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Two exquisite hemipteran galls of India with notes on the physiology of gall induction by Sternorrhyncha[#]

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ABSTRACT: The Indian subcontinent is rich with gall-inducing insects. The varieties of galls they induce offer bountiful opportunities to explain the dynamics of insect-plant interactions. Close to 90% of gall-inducing insects across the world are known to be specific to certain plants and such specialist behaviour offers them for use as ideal models to explain and characterize insect-plant relationships, which bear long-term advantages in managing insects that live and feed on economically important plants. In such a context, I illustrate in this paper, the intimacy of relationships between two gall-inducing Hemiptera (*Apsylla cistellata* tied to *Mangifera indica* and *Mangalorea hopeae* tied to *Hopea ponga*), which are native to the Indian subcontinent. In this article I emphasize that studying the biology of gall-inducing insects unequivocally demands a clear understanding of the stress and reparative physiology of the plant as well, further to that of the feeding biology of the inducing insect. Since all known gall-inducing insects (Hymenoptera excepted) induce galls by feeding action, I have explained the vitality of knowing about mouth parts, salivary secretions, and the mechanisms that arise in plants consequent to insect feeding with regard to the Hemiptera. My plea is that with the vast variety of various gall-inducing insects, we in India have a large canvas to paint the details of the physiology and metabolomics involved in insect-plant interactions clearly, because these insects are highly specialized in selecting their hosts, and also because these insects live embedded within plant tissues for certain period of time. In an ecological context, these insects are more easily amenable to monitor in field contexts than other free-living insects.

KEY WORDS: Peninsular India, Indo-Gangetic Plains, *Mangalorea hopeae, Apsylla cistellata*, *Contarinia manii*, dynamics of interactions

INTRODUCTION

Insect-induced galls have been recognized in India for long. For example, the medicinal relevance of the pouch galls that arise on the leaves of *Terminalia chebula* (Combretaceae) is mentioned in *Amarasimha*'s *Amarakôsã* of the 4th Century AD (Peyer, n.d). We know today that these galls are induced by *Dixothrips onerosus* (Thysanoptera: Phlaeothripidae) (Ananthakrishnan and Raman, 1989; Raman, 2013). Mani's *Cecidotheca Indica* (1959) served as a useful primer for Indian galls; revised editions of this monograph appeared as *Plant Galls of India* in 1973 and 2000.

In 2007(a), I wrote highlighting many of the ignored dimensions of this branch of entomology, intending that it would stimulate the study of the curious

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biologies of these specialist insects. On various scores, the gall-inducing insects of India are unique: a majority of the peninsular-Indian gall-inducing insect elements are endemic to this region, whereas a majority of the northern-Indian gall-inducing insect elements are not, mainly because of the interconnectedness of the Indian plate with the European plate. The restriction of the gall-inducing Cynipoidea (Hymenoptera) and Aphidoidea (Hemiptera) to the foothills and slopes of the Himalaya and the near cent-percent absence of gall-inducing Cynipoidea and Aphidoidea in Peninsular India (Raman, 2007b) reiterate the above. Nevertheless, given the long time periods over which the plants and animals of the Indian subcontinent have been evolving, galls - the expressed phenotypic expressions of tight interactions between two unrelated genomes - present an astonishing variety, concurrently raising umpteen scientific questions (see Raman 2007a, 2009a). Mani (2000) reports nearly 2000 types of galls with a majority of them displaying amazing morphologies. One extraordinary example will be the cylinder-piston gall induced on the opposite leaflets of *Acacia ferruginea* (Leguminosae, http://www.theplantlist. org/tpl1.1/record/ild-31791) from the vicinity of Coimbatore (Rohfritsch, 1971) (Fig. 1), which stand unmatched in the biological world. Keith Harris described the inducing Cecidomyiidae of these galls as *Contarinia manii* (Diptera) in 2010, whereas Mani when first found it in Walayar (Palghat gap, 10°232 N, 76°522 E) placed the insect under *Lobopteromyia* (Mani, 1953).

Unlike the bacterium-, fungus-, and nematode induced plant abnormalities, which I prefer to designate as ‘tumours’, those induced by insects (used heré to include the Acarina as well), usually presenting impressively symmetrical shapes, I prefer to call ‘galls’ (Raman, 2003, 2007a, 2009a). The tumours are amorphous, whereas galls are of definite, usually symmetrical, shapes.

In this article, I will be dealing with the biologies of and the sea-urchin like galls on *Hopea ponga* (Dipterocarpaceae) induced by *Mangalorea hopeae* (Hemiptera: Coccoidea: Beesoniidae) (Fig. 2) and the fir-cone like galls on *Mangifera indica* (Anacardiaceae) induced by *Apsylla cistellata* (Hemiptera: Psylloidea: Aphalaridae) (Figs. 3, 4). One reason for the choice of these examples is that both galls are induced on the axillary vegetative shoot buds by two Hemiptera. The *M. hopeae* populations occur restricted to the western coastal plains (Peninsular India, the Malabar Coast, Konkan Coast), whereas *A. cistellata* populations to the wider Gangetic Plains (27°152 N; 80°302 E). While consolidating known information of these two galls, I will speculate some details, further to offering a few general remarks on the gall flora and the inducing fauna of India. The speculation, I am confident, would encourage the present generation of Indian entomologists, especially those interested in exploring the ecology and physiology of insect–plant interactions, in proving me either right or wrong.

HEMIPTERAN GALLS

MANGALOREA HOPEAE AND GALLS ON *HOPEA PONGA*

Mangalorea hopeae belongs to the Beesoniidae (Coccoidea) (Raman and Takagi, 1992; Saleem and Nasser, 2015). Presently we know of *Beesonia* (four species), *Gallacoccus* (five species), and *Mangalorea*, *Echinogalla*, and *Danumococcus* (one species each). Except *Beesonia napiformis* and *B. brevipes* living on different Fagaceae in warm temperate eastern Asia, the remainder live on various species of the Dipterocarpaceae in warm, humid southern and south-eastern Asia (Takagi, 2007). A Neotropical taxon *Limacoccus* living on species of Arecaceae is currently listed under the Beesoniidae (Limacocciini) (Foldi, 1995), which appears odd. The curiosity is that the Fagaceae-infesting warm-temperate eastern Asian species of the Beesoniidae do not induce galls, whereas the known Dipterocarpaceae-infesting subtropical-tropical taxa induce galls (Takagi, 1987). Presently, the relationships within the Beesoniidae-those on Fagaceae and those on Dipterocarpaceae-remain unexplained (Takagi, 2007).

The earliest trigger to establishing the Beesoniidae, a unique family of the Coccoidea, was from India. Edward Ernest Green (Williams, 1999), a tea planter in Ceylon (Sri Lanka) and an amateur mycologist-entomologist, described *Beesonia dipterocarpi*, which induces chrysanthemum flower-like galls on the vegetative shoot buds of *Dipterocarpus tuberculatus* in Burma, after he retired to UK (Beeson, 1941, pp. 743-744). The *B. dipterocarpi* specimens were sent to Green, from the Entomologist's office, Forest Research Institute (Dehra Dun) in 1926. Green refers to this 'new' insect as 'remarkable' and names it after Cyril Frederick Cherrington Beeson. Green (1928) offers emendations to his 1926 description and provides supplementary notes. Green, in 1926, did not assign this taxon to any subfamily then known (MacGillivray, 1921). He suspected that it could be a member of Tachardiinae; and at the same time, he also indicated that the adult males resemble those of *Conchaspis* (Conchaspinae) (Raman and Singh, 2014).

The galls of *Hopea ponga,* presenting similar to sea urchins, occur generally in leaf axils and rarely at the shoot terminals. Mature galls are dark green and spherical, endowed with numerous stiff and sharp structures (appendages, spines). With maturation, galls turn from pale to dark green, then to brownish green, and finally to grey, losing simultaneously their spherical shape and developing cracks. Usually only one gall occurs at an axil, although occasionally more occur. The following details are paraphrased from Raman and Takagi (1992).

Soon after the monsoon rains, the neonate female nymphal instars of *M. hopeae* invade the axillary angles of vegetative buds, exploiting the naturally occurring space due to extra-axillary position of the vegetative axillary bud. Once settled, the nymph feeds on the cortical parenchyma of the bud. The feeding stimulus restricts the bud from growing into a vegetative branch; instead, it develops into a gall, resulting in a structure that includes an eccentrically grown 'columella' that arches over the inducing nymph. Vascular traces ramify through the columella. Subsequent growth of the columella takes place essentially due to division of cells of the central cortex of the columella. Simultaneously with the arching growth of the bud meristem, some of the epidermal cells differentiate into multicellular, vascularized spiny structures. The stimulus provided by the feeding activity of the growing female nymph (the gall inducer) that occupies the space in the leaf axils of *Hopea* activates the epidermal cells to become multicellular, spiny structures. These structures on mature galls have lignified walls and polyphenolic inclusions.

In old galls, the columella is more striking than that of the spiny structures. With ageing, the parenchyma cells of the columella become lignified. Rupture of vascular strands disrupts water and nutrient supply to the gall. Lignified parenchyma cells separate from one another due to dissolution of middle lamella and develop large intercellular spaces. Cells bordering the gall stretch horizontally pulling the spine-like appendages on the lateral axis. Such lateral movement of appendages facilitates the escape of adults (to occur) from the gall.

APSYLLA CISTELLATA AND GALLS ON *MANGIFERA INDICA*

Galls of *Apsylla cistellata*, resembling the cones of Coniferae (now referred as Pinophyta), arise at the leaf axils of *Mangifera indica* through the modification of axillary vegetative shoot buds. Usually one gall arises at one leaf axil, although several may arise at the ends of branches. *Apsylla cistellata* is presently placed under Rhinocolinae, Aphalaridae of the Psylloidea (Burckhardt and Ouvrard, 2012). George Buckton described this taxon as *Psylla cistellata* in 1896 based on specimens sent to him from Dehra Dun. While describing *P. cistellata*, Buckton remarks that this taxon appears so 'curious' that a change of its generic name and status may be necessary. David Crawford, then at Hawaii, parked this taxon under a new name *Apsylla* in 1912. Mathur (1975) treated *A. cistellata* under Pauropsyllinae (Psyllidae). White and Hodkinson (1985) treated *A. cistellata* under the Calophyidae, with Psylloidea being recognized as a superfamily. A comprehensive list of previous papers dealing with cursory biological investigations of *A. cistellata* is available in Raman *et al*. (2009a). Later papers on *A. cistellata* by Shivankar and Rao (2010) and Jha *et al*. (2013)

essentially deal with the economic damage caused by these insects to *M. indica* and how *A. cistellata* can be managed with chemical applications. Almost all of these papers refer to *A. cistellata* as a 'serious pest' of *M. indica*, but none clarifies to what extent *A. cistellata* either affects economic productivity or damages *M. indica*.

In spite of scores of papers published on the management of *A. cistellata*, including the lengthy monograph by Gajendra Singh (Singh, 2003), a clear knowledge of the bionomics of this curious insect is still deficient. I summarize the details available in various papers of Gajendra Singh here: Gravid females insert 75-150 eggs along the midribs of newly flushed leaves in March-April in two parallel rows. The newly deposited, oval eggs are whitish and translucent with its tip partly exposed (Singh and Misra, 1978). The eggs hatch in either mid-September or early October, approximately 200 days after oviposition. Nymphal phase includes five instars and the development into adults takes *c*. 140 days. Gravid females never oviposit on the leaves of seedlings, but only on the tender leaves of older plants that are about to flower and bear fruits (Singh, 2003). Feeding action of the first-nymphal instar initiates the gall. The neonate nymphal instars remain partly within egg shells and feed on the same leaf where the adult female oviposited (Singh *et al.*, 1975). The feeding effect of multiple neonate nymphs results in the modification of 'adjacently' occurring vegetative shoot buds into galls in about 30 days. Singh (2000) indicates that an increase in endogenous auxin levels and a decrease in total phenols and levels of tyrosine and tryptophan occurs in the shoot buds of *M. indica* that grow into galls. Singh (2003) further indicates a correlation between age of flowering and gall incidence.

The emerging message is that the neonate nymphal instars of *A. cistellata* feed on *M. indica* leaves, particularly on those, which harbour eggs. Feeding action stimulates gall development, not at the same site, but at a site farther away, *viz.*, the vegetative axillary shoot bud by translocating a chemical 'stimulus'.

REMARKS

By talking about two extremely fascinating galls of India, I aim to instil curiosity and interest in Indian entomologists and ecologists who deal with insect-plant interactions, so as to explore these dynamic systems further. I also attempt to compare these systems with a few explained galls induced by other Sternorrhyncha and a few Auchenorrhyncha. At this juncture, it would be pertinent to recognize that the claims of gall induction by the Auchenorrhyncha are of recent times (Matsukura *et al.*, 2009, 2010). They are questionable in terms of the concept of a gall, but are indicated as galls by their authors. For those interested in the study of galls, reading Meyer (1987) would be most fundamental, which explains the basic concepts in gall-inducing insect–plant interactions fascinatingly, with hundreds of examples drawn from all over the world, although several other books on the biology and ecology of gall-inducing insects have appeared later (*e.g.*, Shorthouse and Rohfritsch, 1992; Raman *et al.*, 2005a).

APSYLLA CISTELLATA AND *MANGALOREA HOPEAE*

Gall-induction behaviour of *A. cistellata* stands strikingly different from what could be perceived as the basic pattern among the other better known and more diverse gall-inducing Psylloidea - the Triozidae (Burckhardt, 2005). Before I proceed to make any comparisons, it would be pertinent to recall the biology of feeding by the Adelgidae (Hemiptera: Aphidoidea) here. Adelgidae bear very long stylets; much longer than their total body lengths and longer than the other Aphidoidea do (Rohfritsch, 1990). For example, the stylet bundle lengths of nymphal instars of *Adelges piceae* (Adelgidae) are nearly five times longer than their body lengths. The staggering length of stylets in the Adelgidae is adapted not just for feeding, but also to anchor them on the shoots they feed on (Young *et al.*, 1995). Similar details are available in Rohfritsch (1990) referring to *A. laricis* and *A. abietes* that induce shoot bud galls on *Picea excelsa* in Europe. In

Adelges cooleyi, which induces galls on the vegetative shoot buds of *Picea glauca* × *P. engelmannii* hybrid in North America, Sopow *et al.* (2003) indicate that a dose-dependent chemical stimulus either moves actively or is moved passively over long distances from the point where the gall-founding female occurs. The overall gall-inducing behaviour of the Indian taxon *A. cistellata* appears highly similar to what is known in the European and North-American Adelgidae, which leaves us baffled with several questions: Is the behaviour known in the Adelgidae, an aphidoid, reappears in *A. cistellata*, a psylloid? Is the stylet of *A. cistellata* immensely long, which is inserted at one point (*viz.*, the leaf on which the neonates emerge) and their tips reach a distant point (*viz.*, the vegetative bud at the leaf axil), similar to what has been shown in *A. piceae*, *A. laricis*, and *A. abietes*? On the contrary, the stylet tip does not reach the vegetative buds, but as shown in *A. cooleyi* the salivary secretions (the stimulus) are transmitted to a distant point thus triggering gall development at another site? In spite of an apparent similarity, in the *A. cistellata*-induced bud galls on *M. indica*, the first-instar nymphal instars of *A. cistellata* are the gall initiators, whereas in the bud galls induced by various Adelgidae, adult females are the gall initiators (= the *fundatrigeniae*). Notwithstanding the above similarity in insect behaviour by stimulating galls at sites far away from where actually the initiating insect stages reside, the question raised by Prasad (1957), whether *A. cistellata* plays a vectorial role in transmitting a virus, which possibly stimulates gall development, merits investigation given that many Psylloidea are established vectors of plant pathogens.

Apsylla cistellata populations remain restricted to the Indo-Gangetic Plains and lower valleys of the Himalaya; however, Kandasamy (1986) has reported its incidence in the Shevaroy Hills (11°46'N; 78°12'E; 700–1200 m a.s.l.) in humid, tropical peninsular India, which has not been verified subsequently. Although *M. indica* grow extensively in several warm parts of the world, *A. cistellata* is not known to occur in any geographical area other than the northern plains of the Indian subcontinent including parts of Pakistan, Bangladesh, and Nepal. A possible reason for the localized incidence of *A. cistellata* is the annual rainfall of more than 1100 mm and a difference of more than 30°C between the highest maximum and lowest minimum temperatures (Singh 2003).

Two principal life stages of *Mangalorea hopeae* participate in *Hopea* gall system: (i) one female first-nymphal instar initiates the gall on a vegetative shoot bud exploiting the extra-axillary space; (ii) several male nymphal instars, emerging from that female after its maturation and mating, move and occupy spaces between the sharp spiny structures. The males occurring between such structures alter gall physiology by their feeding, particularly in ageing galls. Because of their number, they utilize nutrients more vigorously than what an ageing gall can mobilize, which accelerates drying of galls. The occupation of the maternal gall by several male nymphal instars is not unique to *M. hopeae*. *Cystococcus* (Coccoidea: Eriococcidae) shows this behaviour that the male offspring complete their development within the maternal gall on *Eucalyptus,* feeding on a layer of nutritive tissue lining the gall cavity (Gullan and Cockburn, 1986). Gullan and Cockburn (1986) also speak of dispersal of the second and subsequent generations of nymphal instars by the first generation of winged males, which explains dispersal of apterous female nymphal instars. Does a similar phoretic phenomenon possibly occur in the biology of *M. hopeae*? This question needs to be answered.

The terminal regions of generative buds are not damaged during gall induction, since the gall-founding female *M. hopeae* feeds only along the sides. The cecidogenetic gradient activated by the feeding stimulus spreads to apical segments of the gall, promoting an expansive growth of the host bud establishing the gall columella. With the disturbance of normal morphogenetic controls, the transformed apex, instead of initiating leaf primordia (and later, the branch), undergoes intense parenchymatization and negotiates a curvature, providing cover to the gall-initiating female simultaneously. Cecidogenetic stimulus also triggers a rare developmental course transforming columella's surface cells into multicellular, vascularized structures. During their initial phase of growth, the terminal, lance-like parts of the spiny structures exhibit a more active growth than the lower stalk regions of these appendages. The lance-like parts of adjacently occurring spiny structures occur so closely that they physically protect inhabiting nymphal instars. Lower stalk region of each spiny structure elongates more intensely by stretching than by cell division and the entire appendage complex is strengthened by the vascular network of the columella. With maturation, the columella cells stretch in the horizontal axis due to desiccation resulting in the separation of appendages, thereby facilitating the escape of adult males.

GALL - INDUCING BEHAVIOUR OF *APSYLLA CISTELLATA* AND *MANGALOREA HOPEAE VIS-À-VIS* OTHER HEMIPTERA

A few common patterns can be discerned in the gall-inducing behaviour in the Sternorrhyncha: (i) gall initiation is usually by the feeding action of a single, adult female; (ii) the gall-founding females disperse over short distances seeking juvenile plant organs, such as tender shoot terminals and differentiating leaves (Raman 2012a). The gall-inducing Adelgidae and Beesoniidae differ from this pattern in such a way that, neonate, female nymphal instars initiate galls. Among the gall-inducing Triozidae (Psylloidea) the first-instar nymphs initiate galls by settling on stomatal apertures and feeding through the stomatal apertures. However, in the Triozidae, whether the initiating nymphal instar is a female or a male is uncertain presently, although the chances of a male inducing a gall are highly unlikely. Among the Psylloidea, the gall-inducing behaviour of *A. cistellata* appears markedly different compared with those of the gall-inducing Triozidae and Psyllidae (Psylloidea).

In the gall-inducing Triozidae, gravid females deposit their eggs at the same site where the galls would develop, and only the egg stalks remain buried in the plant tissue. In contrast, the eggs of *Apsylla cistellata* remain 'partly buried' on the leaves of *M. indica* and the nymphal instars that emerge from those eggs feed on the same leaf, but their feeding action triggers gall induction on the axillary vegetative buds, at least 10 cm away. Samui and Jha (2009) provide a slightly more detailed description of *A. cistellata*'s oviposition behaviour: (i) the eggs are laid singly in slits cut using the ovipositor, those eggs remain embedded in midrib tissues along the under sides of new leaves; (ii) eggs are inserted alternatively by puncturing the tissue along both sides of the dorsal face of the midrib; (iii) the intensity of egg laying depends on the availability of new flush of tender leaves and the number of adults emerging, and (iv) if several females had only a few leaves for egg laying, then they lay eggs along both sides of lateral veins along the under sides of *M. indica* leaves. Burying eggs in host tissue, as evident in the behaviour of *A. cistellata*, therefore, emerges as a special, non-Triozidae trait in the Psylloidea.

Claims of gall induction by the Auchenorrhyncha need to be referred here. The earliest records of Auchenorrhyncha-induced 'galls' exist from the 1920s, referring to *Philaenus spumarius* (Cercopoidea: Aphrophoridae) on *Oenothera* (Onagraceae) and *Ceresa bubalus* (Cicadoidea: Membracidae) on *Medicago sativa* (Leguminosae) (Meyer, 1987: pages 92-93). In terms of general biology, more details are available for the Tingidae (Heteroptera: Cimicomorpha), which prefer to feed on the abaxial-leaf sides seeking humid microenvironments - a trait shared by many gall-inducing Sternorrhyncha. Nonetheless, among the supposed gall-inducing Tingidae (*e.g.*, *Copium* and *Paracopium*), their preference for flowers and capability to induce floral galls impress as specialized traits among gall-inducing Hemiptera (Schaefer, 2005), because floral galls induced by the Sternorrhyncha are not known. Gall-bearing *Teucrium polium* (Lamiaceae) (Sinai desert, Egypt; 29^{o}30'N; 33^{o}50'E) include leaves and floral axes reduced in overall size, although the petals in galled flowers were 'enlarged' (Zalat *et al*., 2000). The other key behaviour that distinguishes gall-inducing *Copium* from gall-inducing Sternorrhyncha is that they bury their eggs- nearly fully - in host tissues (Behr, 1952; Monod and Carayon, 1958). A differently structured internal reproductive system in *Copium* is implicated to be better adapted for such a specific behaviour (Schaefer, 2005).

Fig.1. Cylinder-piston galls on *Acacia ferruginea* induced by *Contarinia manii* in southern India. Inset:: vertical longisectional drawing showing the position of the inducing larva (L).

Fig. 2. Sea-urchin shaped galls on the shoot buds of *Hopea ponga* induced by *Mangalorea hopeae* along the Malabar Coast. (Photo courtesy: M. Nasser, Calicut University, Calicut).

Fig. 3. Coniferae cone like galls on the shoot buds of *Mangifera indica* induced by *Apsylla cistellata* distributed along the Indo-Gangetic Plains.

Fig. 4. Vertical longisectional view of one gall showing nymphal instars and chambers.

Parallelism in the 'gall'-inducing behaviour in Auchenorrhyncha on the one hand and in the few gall-inducing Terebrantia (Thysanoptera) (*e.g.*, *Aneurothrips preisneri*, Thripidae, on *Cordia dichotoma*, Boraginaceae) on the other is more striking. *Scenergates viridis* (Hemiptera: Cicadellidae) are indicated to induce 'gall'-like structures by modifying the entire leaves of *Alhagi maurorum* (Leguminosae) (Ratikov and Appel 2012), which strikingly resemble the leaf-fold galls induced by *Gynaikothrips ficorum* (Thysanoptera: Phaleothripidae) on the leaves of *Ficus microcarpa* (Moraceae). Among the known instances of gall induction in the Cicadellidae (Mitjaev, 1968; Matsukura *et al.,* 2010), a common behaviour is that both the juveniles and adults induce galls, which are different from that known among gall-inducing Sternorrhyncha. Nymphal instars and adults of

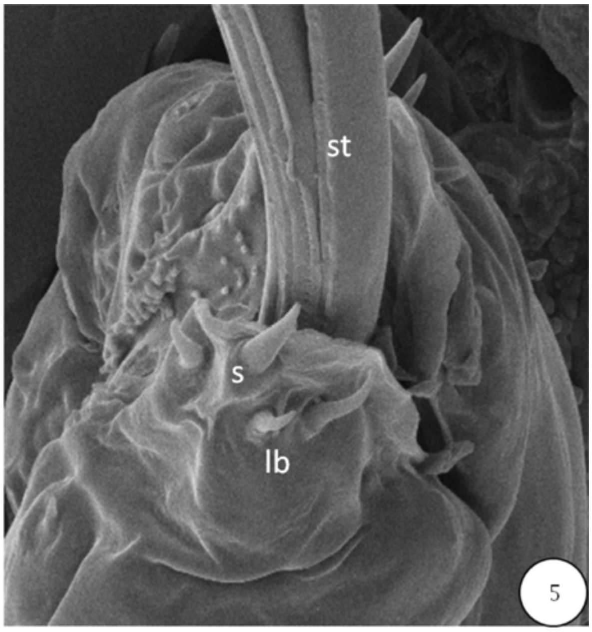

Fig. 5. Mouth parts of a gall-inducing species of *Glycaspis* (*Synglycaspis*) (Psylloidea: Aphalaridae). s – sensillum; lb – labium; st – stylet bundle
(Source: Sharma *et al*., 2015)

Cicadulina bipunctata (Hemiptera: Cicadellidae) induce galls not only at the locations they feed but also on distant leaves through dose-dependent stimulation (Matsukura *et al*., 2009); this behaviour is similar to the gall-inducing behaviour of *A. cistellata* and *A. cooleyi*. As of the present, I will summarize that gall-inducing behaviour is uniquely preserved predominantly among the Aphidoidea, Psylloidea, and Coccoidea and to an insignificant extent in the Aleyrododoidea (one biotype of *Bemisia tabaci* inducing colourful, parenchymatous galls on the leaves of *Achyranthes aspera* (Amaranthaceae)) in the Indian subcontinent. Sporadic papers refer to certain plant abnormalities due to sucking-feeding behaviour among various Auchenorrhyncha, similar to the papers that refer to gall induction by a species of the Chironomidae (Diptera) on the different aquatic plants (Raman, 2009b; Jäger-Zürn *et al.*, 2013). In such vague contexts, it is but critical that we progress ideas with extreme care.

MOUTH PARTS, FEEDING BIOLOGY, AND PHYSIOLOGY OF GALL INDUCTION IN STERNORRHYNCHA

Many recent papers explain the morphology of mouth parts of plant-feeding Hemiptera, mostly referring to the Aphidoidea, which we therefore need to use as a basic model. The mouth parts include the labrum, labium, and a sclerotized stylet bundle, which in turn, includes paired mandibular and maxillary stylets. This ‘mouth-parts complex’ is essentially tubular and devoid of either labial or maxillary palpi. The labral cone, usually endowed with sensilla, is attached proximally to the clypeus and occurs overarching the labial groove. The included stylets are pointed and are elaborately sculpted both at the tips and along the edges. The first maxillae are tightly adpressed to each other so that the oppositely lying grooves along their interfaces arrange in such a manner that they bear two superposed capillary tubes (Fig. 5). Through one, the feeding Hemiptera flushes its saliva and through the other, sucks plant sap. Endowed with a variety of sensilla, the distal tip of the labium guides the stylet into the host organ. The second maxilla fused into a labium constitutes the rostrum, with a groove in which the distal parts of the stylets slide. Each stylet is manipulated by two sets of retractor and protractor muscles. Muscles attached to the ceiling of the cibarium provide suction, which helps in either drawing or injection through the food and salivary canals that lie between the maxillary stylets. The two maxillary stylets interlock with each other along their full length, thus constituting a smooth hollow tube that bears an armature of denticles at the tips (Hori, 2000). The articulation on the opposite side of the stylet bears the salivary canal, which opens terminally between the denticles and the extreme end of the stylets. Although each maxillum is similar in shape and dimension, lengths of stylets change as the insect grows: for example, in the first nymphal instars of Psylloidea it is usually 300 - 600 mm long, whereas in adults of Psylloidea it is 1000 - 1400 mm. Because the stylet bundles become longer with each successive moult of nymphal instars, developing nymphs shift feeding sites from superficial to deeper-lying plant cells as they mature. For example, the gall-founding female

Adelgidae change their feeding sites several times during gall development (Rohfritsch and Anthony, 1992). During feeding, the labium does not pierce the plant tissue, but is positioned perpendicular to the surface so as to push the stylets into the plant. Although a majority of the Sternorrhyncha feed passively on phloem contents, several studies on gall-inducing Sternorrhyncha, especially on the nymphal instars, indicate them to be nonvascular tissue feeders (*e.g.*, parenchyma) (Raman, 1991; Rohfritsch and Anthony, 1992; Sharma *et al.*, 2014).

Hemiptera, specifically the Aphidoidea, produce two types of saliva. The first is dense and proteinaceous, which gels around the stylets forming stylet sheaths, isolating the plant tissues from the mouth parts, and preventing any possible adverse plant reactions (Felton and Eichenseer, 1999). On reaching the target feeding site, they secrete the second type of saliva - less dense, and therefore the watery saliva - which is injected directly into plant tissues. The watery saliva contains diverse digestive and lytic enzymes. The feeding action inflicts a 'subtle' wound, but the salivary proteins interact with Ca^{2+} of host-plant tissues (Will *et al*., 2007; Sharma *et al.*, 2014) preventing the possible wound-healing effort made by the plant. In general, wounding does not either induce or result in cell necrosis. Stylet penetration occurs by changes in the position of the head during feeding; the head is bent over the labium, which is attached to the plant surface, forcing the stylet bundle down the labial groove, and into the host tissue (Freeman *et al*., 2001). Stylet tracks (the proteinaceous sheaths) are left behind within host tissues by the gall-inducing Sternorrhyncha after the withdrawal of the stylets. These tracks accept colouring by cationic dyes (*e.g.,* methylene blue, bismark brown) and can be easily detected under a good-quality light microscope. In some species, the track is straight, as evident in *Eriosoma lanigerum* (Aphidoidea: Pemphigidae), whereas in others it could be meandering and branched, as evident in *Adelges abietes* (Aphidoidea: Adelgidae). Some sternorrhynchs extensively explore the plant surface before commencing feeding (Lewis and Walton, 1958), whereas others do not (*e.g. Daktulosphaeria vitifoliae*, Aphidoidea: Phylloxeridae; Raman *et al.*, 2009c). In a majority of instances, the stylet path travels intercellularly dissolving the middle lamella, principally made of pectic compounds (Rohfritsch, 1976, 1988). Pectinase activity in aphid saliva is known from the time of Jacques Auclair (1963).

Injection of saliva alters the hormonal balance in the host, leading to gall development. For a detailed commentary on the presently valid explanations of gall-induction mechanisms, please refer to Raman et al. (2005b). A few supplementary points are summarized here: Triacylglycerides containing (E,E,E)-octa-2,4,6-trienoic acid from the galls induced by *Colopha moriokaensis* (Aphididae: Pemphiginae) on *Zelkova serrata* leaves (Ulmaceae) are indicated to be responsible for cell hypertrophy (Otha *et al.,* 2000). Soluble proteins in the saliva of the nymphs of *Trioza jambolanae* have been implicated as a critical factor for gall development (Rajadurai *et al.*, 1990). In the saliva of *Trioza apicalis*, an undetermined amine has been shown, which is indicated as the stimulating chemical (Markkula *et al.*, 1976). Gall-inducing Sternorrhyncha vigorously take up oxygen from the gall tissue (several examples in Miles, 1999), along with a stimulation of auxin activity. Use of oxygen in the tissues under arthropod attack might be so great that the IAA-oxidase activity that regulates the concentration of IAA might be deprived of oxygen and therefore inhibited. Such a deprivation of oxygen (Florentine *et al.,* 2002) results in the concentration of IAA increasing disproportionately at feeding sites with a consequential hypertrophy of meristematic plant tissues. Although the specific agent in the hemipteran saliva that induces galls has not been determined, salivary oxidases should be playing a role in the disruption of IAA-oxidase pathway.

CONCLUSION

One key characteristic of gall-inducing insects is their specificity to particular host plants. One possibility is the absence of resistance-breaking genes in gall-inducing insects. Lack of such genes explains why these organisms have not radiated and diversified aggressively as many other insects have. On the contrary, host-plant populations are restricting the gene flow between specific gall-inducing insect populations, through their secondary chemistry because, the host-plant mediated impediments on the breeding behaviours impact on the radiation of gall-inducing insects (Raman 2012b). What can be said in conclusion is that the gall-inducing insects of the Indian subcontinent, more especially the Cecidomyiidae (Diptera), show features of conservative diversification (Raman et al. 2009a), whereas we know either little or nothing of the gall-inducing Hemiptera. Nevertheless, whatever little has been documented so far, appear to be strongly plant mediated, as evident in the instance of *Trioza fletcheri minor* (Hemiptera: Triozidae), which induces galls on more than one species of *Terminalia* (Combretaceae) (Raman *et al*., 1997). Within the Hemiptera, gall-inducing habit appears to have evolved multiple times, most of species diversity restricted to within few groups of the Aphidoidea, Psylloidea, and Coccoidea. More critically, gall-inducing behaviour varies strikingly even within the Hemiptera pointing to their independent evolution over time.

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REFERENCES

Ananthakrishnan T.N. and Raman A. (1989) Thrips and Gall Dynamics, E.J. Brill, Leiden, The Netherlands, 124 pp.

Auclair J.L. (1963) Aphid feeding and nutrition. Annual Review of Entomology 8: 439–490.

Beeson C.F.C. (1941) The Ecology and Control of the Forest Insects of India and the Neighbouring Countries. The Government of India, Dehra Dun, 1007 pp.

Behr L. (1952) Über die Blütengalle des *Teucrium chamaedrys* L. Berichte der Deutschen Botanischen Gesselschaft 65: 326–330.

Buckton G.B. (1896) The mango shoot *Psylla*. Indian Museum Notes 3: 91–92.

Burckhardt D. (2005). Biology, ecology, and evolution of gall-inducing psyllids (Hemiptera: Psylloidea). In: Biology, Ecology, and Evolution of Gall-inducing Arthropods (A. Raman, C.W. Schaefer, T.M. Withers, eds), Science Publishers, Enfield, NH, USA, 143–157.

Burckhardt D. and Ouvrard D. (2012) A revised classification of the jumping plant-lice (Hemiptera: Psylloidea). Zootaxa 3509: 1–34.

Crawford D.L. (1912) Indian Psyllidae. Records of the Indian Museum 7: 419–435

Felton G.W. and Eichenseer H. (1999) Herbivore saliva and its effects on plant defense against herbivores and pathogens. In: Induced Plant Defences against Pathogens and Herbivores (A.A. Agrawal, S. Tuzun, E. Bent, eds), APS Press, St Paul, USA, 19–36.

Foldi I. (1995) A taxonomic revision of *Limacoccus* Bondar with a cladistic analysis of its relationships with other scale insects (Hemiptera: Coccoidea). Systematic Entomology 20: 265–288.

Florentine S.K., Raman A. and Dhileepan K. (2002) Responses of the weed *Parthenium hysterophorus* (Asteraceae) to the stem gall-inducing weevil *Conotrachelus albocinereus* (Coleoptera: Curculionidae). Entomologia Generalis 26: 171–182.

Freeman T.P, Buckner J.S, Nelson D.R., Chu C.C. and Henneberry T. J. (2001) Stylet penetration by *Bemisia argentifolii* (Homoptera: Aleyrodidae) into host leaf tissue. Annals of the Entomological Society of America 4: 761–768.

Green E.E. (1926) On some new genera and species of Coccidae. Bulletin of Entomological Research 17: 55–65.

Green E.E. (1928) Further observations on *Beesonia dipterocarpi* Green. Bulletin of Entomological Research 19: 205–207.

Gullan P.J. and Cockburn A. (1986) Sexual dichronism and intersexual phoresy in gall-forming coccoids. Oecologia 68: 632–634.

Harris K.M. (2010) *Contarinia manii* sp. n. (Diptera, Cecidomyiidae): inducer of a remarkable gall on *Acacia ferruginea* in southern India. Zootaxa 2423: 63–68.

Hori K. (2000) Possible causes of disease symptoms resulting from the feeding of phytophagous Heteroptera, In: Heteroptera of Economic Importance (C.W. Schaefer, A.R. Panizzi, eds), CRC Press, Boca Raton, USA, 11–35.

Jäger–Zürn I., Spies M., Philbrick C.T. and Mora-Olivo A. (2013) Plant galls (cecidia) in Neotropical water plant family Podostemaceae induced by larvae of Chironomidae (Diptera). Spixiana 36: 97**–**112**.**

Jha S., Samui G., Mondal S. and Hasan A. (2013) Studies on bio-ecology of mango shoot gall psyllid (*Apsylla cistellata* Buckton) and its management. Acta Horticulturae 992: 467–474.

Kandasamy C. (1986) Taxonomy of south Indian psyllids. Records of the Zoological Survey of India 84: 1–111.

Lewis I.F. and Walton L. (1958) Gall formation on *Hamamelis virginiana* resulting from material injected by the aphid *Hormaphis hamamelidis*. Transactions of the American Microscopical Society 77: 146–200.

MacGillivray A. D. (1921) The Coccidae. The Scarab Company, Urbana, IL, 502 pp.

Mani M.S. (1953) On a collection of plant galls and gall midges from India. Agra University Journal of Research (Science) 2: 246–266.

Mani M.S. (1959) *Cecidotheca Indica*. Agra University Journal of Research (Science) 8: 91–220.

Mani M.S. (1973) Plant Galls of India. Macmillan India, New Delhi, India, 354 pp.

Mani M.S. (2000) Plant Galls of India (Second edition), Science Publishers, Enfield, USA, 477 pp.

Markkula M., Laurema S. and Tiittanen K. (1976) Systemic damage caused by *Trioza apicalis* on carrot. Symposium Biologica Hungarica 16: 153–155.

Mathur R.N. (1975) Psyllidae of the Indian subcontinent, Indian Council of Agricultural Research, New Delhi, India, 429 pp.

Matsukura K., Matsumura M. and Tokuda M. (2009) Host manipulation by the orange leafhopper *Cicadulina bipunctata*: gall induction on distant leaves by dose dependent stimulation. Naturwissenschaften 96: 1059–1066.

Matsukura, K., Matsumura, M. and Tokuda, M. (2010) Both nymphs and adults of the maize orange leafhopper induce galls on their host plant. Communicative and Interactive Biology 3: 388–389.

Miles P.W. (1999) Aphid saliva. Biological Reviews 71: 44–85.

Mitjaev I.D. (1968) A gall-forming leafhopper. Trudy Instituta Zoologii Akademii Nauk Kazakhskoi SSR (Proceedings of the Institute of Zoology of the Academy of Sciences of the Kazakhskoi SSR) 30: 205–206 [In Russian].

Monod Th. and Carayon J. (1958) Observations sur les *Copium* (Hemipt., Tingidae) et leur action cécidogène sur les fleurs *Teucrium* (Labiacées). Archives de Zoologie Expérimentale et Générale 95: 1–31.

Otha S., Kajino N., Hashimoto H. and Hirata T. (2000) Isolation and identification of cell hypertrophy-inducing substances in the gall forming aphid *Colopha moriokaensis*. Insect Biochemistry and Molecular Biology 30: 947–952.

Peyer A. (no date) *Amarasimhã: Nãmalingãnusãsana* (*Amarakôsã*), 2. *Dvitîyam Kãndam*, 5. *Vanausadhivargah* II, Vers 1–22 (Über Pflanzen), http://www.payer.de/amarakosa/amara205a.htm, accessed on 4 August 2016.

Prasad D. (1957) On the distribution, bionomics, and control of the mango shoot gall psyllid *Apsylla cistellata* Buckton. Indian Journal of Entomology 19: 78–83.

Rajadurai S., Mani T., Balakrishna P. and Raman A. (1990) On the digestive enzymes and soluble proteins of the nymphal salivary glands of *Trioza jambolanae* Crawford (Triozinae: Psyllidae: Homoptera), the gall maker of the leaves of *Syzygium cumini* (L.) Skeels (Myrtaceae). Phytophaga 3: 47—53.

Raman A. (1991) Cecidogenesis of leaf galls on *Syzygium cumini* (L.) Skeels (Myrtaceae) induced by *Trioza jambolanae* Crawford (Homoptera: Psylloidea). Journal of Natural History 25: 653–663.

Raman A. (2003) Cecidogenetic behaviour of some gall-inducing thrips, psyllids, coccids, and gall midges, and morphogenesis of their galls. Oriental Insects 37: 359–413.

Raman A. (2007a) Insect-induced galls of India: unresolved questions. Current Science 92: 748–757.

Raman A. (2007b) Biogeographical implications in species richness, biological diversity, and evolution of gall-inducing insects of the Orient and the eastern Palearctic. Oriental Insects 41: 9–25.

Raman A. (2009a) Morphogenesis of insect-induced plant galls: facts and questions. Flora 206: 517–533.

Raman A. (2009b) *Stenochironomus nelumbos* infesting leaves of *Nelumbo nucifera* and use of the term 'gall'. Current Science 96: 449.

Raman A. (2012a) Gall induction by hemipteroid insects. Journal of Plant Interactions 7: 29–44.

Raman A. (2012b) Adaptive radiation and diversification in gall-inducing insects in the Indian subcontinent: search for a pattern. Deutsche Entomologishe Zeitschrift 59: 177–187.

Raman A. (2013) Historical references to galls induced by *Dixothrips onerosus* (Thysanoptera) on the leaves of *Terminalia chebula* (Combretaceae) in India. Archives of Natural History 40: 163–165**.**

Raman A. and Takagi S. (1992) Galls induced on *Hopea ponga* (Dipterocarpaceae) in southern India and the gall-maker belonging to the Beesoniidae (Homoptera: Coccoidea). Insecta Matsumurana (New Series) 47: 1–32.

Raman A. and Singh S. (2014) Remarkable gall-inducing *Beesonia dipterocarpi* (Hemiptera: Beesoniidae) and their equally remarkable galls on *Dipterocarpus tuberculatus* (Dipterocarpaceae) described from the Indian subcontinent in the 1920s. Oriental Insects 48: 108–122.

Raman A., Singh, R.N. and Maryanska-Nadachowska A. (1997) Biology and karyology of a cecidogenous psylloid, *Trioza fletcheri minor* (Homoptera: Psylloidea) and morphogenesis of galls on the leaves of *Terminalia tomentosa* and *T. arjuna* (Combretaceae). Insecta Matsumuarana (New Series) 53: 117–134.

Raman A., Schaefer C.W. and Withers T.M. (2005a) Biology, Ecology, and Evolution of Gall-inducing Arthropods, Science Publishers, Enfield, USA, 817 pp.

Raman A., Schaefer C.W. and Withers T.M. (2005b) Galls and gall-inducing arthropods: an overview of their biology, ecology, and evolution. In: Biology, Ecology, and Evolution of Gall-inducing Arthropods (A. Raman, C.W. Schaefer and T.M. Withers, eds) Science Publishers, Enfield, USA, 1—34.

Raman A., Burckhardt D. and Harris K.M. (2009a) Biology and adaptive radiation in the gall-inducing Cecidomyiidae (Insecta: Diptera) and Calophyidae (Insecta: Hemiptera) on *Mangifera indica* (Anacardiaceae) in the Indian subcontinent. Tropical Zoology 22: 27–56.

Raman A., Beiderbeck R. and Herth W. (2009b). Early subcellular responses of susceptible and resistant *Vitis* taxa to feeding by grape phylloxera *Daktulosphaira vitifoliae*. Botanica Helvetica 119: 31–39.

Rakitov R. and Appel E. (2012) Life history of the camelthorn gall leafhopper, *Scenergates viridis* (Vilbaste) (Hemiptera, Cicadellidae). Psyche (article ID: 930975), doi: http://dx.doi.org/10.1155/2012/930975.

Rohfritsch O. (1971) Étude d'une galle de *Lobopteromyia* sp. sur *Acacia* (*A. ferruginea* DC.?). Marcellia 39: 139–149.

Rohfritsch O. (1976) Trâces de succion de deux Chermisidae: *Chermes abietes* L. et *Chermes strobilobius* Kalt. dans les bourgeons de *Picea excelsa* L. Marcellia 39: 69–84.

Rohfritsch O. (1988) A resistance response of *Picea excelsa* to the aphid *Adelges abietes* (Homoptera: Aphidoidea). In: Mechanisms of Woody Plant Defences against Insects: Search for Pattern, Springer, New York, USA, 253–266.

Rohfritsch O. (1990) Aphid stylet movement and host-plant reaction in the case of Adelgidae on spruce. In: Aphid-Plant Genotype Interaction (R. K. Campbell, R. D. Eikenbary, eds), Elsevier Science Publications, Amsterdam, pp. 101—116.

Rohfritsch O. and Anthony M. (1992) Strategies in gall induction by two groups of homopterans. In: Biology of Insect-induced Galls, Oxford University Press, New York, USA, 102–117.

Saleem, U.K.A. and Nasser, M. (2015) Insect-induced galls of the Malabar bioregion, Southern India. Oriental Insects 49: 165–197

Samui G. and Jha S. (2009) Biology, seasonal incidence and management of *Apsylla cistellata* Buckton on mango in West Bengal. Journal of Plant Protection Science 1: 16–20.

Schaefer C.W. (2005). Gall-inducing heteropterans (Hemiptera). In: Biology, Ecology, and Evolution of Gall-inducing Arthropods (A. Raman, C.W. Schaefer, T. M. Withers, eds), Science Publishers, Enfiend, NH, USA, 231–238.

Sharma A., Khan A.N., Subrahmanyam S., Raman A., Taylor G.S. and Fletcher, M.J. (2014) Salivary proteins of plant-feeding hemipteroids — implication in phytophagy. *Bulletin of Entomological Research* 104, 117–136.

Sharma A., Raman A., Taylor G.S., Fletcher M.J. and Nicol H. I. (2015) Feeding and oviposition behaviour of a gall inducing species of *Glycaspis* (*Synglycaspis*) (Hemiptera: Psylloidea: Aphalaridae) and development of galls on the leaves of *Eucalyptus macrorhyncha* (Myrtaceae) in central western New South Wales, Australia. European Journal of Entomology 112: 75–90.

Shivankar V.J. and Rao C.N. (2010) Psyllids and their management. Pest Management in Horticultural Ecosystems 16: 1–4.

Shorthouse J.D. and Rohfritsch O. (1992) Biology of Insect-induced Galls. Oxford University Press, New York, U.S.A, 285 pp.

Singh G. (2000) Physiology of shoot gall formation and its relationship with juvenility and flowering in mango. *Acta Horticulturae* 509: 803–810.

Singh G. (2003) Mango Shoot Gall: Its Causal Organism and Control Measures, Indian Council of Agricultural Research, New Delhi, India, 94 pp.

Singh G. and Misra P.N. (1978) The mango shoot gall psyllid *Apsylla cistellata* Buckton and its control. *Pesticides* 12: 15–16.

Singh G., Kumar A. and Everrett T.R. (1975) Biological observations and control of *Apsylla cistellata* Buckton (Psyllidae: Homoptera). *Indian Journal of Entomology* 37: 46–50.

Sopow S. L., Shorthouse J.D., Strong W. and Quiring D.T. (2003) Evidence for long distance chemical gall induction by an insect. Ecology Letters 6: 102–105.

Takagi S. (1987) Notes on the Beesoniidae (Homoptera: Coccoidea). Insecta Matsumurana (New Series) 37: 27–41.

Takagi S. (2007) The gall-inducing coccoid family Beesoniidae (Hemiptera): facts, speculations, and perspectives. Oriental Insects 41: 67–91.

White I.M. and Hodkinson I.D. (1985) Nymphal taxonomy and systematics of the Psylloidea (Homoptera). *Bulletin of the British Museum (Natural History) (Entomology Series)* 50: 153–301.

Will T., Tjallingii W.F., Thonnessen A. and van Bel A.J.E. (2007) Molecular sabotage of plant defence by aphid saliva. Proceedings of the National Academy of Sciences of the USA 104: 10536–10541.

Williams D.J. (1999) E. E. Green's The Coccidae of Ceylon, 1896–1922. Entomologist's Monthly Magazine 135: 189–191.

Young R.F., Shields K.S. and Berlyn, G.P. (1995) Hemlock woolly adelgid (Homoptera: Adelgidae): stylet bundle insertion and feeding sites. Annals of the Entomological Society of America 88: 827–835.

Zalat S., el-Akkad S., Henediq S., Gadalla S. and Gilbert F. (2000) An insect–plant interaction in the Sinai desert ecosystem. Egyptian Journal of Biology 2: 8–14.

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