narzikulovi</i> , <i>A. neomonardae</i> , <i>A. panzeriae</i> , <i>A. passeriniana</i> , <i>A. pulegii</i> , <i>A. sp. nr. clinepetae</i> , <i>A. sp. nr. serpylli</i> , <i>A. stachydis</i> , <i>A. tashevi</i> , <i>A. teucii</i> <i>A. myopori</i>	15 1
Total Herbaceae				231
1.	Liliales (95)	Liliaceae Smilacaceae	<i>A. antherici</i> , <i>A. coweni</i> , <i>A. liliophaga</i> , <i>A. ogilviei</i> , <i>A. takagii</i> , <i>A. veratrin</i> <i>A. smilacisina</i>	6 1
2.	Alstroemeriales (96)	Alstroemeriaceae	<i>A. alstroemeriae</i>	1
3.	Typhales (98)	Typhaceae	<i>A. typhae</i>	1
4.	Iridales (100)	Iridaceae	<i>A. neoneiotoni</i> , <i>A. newtoni</i>	2
5.	Orchidales (108)	Orchidaceae	<i>A. epipactis</i> , <i>A. orchidis</i>	2
Total monocot (Corolliferae)				13
1.	Equisetales	Equisetaceae	<i>A. equiseticola</i>	1
Total Gymnosperms				1
Grand Total				413

Numbers in parentheses indicate position of an order on evolutionary scale

When host affiliation of all the 608 species was computed, a very similar picture emerged as in case of monophagous species (Table 2). Dicotyledons harboured 94.48% host plants and herbaceae had 8.77% edge over lignosae. Rest shared by monocotyledons and others (gymnosperms). In dicotyledons, the similar percent of genera, families and orders gave to similar percent of host species. However, this trend was not followed by other host categories.

Table 2. Affinity of *Aphis* species to their host taxonomic groups

Parameters	Host plants						Total
	Dicotyledons		Monocotyledons			Others*	
	Lignosae	Herbaceae	Calyciferae	Corolliferae	Glumiflorae		
Species	2972 (42.85)	3580 (51.62)	47 (0.68)	222 (3.20)	81 (1.17)	33 (0.48)	6935
Genera	1666 (41.82)	2066 (51.86)	34 (0.85)	142 (3.56)	56 (1.41)	20 (0.50)	3984
Families	629 (43.29)	713 (49.07)	23 (1.58)	62 (4.27)	11 (0.76)	15 (1.03)	1453

Orders	528 (41.67)	637 (50.28)	17 (1.34)	60 (4.74)	11 (0.87)	14 (1.10)	1267
Total	5795 (42.49)	6996 (51.29)	121 (0.89)	486 (3.56)	159 (1.17)	82 (0.60)	13639

* Host-plants other than Angiosperms; Figures in parentheses are % values

Affinity to different taxonomic groups revealed that *Aphis* species alienated in greater numbers to Rosaceae (64, 10.53%) followed by Fabaceae (51, 8.39%), Euphorbiaceae (33, 5.43%) in lignosae. The similar trend was observed in monophagous species. In herbaceae group, Asteraceae (117, 19.29%), Apiaceae (54, 8.88%), Lamiaceae (43, 7.07%), Scrophulariaceae (33, 5.43%), Polygonaceae (29, 4.77%) and Ranunculaceae (23, 3.78%) contributed *Aphis* species. In monocots, Liliaceae (17, 2.80%) and Poaceae (9, 1.48%) shared some *Aphis* species. In gymnosperms (7, 1.15%) host sharing was observed. Aforesaid information, therefore, reveals that above families are of co-evolutionary significance in general. Nevertheless, individual species has its own preference and taxonomic affiliation.

To distinguish morphologically similar populations, taxonomist employ information obtained on life cycle and host plant relationships [9]. According to Guldmond and Mackenie [10] changes in life cycle and/or host relations acting as the primary isolating mechanism and trigger for speciation, rather for special isolation. Such crucial evidence that speciation process may operate has been provided by Hawthorne and Via [11]. Such types of groups have been recognized by Blackman and Eastop [12] in case of *Aphis fabae* complex (*A. fabae*, *A. solanella*, *A. fabaecirsiiacanthoides*, *A. euonymi*, *A. fabaemordvilkoii*) and others. Molecular study of Kim and Lee [13] showed four species- groups centered on *A. craccivora*, *A. fabae*, *A. gossypii* (= *A. frangule gossypii*) and *A. spiraeicola*. When authors compared the acceptance of host plants by different species-groups based on taxonomic classification, irrespective of primary hosts, was highly varied. For e.g., *A. craccivora* group comprised *A. craccivora*, *A. cracciae*, *A. coronille* and *A. cytisorum* as they are preferring host plants in family Fabaceae. We observed that in addition of the foregoing species *A. coronillae* ssp. *arenares*, *A. craccivora* ssp. *canavaleae* and *A. craccivora* ssp. *pseudocaciae* feed exclusively on Fabaceae. These species are showing strong affinity also to Fabaceae and may be co-evolving on it. However, *A. craccivora* is reported to feed on 696 host species from more than 70 families [4, 7]. Out of these 308 host species were from Fabaceae and 66 Asteraceae. It means *A. craccivora* is co-evolving with Fabaceae and Asteraceae.

In the fabae-group six species viz., *A. fabae*, *A. fukii*, *A. hederiae*, *A. neospiraeae*, *A. neotoni* and *A. rumicis* were in the same clade, appeared to be closely related and morphologically

very similar [13]. This species-group is molecularly similar by being in the same clade but vary in their host preference. *A. fabae* is highly polyphagous and invades 636 host species from more than 100 families though showing greater preference towards Asteraceae (233), Apiaceae (94) and Fabaceae (47). *A. fukii* is oligophagous and feeds on Asteraceae, *A. hederiae* and *A. rumicis* are also polyphagous. *A. hederiae* feeds on host plants from 7 families, both in dicots and monocots, whereas *A. rumicis* prefers hosts from Polygonaceae. *A. neotoni* and *A. neospiraeae* being monophagous infest plants from family Iridaceae (monocot) and Rosaceae (dicot), respectively. Species in fabae-group are morphologically similar, phylogenetically in the same clade but widely differing in their host preference.

A. gossypii species-group consisted of 10 species in the same clade viz., *A. gossypii*, *A. taraxacicola*, *A. egomae*, *A. clerodendri*, *A. sumiro*, *A. hypericephaga*, *A. ichigo*, *A. ichigocola*, *A. glycines* and *A. sanguisorbicola*. *A. gossypii* was sister to all the aforesaid species in the clade [13]. *A. gossypii* feeds on 1687 host species from 147 families with a greater preference to Asteraceae (263), Fabaceae (117), Malvaceae (85), Lamiaceae (83), Verbenaceae (53), Cucurbitaceae (37), Polygonaceae (33), Rosaceae (23) and so on. *A. glycines* loves feeding on Fabaceae and representatives of three other families. *A. sanguisorbicola*, *A. ichigocola* and *A. ichigo* prefer Rosaceae i.e. *Sanguisorba* spp. by *A. sanguisorbicola* and *Rubus* spp. by *A. ichigocola* and *A. ichigo*. The other 5 species *A. clerodendri*, *A. egomae*, *A. hypericephaga*, *A. sumeri* and *A. taraxacicola* prefer host species from Verbenaceae, Lamiaceae, Clusiaceae, Violaceae and Asteraceae, respectively. All the aforesaid *Aphis* spp. are congeneric, confamilial and conclave but their host preferences differ drastically. Host affinity appears to be species specific in most of the *Aphis* species in this group. Each species in this group shows some differences in colouration and host specificity [13]. Members of this monophyletic species-group may have adopted different host plants diverging from recent ancestor [13]. Vanlerberghe-Masutti and Chavigny [14] found certain RAPD bands that were fixed in population of *A. gossypii* collected from cucurbits and absent from those collected from non –cucurbit hosts, therefore, clustered in two groups according to host plants. Host association was also observed in glasshouse study where *A. gossypii* obtained from chrysanthemum did not colonize on cucurbits and vice-versa [15, 16].

Species-group consisting of *A. spiraeicola* and *A. kurosawai* is a sister group of *A. fabae*-group and both species share host plants such as Artemisia and Chrysanthemum in the family Asteraceae [17, 18]. According to Blackman and Eastop [1, 4], *A. spiraeicola* infests 676 host plants in 107 families and the important ones are viz., Asteraceae (159), Rosaceae (59),

Rubiaceae (37), Apiaceae (20), Fabaceae (17) and so on. Similarly, *A. kurosawai* feeds on 15 host plants from 3 families: Asteraceae (13), Ericaceae (1), Thymelaceae (1). It will be appropriate to say that first line of co-evolution in both the species is with Asteraceae. Nevertheless, *A. spiraecola* is simultinaceously co-evolving with other host taxa.

A. craccivora appeared to be closely related to the fabae - group and spiraecola- group as sister taxon in the clade in the molecular study [13] and, therefore, they considered (craccivora- group + fabae- group + spiraecola- group) as originating from different lineage of gossypii- group.

Species *A. oenotherae* and 4 distinct species viz., *A. crinosa*, *A. horii*, *A. nerii* and *A. farinosa* appear to be separated into two distinct lineages. Host plants of these *Aphis* species reported by Blackman and Eastop [1, 4, 7] also show that they greatly differ in their host affinity not only on conspecific or congeneric but drastically on confamilial levels also. But one thing is common that all the aforesaid species feed only on dicotyledonous plants except *A. nerii* on representatives of Liliaceae in monocotyledons. *A. oenotherae*, *A. nerii* and *A. horii* share plants both from lignosae and herbaceae, whereas *A. crinosa* and *A. farinosa* only from lignosae i.e. Caprifoliaceae and Salicaceae, respectively.

To compare the host affinity on evolutionary scale, an important representative of each *Aphis* species-group was selected and their host species were aligned with families and orders. In *A. craccivora* primitive order Delleniales gave rise to 3 orders- Rosales, Theales and Bixales.

Rosales stock contributed more plant species because of Fabaceae. On the other hand, host species were widely distributed in large number of families and orders in Bixale stock. The following potential lineages were observed

In lignosae:

1. Rosales—Leguminales=320 host species,
2. Tiliales—Malvales—Euphorbiales—Malpighiales—Rhamnales=56 host species.

In herbaceae:

1. Ranales—Caryophyllales—Polygonales— Chenopodiales =contributed 71 host species,
2. Ranales—Saxifragales—Solanales—Personales = 20 species,
3. Ranales—Rhoeadales—Brassicales—Resedales= 19 species.

In herbaceae, Asterales (Asteraceae) does not fit in any evolutionary lineage but contributed 66 host species indicating higher host affinity and independent evolution. In monocotyledons most of the host orders evolved from Liliales stock.

A. gossypii feeds on 9 host species from gymnosperms and 12 from 4 primitive orders (Laurales, Annonales, Delleniales, Coriariales) from the angiosperms. The prominent lineages were:

1. Rosales—Leguminales = contributed 163 host species,
2. Bixales—Tiliales—Malvales—Euphorbiales—Malpighiales—Rhamnales—Ebenales = 151 host species,
3. Bixales—Tiliales—Celastrales—Loganiales—Rubiales—Apocynales—Verbenales—Bignoniales = contributed 210 host species.

Here, Bixale stock contributed 2.4 times more host species than Rosales Stock. In herbaceae 8 lineages were observed but 4 of them were most prominent.

1. Ranales—Saxifragales—Campanales—Valerianales—Goodeniales—Asterales = contributed 298 host species,
2. Ranales—Saxifragales—Salanales—Personales = 158 host species,
3. Ranales—Geraniales--Polemoniales—Boraginales—Lamiales = 129 host species and
4. Ranales—Caryophyllales—Polygonales— Chenopodiales— Primulales—Plantaginales = 98 host species.

Primitive families like Ranunculaceae, Nymphaeaceae in order Ranales contributed plant species in the host range of this aphid.

In monocotyledons, Calyciferae, Corolliferae and Glumiflorae reported to have 23, 67 and 51 host species, respectively. The Commelinales stock possessed 23 host plants, whereas Liliales stock 118 host species indicating much greater affinity to host species in the later one.

Aphis fabae also reported to infest large number of host species. The evolutionary lineages in lignosae were:

1. Rosales—Leguminales = 72 host species,
2. Rosales—Cunoniales—Styracales— Araliales = 47 host species,
3. Bixales—Tiliales—Malvales—Euphorbiales—Malpighiales—Rhamnales = 24 host species and
4. Loganiales—Rubiales— Apocynales— Verbenales— Bignoniales = 41 host species.

This aphid feeds 3 primitive plant species in orders Magnoliales and Annonales. Bixale and Rosales stocks have similar number of host species but with slight edge in favour of Rosales. In herbaceae, feeding on host plants also starts from very primitive family in Ranales. The evolutionary lineages were:

1. Ranales—Saxifragales—Campanales—Valerianales— Asterales = 281 host species,

2. Ranales—Caryophyllales—Polygonales—Chenopodiales = 118 host species,
3. Ranales—Caryophyllales—Gentianales—Primulales—Plantaginales = 53 host species,
4. Ranales—Saxifragales—Umbellales = 111 host species and
5. Ranales—Saxifragales—Solanales—Personales = 75 host species.

Caryophyllales stock (in 2 and 3) contributed 146 host species. In monocotyledons, affinity to Calyciferae, Corolliferae and Glumiflorae host species were to the tune of 6, 55 and 8, respectively.

The 4th *Aphis* species-group representative *A. spiraecola* is a polyphagous species and feeds on host species belonging to several families and orders right from gymnosperms to most primitive families in angiosperms. It prefers plants both from Rosales and Bixales stocks in lignosae. The most contributing evolutionary lineages in lignosae are:

1. Rosales—Leguminales—Cunoniales—Araliales = 104 host species,
2. Bixales—Tiliales—Celastrales—Loganiales—Apocynales—Rubiales—Verbenales—Bignoniales = 86 host species,
3. Bixales—Tiliales—Malvales—Euphorbiales—Malpighiales—Rhamnales—Myrsinales—Ebenales = 42 host species.

In herbaceae, this aphid species was also feeding on primitive families like Paenoniaceae, Ranunculaceae, Berberidaceae, etc. and the most advanced like Asteraceae, Lamiaceae, etc.

The possible evolutionary lineages are:

1. Ranales—Saxifragales—Campanales—Asterales = 168 host species,
2. Ranales—Saxifragales—Solanales—Personales = 43 host species,

In monocot, Liliales stock contributed most of the species and in all the species-group one lineage is common i.e. from Bixale to Ebenales.

ACKNOWLEDGEMENTS

Authors are sincerely grateful to Mr. Akhilesh Rathore for providing all help in retrieving the information.

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