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Review Article

Galling Aphids (Hemiptera: Aphidoidea) in China: Diversity and Host Specificity

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Gall formation is an interesting plant response to aphid feeding. This paper presents a review of galling aphids in China. Altogether, 157 species and subspecies in ten families and subfamilies are found to induce galls on their host plants. As many as 39% species are endemic to China. The Eriosomatinae include the highest percentage of gall-inducing species. The great diversity of gall morphology may be described in terms of five characteristics: type, site, size, shape, and structure. The host association and host specificity of galling aphids are also discussed.

1. Introduction

Aphids (Hemiptera: Aphidoidea) are an important group of phloem-feeding insects that may limit plant productivity [1] and transmit plant viruses [2]. They feed from the phloem sieve elements by penetrating their slender stylets intercellularly during which specific plant responses are triggered [3, 4]. A remarkable and interesting plant response is the formation of galls. These atypical plant tissue growths, the result of interactions between the inducer and the plant [5], reflect the complex and intimate relationship between plants and insects. Galls provide abundant nutrition [6–11], a favorable microenvironment [6, 7, 12, 13], and protection against natural enemies [6, 7, 14] to the inducer and its offspring. They also mitigate clonal mixing and maintain the genetic integrity [15, 16]. Therefore, galling aphids have been viewed as a useful model system for studying herbivore-plant interactions. Approximately 10–20% of the 4,700 aphid species known worldwide can induce galls on their host plants [17]. Gall traits are important biological characteristics of galling aphids. The shape, structure, and site of galls are highly species specific [18]. Thus, galls are commonly regarded as the extended phenotype of aphids [19–21] and hence helpful for aphid identification and phylogenetic study.

A total of approximately 1,100 aphid species are now known from China, constituting at least 23% of the world's aphid fauna [22]. Studies of galling aphids in China focus primarily on the subfamilies Eriosomatinae and Hormaphidinae. Zhang et al. [23] and Chen and Qiao [24] systematically studied the diversity of the galls of these two subfamilies, respectively. The evolution of galls in the tribes Fordini and Pemphigini of Eriosomatinae was also discussed [10, 11]. In this paper, galling aphids in China are reviewed with special emphasis on the diversity of gall-inducing species and gall morphology. Host association and host specificity are also considered.

The aphid species information in this paper was obtained from the species records of specimens deposited in the National Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences, Beijing, China (NZMCAS) and identified by aphid taxonomists of our research group. The information about galls and host plants was taken from field collection records. The host plant species were identified by plant taxonomists of the Institute of Botany, Chinese Academy of Sciences and Beijing Forestry University.

The aphid classification system used in this paper follows G. Remaudière and M. Remaudière [25].

2. Galling Aphid Diversity

At present, approximately 157 species and subspecies (14% of the total number of Chinese aphid species) are known to induce galls on their specific host plants in China. They are restricted to ten families and subfamilies, that is, Adelgidae, Phylloxeridae, Eriosomatinae, Hormaphidinae, Aphidinae, Chaitophorinae, Mindarinae, Myzocallidinae, Phyllaphidinae, and Thelaxinae. Of these gall-inducing aphid species, 83 species belong to the subfamily Eriosomatinae, 37 to Aphidinae, and 19 to Hormaphidinae. The principal groups of galling aphids and the host plants bearing galls in China are listed in Table 1.

Out of these galling aphids, 61 species and subspecies are endemic to China, accounting for 39% of the total galling species. Endemic species, localities (province) where galls were collected, host plants bearing galls, and gall morphology are listed in Table 2.

3. Gall Morphological Diversity

3.1. Type. Aphids can induce both pseudogalls and true galls on their host plants. Pseudogalls are commonly found on leaves and appear as leaf folds, leaf rolls, leaf curls, or leaf blisters. In the subfamilies Aphidinae, Chaitophorinae, Mindarinae, Myzocallidinae, Phyllaphidinae, and Thelaxinae, only pseudogalls are produced. *Hyalopterus pruni* (Geoffroy) produces noticeable leaf-roll pseudogalls on *Prunus armeniaca* in the spring (Figure 1(n)). *Cryptosiphum artemisiae* Buckton causes leaves to swell and roll on *Artemisia* (Figure 1(o)). Different from pseudogalls, true galls are more diverse in shape, complex in structure, and not only located on the leaves. The Adelgidae and Phylloxeridae induce true galls on their host plants. In the Eriosomatinae and Hormaphidinae, both pseudogalls and true galls are formed. A species of Hormaphidinae, *Tuberaphis takenouchii* (Takahashi), forms broccoli-head-like galls on the twigs of *Styrax formosana*, found in Taiwan. However, its congeneric species *T. viscisucta* (Zhang), which occurs in Yunnan, feeds on the leaves of *Viscum album* and causes the leaf edges to curl downward.

3.2. Site. The fundatrix (the first spring generation that hatches from overwintering eggs) of each galling aphid species induces its gall at a specific site on a specific host [26]. Galls may occur on the leaf blade, the leaf vein, the petiole, the main axis of a compound leaf, twigs, branches, and roots. *Viteus vitifoliae* (Fitch) causes galls on grape leaves and gall-like swellings on grape roots. *Pemphigus bursarius* (Linnaeus) produces galls on the petioles of *Populus simonii* (Figure 1(e)). The galls of *Floraphis meitanensis* Tsai & Tang are located on the main axis of the compound leaf of *Rhus punjabensis* var. *sinica*. Among these galls, the leaf gall is the most common type.

The galling site is closely related to the sink strength of galls and therefore has important effects on the reproductive success of the fundatrix [18, 27–29]. Fundatrices compete for galling sites. Intraspecific fights have been reported in different aphid species [28, 30, 31]. Furthermore, one plant species can host several galling aphid species. These species coexist by attacking different organs of a single host plant. In China, *Distylium chinense* harbors at least four species of Hormaphidinae, that is, *Asiphonipponaphis vasigalla* Chen, Sorin & Qiao, *Neothoracaphis yanonis* (Matsumura), *Metanipponaphis* sp., and *Nipponaphis* sp.. They form specific galls on the leaf midrib (Figure 1(j)), the leaf blade (Figure 1(l)), the petiole (Figure 1(k)), and the twig (Figure 1(m)), respectively. This observation indicates an adaptive radiation of galling aphids that exploit different ecological niches within a host plant.

3.3. Size. Gall size is also highly variable. Some aphids make very small galls. For example, the galls of *Acanthochermes similiquercus* Jiang, Huang & Qiao (Figure 1(b)) are small bean sized. Each gall contains only one aphid. In contrast, some galls are extremely large. The galls of *Ceratoglyphina styracicola* (Takahashi) in Taiwan can reach a diameter of 9 cm and contain 100,000 aphids [32]. It is obvious that gall size is directly linked to aphid colony size. Like the galling site, size is also an important factor influencing the gall sink strength [18, 29]. The species of Hormaphidinae on *Distylium chinense* serve to illustrate this principle. Large galls of *Nipponaphis* sp. (Figure 1(m)) divert nutrients from neighboring shoots. The smaller galls of *Metanipponaphis* sp. (Figure 1(k)) divert nutrients only from neighboring leaves on the same shoot. The smallest galls of *Neothoracaphis yanonis* (Figure 1(l)) use only the leaf on which they are located.

3.4. Shape. The shapes of aphid galls vary and have been described as chilli-like, cockscomb-like, bag-like, spherical, cucumber-like, flower-like, boat-like, broccoli-head-like, banana-bundle-shaped, and so on. Gall shape is highly species specific. Galls produced by individuals of the same species are distinctively similar in shape [18]. *Chaetogeoica foliodentata* (Tao) produces cockscomb-like galls on *Pistacia weinmannifolia* (Figure 1(h)). *Epipemphigus imaicus* (Cholodkovsky) forms silkworm-like galls on *Populus cathayana* (Figure 1(d)). Different species induces different shaped galls even on the same organ of the same host plant. On the leaves of *Distylium chinense*, for example, *Asiphonipponaphis vasigalla* forms vase-shaped galls (Figure 1(j)), whereas the galls of *Neothoracaphis yanonis* are spherical with a pointed bottom and protrude from both sides of the leaves (Figure 1(l)). This observation suggests that gall shape is determined by the aphids rather than by the plants and gall is an extended phenotype of the aphids [20]. Fundatrix behavior during gall initiation is assumed to play a decisive role in regulating gall shape, especially complex and peculiar shapes [18, 29].

3.5. Structure. Based on the number of cavities, galls can be divided into single-cavity and multiple-cavity types. The single-cavity gall is the simplest and most common type of aphid gall. The multiple-cavity gall is composed of

Table 1: Taxonomy of galling aphids and host plants bearing galls in China.

Family	Subfamily/tribe	Genera	Host plants
Adelgidae		*Adelges*, *Pineus*	*Picea*
Phylloxeridae		*Acanthochermes*	*Quercus*
		Viteus	*Vitis*
Aphididae	Eriosomatinae		
	Eriosomatini	*Aphidounguis*, *Colopha*, *Eriosoma*, *Kaltenbachiella*, *Tetraneura*	*Ulmus*
	Fordini	*Aploneura*, *Baizongia*, *Chaetogeoica*, *Forda*, *Namaforda*, *Smynthurodes*	*Pistacia*
		Floraphis, *Kaburagia*, *Meitanaphis*, *Nurudea*, *Schlechtendalia*	*Rhus*
	Pemphigini	*Epipemphigus*, *Pachypappa*, *Pachypappella*, *Pemphigus*, *Thecabius*	*Populus*
		Prociphilus	Caprifoliaceae, Oleaceae, Rosaceae
	Hormaphidinae		
	Cerataphidini	*Aleurodaphis*	*Sinojackia*
		Astegopteryx, *Cerataphis*, *Ceratoglyphina*, *Ceratovacuna*, *Ktenopteryx*, *Pseudoregma*	*Styrax*
		Tuberaphis	*Styrax*, *Viscum*
	Hormaphidini	*Hamamelistes*	*Betula*
	Nipponaphidini	*Asiphonipponaphis*, *Metanipponaphis*, *Neothoracaphis*, *Nipponaphis*	*Distylium*
	Aphidinae		
	Aphidini	*Aphis*	Malvaceae, *Prunus*
		Cryptosiphum	*Artemisia*
		Hyalopterus	Rosaceae
	Macrosiphini	*Cryptaphis*	*Geranium*
		Cryptomyzus, *Hyperomyzus*	*Ribes*
		Diuraphis	Pooideae
		Dysaphis, *Myzus*, *Ovatus*, *Sappaphis*, *Sorbaphis*, *Tuberocephalus*	Rosaceae
		Hayhurstia	*Chenopodium*
		Lipaphis	Cruciferae
		Neorhopalomyzus	*Lonicera*
		Rhopalosiphoninus	*Deutzia*, *Syringa*
		Semiaphis	*Lonicera*, Umbelliferae
	Chaitophorinae	*Chaitophorus*	*Populus*
		Periphyllus	*Acer*, *Aesculus*, *Koelreuteria*
	Mindarinae	*Mindarus*	*Abies*
	Myzocallidinae	*Tinocallis*	*Sapindus*, *Lagerstroemia*
	Phyllaphidinae	*Phyllaphis*	*Fagus*
	Thelaxinae	*Kurisakia*	*Quercus*

Table 2: Endemic galling aphid species in China.

Species	Distribution	Host plants bearing galls	Gall morphology
Adelgidae			
Adelges (Gilletteella) glandulae (Zhang)	Sichuan, Yunnan	*Picea brachytyla*, *P. likiangensis*, *P. likiangensis* var. *balfouriana*, *P. purpurea*	Leaf gall, cone-like, multiple-cavity, without associated needles [33].
Adelges (Sacchiphantes) roseigallis (Li & Tsai)	Gansu	*Picea asperata*, *P. crassifolia*	Leaf gall, cone-like [34].
Pineus (Pineus) armandicola Zhang, Zhong & Zhang	Yunnan	*Picea likiangensis*	Leaf gall, cone-like or torch-like, multiple-cavity [35].
Pineus (Pineus) sichunanus Zhang	Sichuan, Yunnan	*Picea brachytyla*, *P. likiangensis*, *P. likiangensis* var. *balfouriana*, *P. purpurea*	Leaf gall, broom-like or torch-like, multiple-cavity [33].
Phylloxeridae			
Acanthochermes similiquercus Jiang, Huang & Qiao	Sichuan	*Quercus* sp.	Small spherical gall on the leaf with an opening on the lower surface [36].
Eriosomatinae Eriosomatini			
Eriosoma cerum Zhang	Beijing, Hebei, Inner Mongolia	*Ulmus pumila*	Leaf edge curls downward [37].
Eriosoma fukangense Zhang	Xinjiang	*Ulmus pumila*	Leaf rolls, screw-like [37].
Eriosoma multilocularis Zhang & Zhang	Beijing, Hebei	*Ulmus pumila*	Multiple-cavity gall on the underside of leaves, with longitudinal ridges on lateral sides [38].
Eriosoma spirifolium Zhang	Xinjiang	*Ulmus pumila*	Leaf curls, spiral-shaped [37].
Eriosoma togrogum Zhang	Inner Mongolia, Shaanxi	*Ulmus pumila*	Leaf pseudogall [39].
Eriosoma ulmipumilicola Zhang & Zhang	Hebei	*Ulmus pumila*	Leaf rolls and swellings [37].
Eriosoma usuense Zhang & Qiao	Xinjiang	*Ulmus pumila*	Leaf spirally twisted [37].
Kaltenbachiella glabra Akimoto	Taiwan	*Ulmus uyematsui*	Almost globular gall, without hairs, arising upward from the midrib of leaves [40].
Tetraneura (Indotetraneura) asymmachia Zhang & Zhang	Liaoning	*Ulmus parvifolia*, *U. pumila*	Leaf gall, irregular pouch-like, stalked, smooth, with secondary exit laterally [37].
Tetraneura (Tetraneura) aequiunguis Zhang & Zhang	Inner Mongolia, Shandong	*Ulmus* sp.	Leaf gall [41].
Tetraneura (Tetraneura) persicina Zhang & Zhang	Liaoning, Shandong	*Ulmus pumila*	Leaf gall, peach-shaped, stalked [37].
Tetraneura (Tetraneura) triangula Zhang & Zhang	Hebei, Shandong, Tianjin	*Ulmus pumila*	Irregular-shaped gall on the upper side of leaves [37].
Tetraneura (Tetraneura) ulmicema Zhang	Ningxia	*Ulmus glabra*	Leaf gall, smooth, without hairs [37].
Eriosomatinae Fordini			
Chaetogeoica foliodentata (Tao)	Jiangsu, Shaanxi, Shandong, Sichuan, Yunnan, Zhejiang	*Pistacia chinensis*, *P. weinmannifolia*	Cockscomb-like gall, arising from the midrib on the upper surface of leaves [37].
Chaetogeoica ovagalla (Zhang)	Shandong	*Pistacia chinensis*	Elongate oval gall, arising from the midrib of leaves [42].

Table 2: Continued.

Species	Distribution	Host plants bearing galls	Gall morphology
Chaetogeoica sensucopia (Zhang)	Shandong	*Pistacia chinensis*	Small elongate oval gall, arising from the midrib of leaves [42].
Chaetogeoica ulmidrupa Zhang	Shandong	*Pistacia aculeata*	Dimidiate gall, with a longitudinal ridge [43].
Chaetogeoica yunlongensis (Zhang & Zhong)	Shaanxi, Yunnan	*Pistacia chinensis*	Cucumber-shaped gall, arising from the midrib of leaves [42].
Floraphis choui Xiang	Shaanxi	*Rhus potaninii*	Gall produced on leaflets, branched with every branch obconical [44].
Floraphis meitanensis Tsai & Tang	Guizhou, Hunan, Sichuan	*Rhus punjabensis* var. *sinica*	Gall produced on the main axis of a compound leaf, flattened, branched from base [37, 45].
Kaburagia rhusicola ensigallis (Tsai & Tang)	Guizhou, Hubei, Hunan, Sichuan	*Rhus punjabensis* var. *sinica*	Elongate jujube-like gall, with a pointed tip, arising from the main vein or secondary vein on the base of leaves [37].
Kaburagia rhusicola ovatirhusicola Xiang	Hubei, Shaanxi, Yunnan	*Rhus potaninii*	Gall obovate, outer surface with prominent net-like veins, produced on leaflet [44].
Kaburagia rhusicola ovogallis (Tsai & Tang)	Guizhou, Hubei, Hunan, Sichuan	*Rhus chinensis*, *R. punjabensis* var. *sinica*	Gall ovate, tip rounded, with short hairs, arising from the secondary vein on the base of leaves [37].
Meitanaphis elongallis Tsai & Tang	Guizhou, Hubei, Hunan	*Rhus punjabensis* var. *sinica*	Gall jujube-like, outer surface with many fine longitudinal ridges, arising from the midrib on the lower surface of leaves [37, 45].
Schlechtendalia peitan (Tsai & Tang)	Guizhou, Hunan, Sichuan	*Rhus chinensis*, *R. chinensis* var. *roxburghii*, *R. punjabensis* var. *sinica*	Gall ovate, somewhat flattened, with short soft hairs, arising from the secondary vein on the base of leaves [37].
Eriosomatinae Pemphigini			
Epipemphigus chomoensis (Zhang)	Tibet	*Populus* sp.	Gall cockscomb-like, outer surface uneven with 3 small protuberances, situated along the midrib on the upper surface of leaves, with a primary exit on the lower surface [46].
Epipemphigus yunnanensis (Zhang)	Guizhou, Yunnan	*Populus bonatii*, *P. cathayana*, *P. yunnanensis*	Gall cockscomb-like, outer surface uneven with 3–5 acute angled protuberances, situated along the midrib on the upper surface of leaves, with a primary exit on the lower surface [46].
Pachypappella aliquipila Zhang	Hebei	*Populus* sp.	Leaf folds [37].
Pemphigus circellatus Zhang & Zhong	Yunnan	*Populus tremula* var. *davidiana*, *P. yunnanensis*	Big opened gall on the branch [47].
Pemphigus cylindricus Zhang	Tibet	*Populus* sp.	Cylinder-shaped leaf gall [48].
Pemphigus mangkamensis Zhang	Tibet	*Populus* sp.	Cockscomb-like gall on the upper side of leaves [48].
Pemphigus sinobursarius Zhang	Heilongjiang, Inner Mongolia, Liaoning, Ningxia, Yunnan	*Populus cathayana*, *P. euphratica*, *P. simonii*	Round pouch-like gall, arising from the base of midrib on the under surface of leaves [46].

Table 2: Continued.

Species	Distribution	Host plants bearing galls	Gall morphology
Pemphigus tibetensis Zhang	Beijing, Gansu, Hebei, Tibet, Xinjiang	*Populus cathayana*	Pomegranate-like gall, with thick wall and a primary exit, produced on the twig [46].
Pemphigus turritus Zhang	Gansu	*Populus purdomii*	Sharp chilli-like or sharp horn-like gall, arising from the midrib on the upper surface of leaves, with a primary exit on the lower surface [37, 49].
Pemphigus wuduensis Zhang	Gansu	*Populus purdomii*	Flattened globular gall, arising from the base of midrib on the upper surface of leaves, with a secondary exit [37, 49].
Pemphigus yangcola Zhang	Yunnan	*Populus yunnanensis*	Semispherical gall on the twig, smooth, with primary exit [46].
Prociphilus (Prociphilus) gambosae Zhang & Zhang	Hebei	*Syringa oblata*	Leaf curls [50].
Prociphilus (Prociphilus) ligustrifoliae (Tseng & Tao)	Guizhou, Shaanxi, Sichuan, Yunnan	*Ligustrum japonicum*, *L. lucidum*	Leaf curls [51].
Thecabius (Oothecabius) sequelus Zhang	Hebei, Xinjiang	*Populus simonii*	Leaf folds and swellings along the midrib, dumpling-shaped [52].
Thecabius (Parathecabius) zhongi Zhang	Gansu	*Populus cathayana*	Dumpling-shaped pseudogall, formed by folding of the two halves of a leaf together [52].
Thecabius (Thecabius) beijingensis Zhang	Beijing, Hebei, Heilongjiang, Liaoning, Shanxi	*Populus beijingensis*, *P. cathayana*, *P. koreana*	Leaf folds and rolls up along the midrib, forming a swollen sausage-shaped pseudogall [52].
Hormaphidinae			
Aleurodaphis sinojackiae Qiao & Jiang	Jiangsu, Zhejiang	*Sinojackia xylocarpa*	Leaf curls, boat-shaped [53].
Asiphonipponaphis vasigalla Chen, Sorin & Qiao	Hunan	*Distylium chinense*	Vase-shaped gall, arising from or near the midrib on the upper surface of leaves, with a flower-shaped opening at the tip when mature [54].
Cerataphis jamuritsu (Takahashi)	Hong Kong, Taiwan	*Styrax suberifolia*	Large bell-shaped gall on the branch, covered with much white wax [55].
Hamamelistes similibetulae (Qiao & Zhang)	Tibet	*Betula albosinensis*	Small conical gall on the upper side of leaves [56].
Ktenopteryx eosocallis Qiao & Zhang	Fujian, Guangxi	*Styrax odoratissima*	Leaf deformation [57].
Tuberaphis cymigalla (Qiao & Zhang)	Fujian	*Distylium racemosum* (unlikely, requiring further confirmation)	Branched gall on the twig [58].
Tuberaphis viscisucta (Zhang)	Yunnan	*Viscum album*	Leaf curls [59].
Aphidinae			
Cryptosiphum artemisiae linanense Zhang	Gansu, Hebei, Heilongjiang, Jilin, Liaoning, Zhejiang	*Artemisia argyi*, *A. atrovirens*, *A. mongolica*, *A. selengensis*	Leaf rolls, fist-like [60].
Cryptosiphum atriplicivorum Zhang	Gansu	*Artemisia* sp.	Leaf rolls and swellings [39].
Neorhopalomyzus lonicerisuctus Zhang, Zhong & Zhang	Sichuan, Yunnan	*Lonicera* sp.	Leaf curls [61].

Table 2: Continued.

Species	Distribution	Host plants bearing galls	Gall morphology
Sappaphis dipirivora Zhang	Beijing	*Pyrus* sp.	Leaf rolls and swellings [62].
Sappaphis sinipiricola Zhang	Hebei, Henan	*Pyrus betulaefolia*	Leaf rolls [62].
Tuberocephalus (Trichosiphoniella) tianmushanensis Zhang	Beijing, Zhejiang	*Prunus pauciflora*	Leaf curls, cylinder-shaped [60].
Tuberocephalus (Trichosiphoniella) tuberculus Su, Jiang & Qiao	Sichuan	An unidentified species of Rosaceae	Pseudogall along the lateral vein of young leaves [63].
Chaitophorinae			
Periphyllus acerihabitans Zhang	Jiangsu, Zhejiang	*Acer buergerianum*	Leaf curls [64].

several subgalls with more complex ontogeny and structure [24, 65]. The Adelgidae and many galling species in the tribe Cerataphidini of Hormaphidinae produce multiple-cavity galls (see [65]). The pineapple-like galls of *Adelges* sp. (Figure 1(a)) are formed from spruce buds in which the developing leaves enlarge laterally and the margins merge into each other, forming multiple chambers within which the aphids feed [66]. Galls can also be categorized into two types of structure: closed and open. Some galls are initially closed and do not open until maturity. However, other galls remain open during their entire period of development. True galls include both closed and open types. In Shandong, the galls of *Tetraneura (Tetraneurella) nigriabdominalis* (Sasaki) (Figure 1(c)) are closed from early May through early June and then split laterally. From these slits, the alatae leave the gall to found colonies on the roots of Gramineae. However, the galls of *Pemphigus bursarius* have a natural lateral opening over an extended period from late May through September (Figure 1(e)). In contrast, pseudogalls are generally open and relatively simple in structure. On *Populus ussuriensis*, *Thecabius* (*Oothecabius*) *populi* (Tao) causes the leaves to fold downward, forming open dumpling-shaped pseudogalls (Figure 1(g)).

Gall shape and structure are closely related to gall fitness, the number of offspring produced within a gall. Together with gall size, gall shape and structure determine the inner surface area of the gall, the most accurate and practical measure of gall fitness [67]. The inner surface area determines the feeding area available to the nymphs within the gall and is thus correlated with the aphid colony size. It would be interesting to investigate the possibility that aphid galls tend to be more complex in shape and structure (e.g., multiple-cavity galls) to support larger colonies.

Aphid galls show great diversity of type, site, size, shape, and structure. However, these gall traits are also highly species specific. Therefore, they help to identify species, especially species that are difficult to distinguish morphologically [68]. Knowledge of the evolutionary driving forces behind the divergence of gall morphology is limited. Natural enemies [6, 7, 14, 21], competition for galling sites [26], and increasing sink strength [8, 10, 11] might have influenced the divergence of gall traits. The great variety of galls is hypothesized to be related to aphid adaptive radiation [5, 69]. Several case studies of selected aphid groups have been conducted to investigate how gall diversification has influenced aphid speciation. The gall-inducing aphid group Fordini is supposed to have radiated primarily by using different sites on the same plant organ and by enlarging the gall size [8, 10]. Its sister group, the gall-inducing Pemphigini, is assumed to have diversified by attacking different plant organs [11].

4. Host Association and Host Specificity

Gall-bearing host plants are richly abundant in China. These gall-bearing plants belong to at least 64 genera and 27 families. The common gall-bearing plants include *Picea*, *Ulmus*, *Populus*, *Styrax*, and *Distylium* (Table 1). Gall-inducing aphids are generally heteroecious, alternate between primary host plants (woody), where galls are produced and the sexual phase of life cycle is completed, and secondary host plants (herbaceous) where only parthenogenetic generations occur. Some aphids, however, are capable of inducing galls on secondary host plants, for example, *Hamamelistes similibetulae* on *Betula albosinensis* and *Cryptosiphum artemisiae* on *Artemisia*.

Galling aphids are strictly associated with their primary hosts. The host specificity is well defined and represented particularly in the Adelgidae, Eriosomatinae, and Hormaphidinae (Table 1). The pattern of host association differs among aphid lineages. The Adelgidae are restricted to *Picea* (Pinaceae). The subfamily Eriosomatinae includes three host-specific tribes: Eriosomatini on *Ulmus* (Ulmaceae), Fordini on *Pistacia* and *Rhus* (Anacardiaceae) (Fordina on *Pistacia*, Melaphidina on *Rhus*, resp.), and Pemphigini on *Populus* (Salicaceae). The Hormaphidinae include three tribes: Cerataphidini on *Styrax* (Styracaceae), Hormaphidini on *Hamamelis* (Hamamelidaceae), and Nipponaphidini on *Distylium* (Hamamelidaceae). But the galling species of Hormaphidini in China are restricted to their secondary host *Betula* (Betulaceae) owing to the absence of primary host in their distribution areas. In Aphidinae, the association is not so rigid. Most gall-inducing species are primarily associated with Rosaceae. Some other remotely related plant species, such as *Lonicera* (Caprifoliaceae) and *Ribes* (Saxifragaceae), are also occupied.

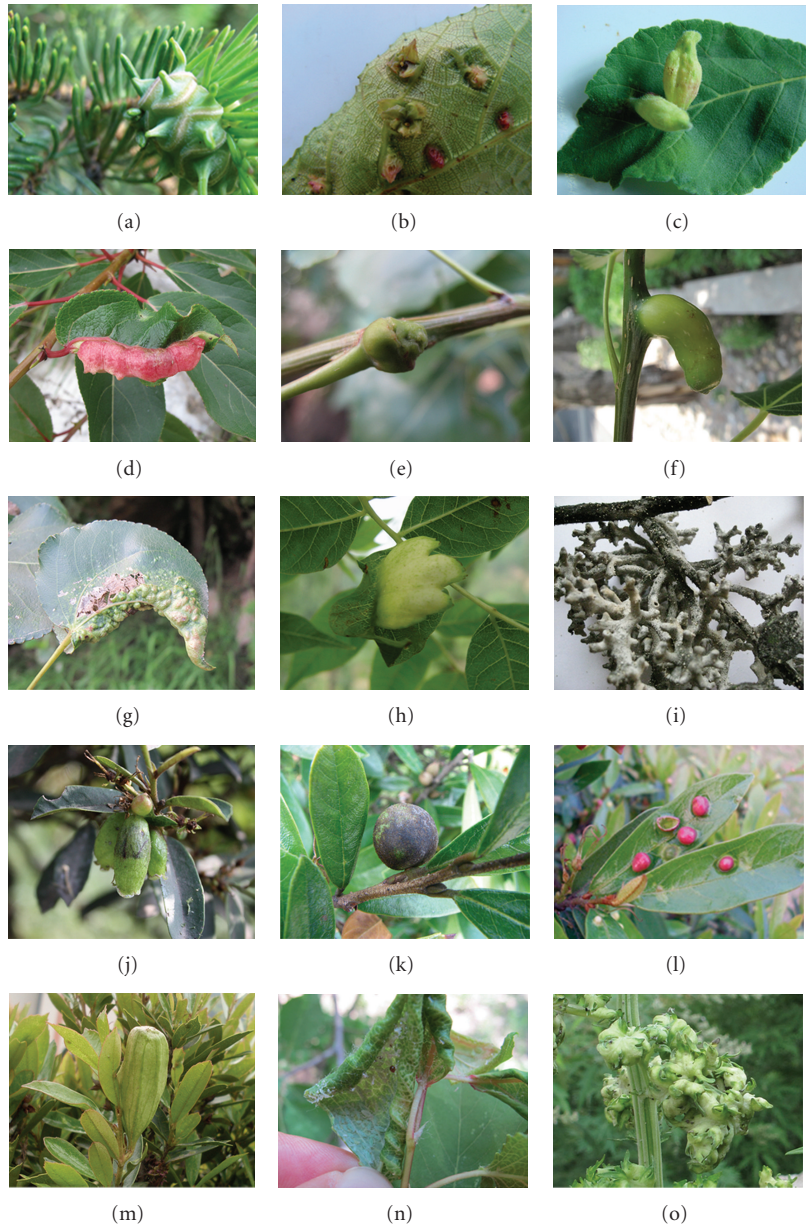

Figure 1: (a) A gall of *Adelges* sp. on *Picea crassifolia* (Huangzhong, Xining, Qinghai, China; 8 July 2009): pineapple-like, multiple-cavity, closed. (b) Galls of *Acanthochermes similiquercus* Jiang, Huang & Qiao on a leaf of *Quercus* sp. (Baoding, Panzhihua, Sichuan, China; 15 April 2005): spherical, single-cavity, some matured ones are open. (c) Galls of *Tetraneura (Tetraneurella) nigriabdominalis* (Sasaki) on a leaf of *Ulmus* sp. (Hulun Buir, Inner Mongolia, China; 1 August 2004): spindle-shaped, single-cavity, closed. (d) A pseudogall of *Epipemphigus imaicus* (Cholodkovsky) on *Populus cathayana* (Shangri-La, Yunnan, China; 27 July 2010): silkworm-like, single-cavity, open on the undersurface of the leaf. (e) A gall of *Pemphigus bursarius* (Linnaeus) on a petiole of *Populus simonii* (Miyun, Beijing, China; 25 July 2009): bag-like, single-cavity, with a natural lateral opening. (f) A gall of *Pemphigus immunis* Buckton on a twig of *Populus* sp. (Miyun, Beijing, China; 25 July 2009): long saccate, single-cavity, closed. (g) A dumpling-shaped leaf-fold pseudogall of *Thecabius* (*Oothecabius*) *populi* (Tao) on *Populus ussuriensis* (Miyun, Beijing, China; 25 July 2009). (h) A gall of *Chaetogeoica foliodentata* (Tao) on the leaf midrib of *Pistacia weinmannifolia* (Qishan, Baoji, Shaanxi, China; 12 July 2004): cockscomb-like, single-cavity, closed. (i) A gall of *Tuberaphis owadai* Kurosu & Aoki on a twig of *Styrax japonica* (Yuanyang, Kunming, Yunnan, China; 10 June 2009): coral-like, single-cavity, with many small openings on the projections. (j) Galls of *Asiphonipponaphis vasigalla* Chen, Sorin & Qiao on the leaf midribs of *Distylium chinense* (Jishou, Hunan, China; 15 April 2010): vase-shaped, single-cavity, open on the bottom. (k) A gall of *Metanipponaphis* sp. on a petiole of *Distylium chinense* (Jishou, Hunan, China; 6 September 2009): global, single-cavity, closed. (l) Galls of *Neothoracaphis yanonis* (Matsumura) on the leaves of *Distylium chinense* (Jishou, Hunan, China; 21 May 2009): spherical with a pointed bottom, protruding from both sides of the leaves, single-cavity, closed. (m) A gall of *Nipponaphis* sp. on a twig of *Distylium chinense* (Jishou, Hunan, China; 5 September 2009): bottle-shaped, single-cavity, closed. (n) Leaf rolls caused by *Hyalopterus pruni* (Geoffroy) on *Prunus armeniaca* (Huangzhong, Xining, Qinghai, China; 8 July 2009). (o) Leaf rolls and swellings caused by *Cryptosiphum artemisiae* Buckton on *Artemisia* sp. (Miyun, Beijing, China; 25 July 2009).

The association of galling aphids with their specific host plants is supposed to be ancient [70]. One hypothesis about what plays an important role in shaping aphid-host plant association is "fundatrix specialization" [71–74]. This hypothesis suggests that the fundatrix is highly specialized to the ancestral host and is less able to acquire new hosts than are other morphs over long evolutionary periods. It should be noted that, with few exceptions, the fundatrix, the morph that hatches from the overwintering egg on the primary host in the spring, is the only morph that can induce a gall [18, 29]. Thus, the phylogenetic constraints on the fundatrix would in some degree explain the high host specificity of galling aphids to their primary hosts.

Aphids have very intimate associations with their host plants. The aphids obtain food resources and habitat from their hosts. It is commonly assumed that host plants have a great influence on aphid diversification [75]. Two of the major hypothesized pathways of diversification in phytophagous insects are cospeciation with host plants [76, 77] and speciation through host shift [78]. Both hypotheses rely on some degree of host specialization and suggest that host plant diversity plays a major role in insect diversification [75, 79]. In particular, galling aphids are closely linked with their host plants and, as a whole, occupy a wide range of plant species. Primary host specificity is strong. Different aphid families, subfamilies, or tribes are strictly associated with different plant families or genera. We think that the high host plant diversity should have considerable influence on the diversification of galling aphids and the adaptation to different host plants in different galling lineages might have driven the divergence of galling aphids at higher taxonomic levels.

5. Conclusion

This paper has presented a preliminary review of gall-inducing aphids in China. The major groups of galling aphids were surveyed. The great diversity of gall morphology was analyzed systematically according to type, site, size, shape, and structure. These traits are highly species specific, and most are closely related to gall fitness. The host plants bearing galls are rich in species, and strong primary host specificity was found. We suggest that host association and varied gall morphology might jointly have driven the diversification and adaptive radiation of galling aphids.

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