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Salivary proteins of plant-feeding hemipteroids – implication in phytophagy

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Abstract

Many hemipteroids are major pests and vectors of microbial pathogens, infecting crops. Saliva of the hemipteroids is critical in enabling them to be voracious feeders on plants, including the economically important ones. A plethora of hemipteroid salivary enzymes is known to inflict stress in plants, either by degrading the plant tissue or by affecting their normal metabolism. Hemipteroids utilize one of the following three strategies of feeding behaviour: salivary sheath feeding, osmotic-pump feeding and cell-rupture feeding. The last strategy also includes several different tactics such as lacerate-and-flush, lacerate-and-sip and macerate-and-flush. Understanding hemipteroid feeding mechanisms is critical, since feeding behaviour directs salivary composition. Saliva of the Heteroptera that are specialized as fruit and seed feeders, includes cell-degrading enzymes, auchenorrhynchan salivary composition also predominantly consists of cell-degrading enzymes such as amylase and protease, whereas that of the Sternorhyncha includes a variety of allelochemical-detoxifying enzymes. Little is known about the salivary composition of the Thysanoptera. Cell-degrading proteins such as amylase, pectinase, cellulase and pectinesterase enable stylet entry into the plant tissue. In contrast, enzymes such as glutathione peroxidase, laccase and trehalase detoxify plant chemicals, enabling the circumvention of plant-defence mechanisms. Salivary enzymes such as M1-zinc metalloprotease and CLIP-domain serine protease as in *Acyrthosiphon pisum* (Aphididae), and non-enzymatic proteins such as apolipophorin, ficolin-3-like protein and 'lava-lamp' protein as in *Diuraphis noxia* (Aphididae) have the capacity to alter host-plant-defence mechanisms. A majority of the hemipteroids feed on phloem, hence Ca^{++}-binding proteins such as C002 protein, calreticulin-like isoform 1 and calmodulin (critical for preventing sieve-plate occlusion) are increasingly being recognized in hemipteroid–plant interactions. Determination of a staggering variety of proteins shows the complexity of hemipteroid saliva: effector proteins localized in hemipteran saliva suggest a similarity to the physiology of pathogen–plant interactions.

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Introduction

Understanding the dynamics of insect–plant interactions provides insights into diverse aspects of relationships between plant-feeding insects and their host plants (Walling, 2000; Mitchell, 2004; Smith, 2005; Ali & Agrawal, 2012; Raman, 2012). Recognition of an appropriate plant by an insect and the consequent response – either resistant or susceptible – of the plant can be examined in different ways. Because such relationships are usually triggered by feeding actions, an analysis of the saliva offers scope to understand insect–plant relationships better. For example, aphid-secreted salivary proteins are considered similar to plant-pathogenic effectors and therefore considered to function by perturbing host-cell processes (Arimura *et al.*, 2011). Adequate evidence exists that the feeding behaviours of phytophagous biting–chewing insects on the one hand and sap-sucking insects on the other are strikingly different: the former triggers a jasmonic-acid signalling pathway, whereas the latter triggers the jasmonic acid–ethylene and salicylic-acid signalling pathways (Zhao *et al.*, 2005). Moreover, understanding the structure and roles of salivary proteins provides scope to determine evolutionary trends in phytophagous insects and their host plants (Howe & Jander, 2008).

Stress in plants is a state in which increasing demands are made on a plant, which leads to an immediate perturbation of its functions, followed by gradual reversal to normality of cell function and usually resulting in a better capacity of resistance (Larcher, 1987). During feeding, insects stress plants in multiple ways by affecting plant tissue (Backus *et al.*, 2005*b*) generating stress-mitigating molecular responses (Moran & Thompson, 2001; Thompson & Goggin, 2006), and redirecting the plant's energy in the production of novel secondary compounds (Mutikainen *et al.*, 2002). Physical symptoms of plant stress could manifest as wilting, lesions and either localized or extended necrosis. Insect induced galls — specialized representations in insect–plant interactions — also manifest plant-stress responses (Raman, 2011). Cells of the stressed tissue present anomalous wall structures, irregular and abnormal-wall thickenings, slack-cell membranes, extended and hyaline cytoplasm including large vacuoles, and callose formation (Raman *et al.*, 2009; Atkinson & Urwin, 2012), which are, by and large, similar to the stress inflicted by abiotic factors on plant cells (Harper & Horne, 2012). When plants are unable to resist the stress effect, they experience production of reactive-oxygen species (Atkinson & Urwin, 2012), resulting ultimately either in cell and tissue death or in cell proliferation resulting in gall.

Feeding strategies

Most hemipteroids belong to the sap-sucking guild. Feeding by sap-sucking insects involves the secretion of saliva and ingestion of plant-cell components. Hemipteran mouth parts consist of mandibles and maxillae that are modified into two pairs of stylets, whereas those of the Thysanoptera have assymetrical mouthparts with either reduced or absent right mandible, which enable them to both salivate and ingest simultaneously and efficiently. They utilize one of the following strategies during feeding: (i) stylet-sheath forming, (ii) osmotic-pump feeding and (iii) cell-rupture feeding. The last strategy consists of four sub-strategies, which include lacerate-and-flush, lacerate-and-sip, lance-and-ingest and macerate-and-flush (Hori, 2000; Backus *et al.*, 2005*b*). Sheath-forming hemipteroids feed mostly on vascular tissues whereas the cell-rupture feeders feed mostly intracellularly on either mesophyll or stem parenchyma cells (Backus, 1988). The cell-rupture feeding strategy occurs in the Typhlocybinae in the Auchenorrhyncha, Cimicomorpha and some families of the Pentatomomorpha in the Heteroptera. This type of feeding behaviour includes variation in movement of the outer – the mandibular – stylets and the inner – maxillary – stylets (Backus, 1988). Cell-rupture tactics include (i) active and rapid laceration without complete salivation in lacerate-and-sip feeding behaviour; (ii) alternate salivation and ingestion with slow movement of stylets in lacerate-and-flush feeding; (iii) long probing time and ingestion from phloem by forming salivary pseudosheaths in lance-and-ingest type of feeding behaviour (Backus *et al.*, 2005*b*) and (iv) enzyme-dependent cell degradation in macerate-and-flush feeding (Hori, 2000). Similar to cell-rupturing technique, sheath former also forms sheaths by either movement of entire stylet into plant tissue (species of Pentatomomorpha and Sternorrhyncha) or by penetrating the maxillary stylets deeper into plant tissue compared with branched mandibular stylets (species of Auchenorrhyncha) (Backus *et al.*, 2005*b*).

In a few hemipterans such as *Myzus persicae* (Aphididae), *Bemisia tabaci* (Aleyrodidae) and *Nilaparvata lugens* (Delphacidae), which are salivary-sheath formers, the insects insert their stylets at the feeding sites damaging a few cells. Some insects with stylet-sheath forming behaviour also employ cell-degrading enzymes, such as cellulase, amylase and pectinase, which facilitate minimal mechanical injury to the plant tissue (Miles, 1999; Hori, 2000; Backus *et al.*, 2012). The stylet-sheath pathway can be either intercellular (e.g., *Brevicoryne brassicae*, *M. persicae*, *Rhopalosiphum padi*, all Aphididae) (Prado & Tjallingii, 2007) or intracellular (e.g., *Nephotettix cincticeps*, Cicadellidae) (Hattori *et al.*, 2012). The Coreidae employ an osmotic-pump feeding strategy by enhancing the osmotic potential of the intercellular fluid, viz., the apoplast (Mitchell, 2004). Whereas in *Mictis profana* (Coreidae) that employ the osmotic-pump feeding mechanism, salivary sucrase increases osmotic concentration of intercellular fluids enabling the insect to suck plant sap (Miles & Taylor, 1994; Taylor & Miles, 1994). The Lygaeidae feed by lacerating and flushing, cut the plant tissue and push-and-pull their stylets during feeding. Other cell-rupturing families, such as the Miridae, on the other hand, feed by macerating and flushing; their feeding action degenerates cell walls using specific cell-wall digesting enzymes, such as

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pectinases and cellulases. For example, in those hemipterans, which feed by macerating and flushing, salivary pectinase macerates the tissue (e.g., *Deraeocoris nebulosus*, Miridae; Boyd *et al.*, 2002). Sap sucking (e.g., *Frankliniella occidentalis*, Terebrantia: Thripidae; Kindt *et al.*, 2003) and sap-sucking–sheath-forming (e.g., *M. profana*, Coreidae; Miles & Taylor, 1994; Taylor & Miles, 1994) hemipteroids are known to feed on host-plant parenchyma and either xylem (e.g., *Philaenus spumarius*, Aphrophoridae; *N. cincticeps*, Cicadellidae; Crews *et al.*, 1998; Hattori *et al.*, 2012) or phloem (*Acyrthosiphon pisum*, Carolan *et al.*, 2009). Selection of the feeding site varies according to developmental stage and stylet length. For example, short-styleted Thysanoptera feed on the upper layers of leaf tissue (Kindt *et al.*, 2003), whereas the long-styleted Hemiptera (e.g., *Kerria lacca*, Kerridae) feed on deeper-lying stem tissues (Ahmad *et al.*, 2012). Stylet passage can be either inter- or intra-cellular and the extent of tissue damage depends on probing strategies (Ahmad *et al.*, 2012).

Feeding behaviour and salivary composition

Salivary glands of the Hemiptera and Thysanoptera vary in the structure and number of lobes. In the Hemiptera, one pair of glands occur, each usually comprising a principal gland functioning as a reservoir, and an accessory gland in supplying the fluid to watery saliva in the form of haemolymph ultrafiltrate (Miles, 1999). In the Thysanoptera, two pairs of glands consist of well-differentiated structures: one pair comprises long, tubular glands that run parallel to the intestine, and a second pair that are short, ovoid and usually confined to the thorax (Del Bene *et al.*, 1999). Feeding behaviour is critical in regulating the salivary chemistry of these insects. Most of the Heteroptera and Sternorrhyncha secrete saliva in two ways: as gelly and watery saliva. The gel saliva is composed of lipoproteins, phospholipids and conjugated carbohydrates whereas watery saliva is mainly composed of different enzymes (Miles, 1999; Backus *et al.*, 2005*b*). Recent developments, however, have enabled us to understand the enzymatic composition of the two different salivary secretions (Miles, 1999). For example, immunolocalization techniques indicate that salivary proteins in the principal and accessory glands of *Schizaphis graminum* (Hemiptera: Aphididae) are different. Proteins of molecular weight of 66–69 kDa proteins were found in the watery and gel saliva, whereas 154 kDa protein in watery saliva (Cherqui & Tjallingii, 2000). However, in the Miridae saliva is secreted as a single type, possibly a combination of gelling and watery components (Miles, 1999). Within the Heteroptera salivary enzymes have been characterized in the Pentatomidae, Coreidae, Lygaeidae, Dinidoridae, Pyrrhocoridae, Miridae, Acanthosomatidae, Aradidae, Cydnidae, Largidae, Scutelleridae, Berytidae and Tingidae. They have been characterized in the Cicadellidae and Delphacidae in the Auchenorrhyncha. In the Sternorrhyncha they have been characterized in the Psyllidae, Aphididae and Aleyrodidae. In Thysanoptera salivary enzymes have been characterized in Terebrantia and Tubulifera (table 1).

Damage caused by hemipteroid feeding

While feeding, the members of the Heteroptera damage plant tissues resulting in tissue thinning, malformation and necrosis (Baxendale *et al.*, 1999; Schaefer & Panizzi, 2000), those of the Auchenorrhyncha inflict tip wilting, plant stunting and chlorosis (Backus *et al.*, 2005*b*), whereas those of the Sternorrhyncha induce necrosis and galls (Miles, 1999). Feeding action of the Terebrantia induces necrosis in plant tissue (Hunter & Ullman, 1989), whereas some of the Tubulifera (e.g., *Liothrips, Gynaikothrips*) result in galls (Raman, 2003). Direct damage is due to mechanical injury caused by movement of stylets as well as chemical injury caused by salivary enzymes (Backus *et al.*, 2005*b*). However sap-sucking hemipteroids do not inflict as much mechanical damage as the biting and chewing coleopteroids would; but hemipteroids may, nevertheless, inflict intense physiological changes in the host. For example, feeding actions of *Diuraphis noxia* and *R. padi* (Aphididae) on *Triticum aestivum* and *Avena sativa* (both Poaceae) alter total-protein contents, activities of peroxidase, catalase and polyphenol oxidase (Ni *et al.*, 2001). In the Pentatomorpha and Miridae, salivary enzymes such as pectinase, protease, amylase and cellulase play specific roles in degrading parts of host cells in facilitating stylet insertion. Sap-sucking insects inflict more intense transcriptomic changes in plants compared with the chewing insects. Feeding by *M. persicae* (Aphididae) triggers changes in the expression of 2181 genes in the host-plant *Arabidopsis thaliana* (Brassicaceae), whereas during feeding of *Pieris rapae* (Lepidoptera: Pieridae) only 186 genes are activated (De Vos *et al.*, 2005).

Apart from affecting host plants through direct interaction resulting either in necrosis or in cell damage or in gall induction, in other subtle physiological changes (Morkunas *et al.*, 2011), sap-sucking hemipteroids also transmit pathogenic microbes (Purcell & Almeida, 2005). Species of the Aphidoidea, Psylloidea, Aleyrodoidea, Cicadoidea, Fulgoroidea (Hemiptera) and the Terebrantia (Thysanoptera) are established vectors of many plant pathogens (Hogenhout *et al.*, 2008*a*). There are two major types of insect-transmitted pathogens: circulative and non-circulative. Circulative pathogens penetrate the gut epithelial cells of their insect vectors, migrate into the haemolymph, and then to the salivary glands before vectors re-introduce them into plants via their saliva (Hogenhout *et al.*, 2008*b*). Immediate salivation of the non-circulative pathogens is necessary (Powell, 2005), since the insect gut does not have an appropriate retention capacity for non-circulative viruses in particular, as shown in the transmission of the cauliflower-mosaic virus, which binds specifically to the lining cells of the salivary canal of *B. brassicae* and has to be quickly transmitted to *Brassica oleracea* var. *botryris* (Brassicaeae) (Uzest *et al.*, 2007). Non-circulative pathogens adhere to the stylets of vectors, subsequently are re-introduced into the plant during feeding, without circulating in the hemolymph. For example, the acrostyle, a recently discovered structure on the maxillary stylets of *A. pisum* is houses the stylet-borne pathogens (Uzest *et al.*, 2010). The acrostyle seems to enable either stiffening of the stylet tip or stimulation of the protein–protein interaction in *Vicia faba* (Fabaceae)–*A. pisum* interactions. It seems that the acrostyle may also be helpful in acquiring the virus from one plant and inoculating it into another, as well as launching appropriate salivary contents at the appropriate time, such as release of Ca^{++}-binding proteins with watery saliva, i.e., after stylet-sheath formation preventing sieve-tube occlusion (Uzest *et al.*, 2010). Foregut-borne, non-circulative pathogens also rely on the saliva for transmission. Salivary β-glucosidase of *Homalodisca vitripennis* (Cicadellidae) enables the dispersal of *Xylella fastidiosa* bacterial cells (Xanthomonadales: Xanthomonadaceae), which occur as a dense biofilm in *Vitis*

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Table 1. Host-plant stress inducing salivary proteins in the hemipteroids.

Protein	Hemipteroid	kDa	Class of protein, mode of action and subclass mode of function (EC – Enzyme Commission number)	References
Detoxifying plant alleochemicals and altering plant-defence mechanism				
Cytochrome-oxidase B subunit	*D. noxia*	29	Detoxifies plant allelochemicals Alters plant-defence mechanism	Nicholson *et al.* (2012)
Glucose–methanol–choline oxidoreductase	*A. pisum*	53–66	EC 1.1.1 Acts on the CH–OH group of donors Mediates oxidative detoxification of plant allelochemicals Suppresses plant-defence mechanism	Carolan *et al.* (2009)
Zinc-binding dehydrogenase (EC 1.1.1.1)[1]	*M. persicae*	67	EC 1.1.1 Acts on the CH–OH group of donors EC 1.1.1.1 With NAD^+ or $NADP^+$ as acceptor Detoxifies plant allelochemicals	Cooper *et al.* (2010)
Glucose dehydrogenase (EC 1.1.1.47)	*A. pisum*, *M. persicae*	128	EC 1.1.1 Acts on the CH–OH group of donors Detoxifies allelochemicals Suppress plant-defence mechanism	Harmel *et al.* (2008), Cooper *et al.* (2010), Carolan *et al.* (2011), Nicholson *et al.* (2012)
Glucose oxidase (EC 1.1.3.4)	*M. persicae*	160	EC 1.1.3 Acts on the CH–OH group of donors, with oxygen as acceptor Causes weak induction of wound response in plants Suppress plant-defence mechanism	Harmel *et al.* (2008)
Phenol oxidases[1]	*A. pisum*, *M. rosae*, *S. avenae*, *Aphis gossipii*, *M. persicae*, *M. euphorbiae*, *Agonoscelis rutilia*, *Eumecopus australasiae*, *Eumecopus punctiventris*, *N. viridula*, *Oechalia schellembergi*, *M. profana*, *Elasmolomus sordidus*, *O. fasciatus*, *Dysdercus sidae*, *Creontiades modestum*, *L. rugulipennis*, *Moisonia importunitas*, *Tectocoris lineola*, *H. theivora*	85–200[2]	EC 1. 10 Acts on diphenols and related substances as donors Detoxifies plant allelochemicals	Miles (1999), Hori (2000), Sarker & Mukhopadhyay (2006)
Laccase (EC 1.10.3.2)	*N. cincticeps*	85	EC 1. 10. 3 Acts on diphenols and related substances as donors, with oxygen as acceptor Detoxifies plant-defence mechanism by rapid oxidation of monolignols (lignin) forming nontoxic polymers	Hattori *et al.* (2005, 2010)
Catechol oxidase (EC 1.10.3.1)	*D. noxia*, *N. cincticeps*, *M. profana*, *H. theivora*	200	EC 1. 10 Acts on diphenols and related substances as donors, with oxygen as acceptor Detoxifies plant allelochemicals	Miles (1999), Hori (2000), Ni *et al.* (2000), Hattori *et al.* (2005, 2010), Sarker & Mukhopadhyay (2006)
Ascorbate oxidase	*R. padi*, *D. noxia*	70[2]	EC 1.10 Acts on diphenols and related substances EC 1.10.3 acts as donors with oxygen as acceptor Detoxifies plant allelochemicals	Ni *et al.* (2000)
Peroxidases[1]	*A. pisum*, *M. rosae*, *T. trifollii maculate*, *S. avenae*, *A. gossipii*, *M. persicae*, *M. euphorbiae*, *D. noxia*, *R. padi*, *H. theivora*	60–100	EC 1.11 Acts on a peroxide as acceptor Detoxifies plant allelochemicals	Miles (1999), Ni *et al.* (2000), Cherqui & Tjallingii (2000), Sarker & Mukhopadhyay (2006)
Glutathione peroxidise (EC 1.11.1.9)	*A. pisum*	85	EC 1.11 Acts on a peroxide molecule as anacceptor EC 1.11.1 Peroxidases Detoxifies plant allelochemicals Reduces lipid hydroperoxides to corresponding alchohols Reduces free H_2O_2 to water	Carolan *et al.* (2011)
Catalase (EC 1.11.1.6)	*D. noxia*	240[2]	EC 1.11 Acts on a peroxide molecule as anacceptor EC 1.11.1 peroxidases Detoxifies plant allelochemicals	Ni *et al.* (2000)

Superoxide dismutase	*R. padi*, *D. noxia*, *E. fabae*	325[2]	EC 1.15 Acts on superoxide as acceptor Detoxifies plant allelochemicals	Ni *et al.* (2000), DeLay *et al.* (2012)
Cytochrome P-450	*D. noxia*	50–55	EC 1.13 Acts on single donors with incorporation of molecular oxygen Detoxifies plant allelochemicals Alters plant-defence mechanism	Nicholson *et al.* (2012)
Trehalase	*A. pisum*, *D. noxia*, *M. persicae*, *Eurydema rugosum*, *O. fasciatus*, *D. koenigii*, *L. rugulipennis*, *Eurydema rugosum*, *O. fasciatus*, *D. koenigii*, *L. rugulipennis*	56	EC 3.2 Glycosylases Detoxifies allelochemicals of plants Suppresses plant-defence mechanism	Hori (2000), Cristofoletti *et al.* (2003), Carolan *et al.* (2011), Nicholson *et al.* (2012)
α-glucosidase (EC 3.2.1.3) α-1,4-glucoside glucohydrolase (3.2.1.20) amyloglucosidase	*M. persicae*, *R. padi*, *P. angulosa*, *Pentatoma rufipes*, *C. signatus*, *C. marginatus*, *Leptocorisa varicornis*, *M. profana*, *Gastrodes errugineus*, *Oxycarenus hyalinipennis*, *Dysdercus cingulatus*, *D. fasciatus*, *P. apterus*, *Adelphocoris auturalis*, *Dryocoropsis laticollis*, *A. curvipes*, *C. tomentosicollis*, *C. shadabi*, *R. dentipes*, *M. jaculus*	95–120	EC 3.2 Glycosylases EC 3.2.1 Glycosidases (hydrolysing O- and S-glycosyl compounds) Hydrolyse glucose molecules and toxic phenolic glycosides of plant Amyloglucosidase hydrolase starch of plant tissue	Miles (1999), Hori (2000), Harmel *et al.* (2008), Soyelu *et al.* (2007)
β-glucosidases[1] (β-1,4-glucoside glucohydrolase) (3.2.1.21) 1,3 glucosidase[1] 1,4 glucosidase[1]	*M. persicae*, *R. padi*, *S. graminum*, *C. marginatus*, *L. varicornis*, *D. fasciatus*	114–330	EC 3.2 Glycosylases EC 3.2.1 Glycosidases (hydrolysing O- and S-glycosyl compounds) Detoxify plant allelochemicals May also attack callose in sieve pores	Miles (1999)
α-galactosidase (3.2.1.22) β-galactosidase[1]	*P. angulosa*, *C. marginatus*, *O. funestus*	46–52[2]	EC 3.2 Glycosylases EC 3.2.1 Glycosidases (hydrolysing O- and S-glycosyl compounds) Detoxify plant allelochemicals	Hori (2000)
Sucrase[1] (β-D-fructofuranosidase,α-D-glucohydrolase,) (EC 3.2.1.26, EC 3.2.1.48)	*R. padi*, *M. profana*, *A. obscuricornis*, *G. tasmanicus*	120	EC 3.2 Glycosylases EC 3.2.1 Glycosidases (hydrolysing O- and S-glycosyl compounds) Degrades cells Detoxify phenolic glycosides	Steinbauer *et al.* (1997), Miles (1999)
Angiotensin converting enzyme-like (M2 metalloprotease)	*A. pisum*	100–110	EC 3.4 Peptidases EC 3.4.17 Metallocarbo-xypeptidase Destroy plant-defence proteins	Carolan *et al.* (2009, 2011)
M1 zinc metalloprotease	*A. pisum*	148–156	EC 3.4 Peptidases Destroy plant-defence proteins	Carolan *et al.* (2009, 2011)
CLIP-domain serine protease	*A. pisum*	38	EC 3.4 Peptidases Inhibit phenol oxidase-based innate defences of plants	Carolan *et al.* (2009)
Alkaline phosphatise (3.1.3.1)	*S. avenae*, *B. tabaci D. noxia*, *Lygus sp. D. koenigii*, *C. janus*	112–120	EC 3.1.3 Phosphoric monoester hydrolases helps in avoiding effect of allelochemicals of host during penetration of stylet into plant tissue	Urbanska *et al.* (1998), Hori (2000), Funk (2001), Cooper *et al.* (2010)
Hydroxymethylglutaryl-CoA lyase, mitochondrial-like isoform 2	*D. noxia*	75	EC 4.1 Carbon–carbon lyases EC 4.1.3 Oxo-acid-lyases Degrades plant protein and interferes with lipid signalling of plant Alters defence metabolite of plant Could play a role as a phytotoxin	Nicholson *et al.* (2012)
PR1-like protein (Pathogenesis-related proteins)	*A. pisum*	18–35	Alters defence mechanism	Carolan *et al.* (2009)

Table 1. (*Cont.*)

Protein	Hemipteroid	kDa	Class of protein, mode of action and subclass mode of function (EC – Enzyme Commission number)	References
SMP-30 (Regucalcin) (Senescence marker protein 30)	*A. pisum*	43	Inactivates the plant-defence mechanism	Carolan *et al.* (2009)
Calreticulin	*A. pisum*	48	Helps insect to feed on phloem sap of plant by preventing sieve element occlusion May circumvent calcium-mediated wound responses of host plant	Carolan *et al.* (2011)
Apolipophorin	*D. noxia*	24	Interacts with plant-defence sterols and suppresses them Interfere with signalling of plant's own cellular immune response	Nicholson *et al.* (2012)
Nuclear lamin L1 alpha	*D. noxia*	121	Alters plant-defence mechanism	Nicholson *et al.* (2012)
Stretchin–myosin light chain kinase	*D. noxia*	1313	Prevents defence mechanism of plants which depends on actin/myosin polymerization	Nicholson *et al.* (2012)
Plant-cell degrading				
Phosphorylase[1]	*P. apterus*	100[2]	EC 2.4 Glycosyl-transferases Degrade glycogen to release glucose	Hori (2000)
Pectinases[1]	*S. graminum*, *P. apterus*, *Capsus ater*, *Creontiades dilutes*, *Helopeltis clavifer*, *Lyglineolaris* sp., *Lygus gemellatus*, *L. hesperus*, *L. pratensis*, *L. punctatus*, *L. rugulipennis*, *Miris dolabratus*, *Moissonia importunitus*, *Poeciloscytus unifasciatus*, *Pseudatomoscelis seriatus*, *Stenodema calcaratum*, *Stenotus binotatus*	40–69[2]	Degrades cells Initiates volatile production in plants	Miles (1999), Hori (2000)
Cellulase[1] β-1,4-glucanase	*R. padi*, *D. noxia*, *A. hilare*, *S. graminum*, *Ragmus importunitus*, *H. vitripennis*	35–55[2]	EC 3.2 Glycosylases Degrade cells	Miles (1999), Hori (2000), Ni *et al.* (2000), Backus *et al.* (2012)
Polygalacturonase (3.2.1.15)	*S. graminum*, *A. pisum*, *M. persicae*, *L. hesperus*, *L. rugulipennis*, *L. pratensis*, *L. lineolaris*, *O. kalmii*, *A. lineolatus*, *C. norwegicus* and *Poecilocapsus lineatus*	35.8–38.1	EC 3.2 Glycosylases EC 3.2.1 Glycosidases (hydrolysing O- and S-glycosyl compounds) Degrade pectin components of plant cells	Laurema & Nuorteva (1961), Ma *et al.* (1990), Miles (1999), Cherqui & Tjallingii (2000), Frati *et al.* (2006), Allen & Mertens (2008), Celorio-Mancera *et al.* (2009)
Amylase[1] and (α- and β-amylase (α-1,4-glucan 4-glucanohydrolase) (EC 3.2.1.1)	*R. padi*, *S. avenae*, *M. persicae*, *T. jambolanae*, *B. tabaci*, *E. fabae*, *Eurygaster integriceps*, *H. theivora*, Pentatomidae, Coreoidea, Lygaeidae, Dinidoridae, Pyrrhocoridae, Miridae, Acanthosomatidae, Cydnidae, Largidae, Aradidae, Scutelleridae, Berytidae, Tingidae *A. ramakrishnae*	50–75 48–52 26–75[2]	EC 3.2 Glycosylases Degrade plant cells	Berlin & Hibbs (1963), Rajadurai *et al.* (1990), Cohen & Hendrix (1994), Miles (1999), Raman *et al.* (1999), Hori (2000), Ni *et al.* (2000), Ozgur (2006), Sarker & Mukhopadhyay (2006), Soyelu *et al.* (2007), Harmel *et al.* (2008), Mehrabadi & Bandani (2009), Zibaee *et al.* (2012), DeLay *et al.* (2012)

α-glucosidase (EC 3.2.1.3) α-1,4-glucoside glucohydrolase (3.2.1.20) amyloglucosidase	*M. persicae*, *R. padi*, *P. angulosa*, *P. rufipes*, *C. signatus*, *C. marginatus*, *L. varicornis*, *M. profana*, *G. errugineus*, *O. hyalinipennis*, *D. cingulatus*, *D. fasciatus*, *P. apterus*, *A. auturalis*, *D. laticollis*, *A. curvipes* *C. tomentosicollis*, *C. shadabi*, *R. dentipes*, *M. jaculus*	95–120	EC 3.2 Glycosylases EC 3.2.1 Glycosidases (hydrolysing O- and S-glycosyl compounds) Hydrolyse glucose molecules and toxic phenolic glycosides of plant Amyloglucosidase hydrolase starch of plant tissue	Miles (1999), Hori (2000), Harmel *et al.* (2008), Soyelu *et al.* (2007)
Sucrase[1] (β-D-fructofuranosidase,α-D-glucohydrolase,) (EC 3.2.1.26, EC 3.2.1.48)	*R. padi*, *M. profana*, *A. obscuricornis*, *G. tasmanicus*	120	EC 3.2 Glycosylases EC 3.2.1 Glycosidases (hydrolysing O- and S-glycosyl compounds) Degrades cells Detoxify phenolic glycosides	Steinbauer *et al.* (1997) Miles (1999)
Peptidases[1]	*D. fasciatus Chrysocoris stollii*	30–80[2]	EC 3.4 peptidases Degrades plant cells	
Cysteine endopeptidases Proteinases (EC 3.4.22)	*A. curvipes C. tomentosicollis*, *C. shadabi*, *R. dentipes*, *M. jaculus*	30–80[2]	EC 3.4 Peptidases Degrades cells	Soyelu *et al.* (2007)
Proteases	*T. jambolanae*, *E. integriceps*, *Aelia acuminate*, *A. sibirica*, *Dolycoris baccarum*, *Clavigralla gibbosa*, *O. fasciatus*, *C. janus*, *Dysdercus koeniggi*, *D. laticollis*, *A. curvipes*, *C. tomentosicollis*, *C. shadabi*, *R. dentipes*, *M. jaculus*, *Brachynema germari*, *H. theivora*, *Arrhenothrips ramakrishnae*	165[2]	EC 3.4 Peptidases Degrade plant cells	Rajadurai *et al.* (1990), Raman *et al.* (1999), Hori (2000), Ozgur (2006), Sarker & Mukhopadhyay (2006), Soyelu *et al.* (2007), Hosseininaveh *et al.* (2009), Bigham & Hosseininaveh (2010)
Phosphatase[1]	*M. profana*, *L. gemellatus*, *L. pratensis*, *L. punctatus*, *P. apterus*	112–130[2]	EC 3.1 Acts on ester bonds Dephosphorylation of proteins	Hori (2000)
Acid phosphatase[1] (3.1.3.2)	*O. fasciatus*, *C. janus*, *D. koenigii*, *L. rugulipennis*, *C. signatus*	130[2]	EC 3.1 Acts on ester bonds EC 3.1.3 Phosphoric monoester hydrolases provide phosphate to tissues that have high energy requirements, during development, growth and maturation	Hori (2000)
Lipase, esterase and pectin methylesterase [1]	*D. noxia*, *S. graminum*, *R. padi*, *T. jambolanae*, *E. integriceps*, *Bryocoropsis laticollis Distantiella theobroma*, *Helopeltis bergrothi*, *D. fasciatus*, *C. janus*, *Oxycarenus hyalinpennis*, *O. fasciatus Chilacis typhae*, *Leptoglossus occidentalis*, *H. theivora*, *Pheaacoccus nianihoti*, *A. ramakrishnae*, *E. fabae*	48–52[2] (L), 65–96 (E) 38 (PME) 43–300[2]	EC 3.1 Acts on ester bonds Degrades cells	Rajadurai *et al.* (1990), Ma *et al.* (1990), Calatayud *et al.* (1996), Miles (1999), Raman *et al.* (1999), Hori (2000), Ni *et al.* (2000), Sarker & Mukhopadhyay (2006), DeLay *et al.* (2012)
Carboxylesterhydrolases[1]	*O. fasciatus*	100[2]	EC 3.1 Acts on ester bonds EC 3.1.1 Carboxylic ester hydrolases Degrades plant cells	Hori (2000)
Hydroxymethylglutaryl-CoA lyase, mitochondrial-like isoform 2	*D. noxia*	75	EC 4.1Carbon–carbon lyases EC 4.1.3Oxo-acid-lyases Degrades plant protein and interferes with lipid signalling of plant Alters defence metabolite of plant Could play a role as a phytotoxin	Nicholson *et al.* (2012)

Table 1. (*Cont.*)

Protein	Hemipteroid	kDa	Class of protein, mode of action and subclass mode of function (EC – Enzyme Commission number)	References
Other proteins (*calcium-binding proteins, effector proteins and other non-enzymatic proteins*)				
β-glucosidases[1] (β – 1,4-glucoside glucohydrolase) (3.2.1.21) 1,3 glucosidase[1] 1,4 glucosidase[1]	*M. persicae*, *R. padi*, *S. graminum*, *C. marginatus*, *L. varicornis*, *D. fasciatus*, *E. fabae*	114–330	EC 3.2 Glycosylases EC 3.2.1 Glycosidases (hydrolysing O- and S-glycosyl compounds) Detoxify plant allelochemicals May also attack callose in sieve pores	Miles (1999), DeLay *et al.* (2012)
Calmodulin	*M. viciae*	20–173	Helps insect to feed on phloem sap of plant by preventing sieve element occlusion	Tjallingii (2006), Will & van Bel (2006), Will *et al.* (2007, 2009)
C002 protein	*A. pisum*	28.1	Helps insect to feed on phloem sap of plant by alters the mechanism of blocking of sieve	Mutti *et al.* (2008)
Calreticulin-like isoform 1	*D. noxia*	46	Helps insect to feed on phloem sap of plant by preventing sieve element occlusion	Nicholson *et al.* (2012)
Calreticulin	*A. pisum*	48	Helps insect to feed on phloem sap of plant by preventing sieve element occlusion May circumvent calcium mediated wound responses of host plant	Carolan *et al.* (2011)
NcSP84	*N. cincticeps*	84	Helps insect to feed on phloem sap of plant by preventing sieve element occlusion	Hattori *et al.* (2012)
MP 10 (Microbial protein 10)	*M. persicae*	20	Causes necrosis and suppress flg22 triggered immunity	Bos *et al.* (2010)
Microbial protein C002	*M. persicae*	25	Increases aphid fecundity by acting as effector to promote aphid infestation	Bos *et al.* (2010)
Microbial protein 42	*M. persicae*	30	Reduces aphid fecundity	Bos *et al.* (2010)
Vesicular-fusion protein Nsf1	*D. noxia*	20	Could possibly disrupt host vesicle formation and fusion in the sieve element itself or in companion cells to redirect and modify cell constituents	Nicholson *et al.* (2012)
Apolipophorin	*D. noxia*	24	Interacts with plant-defence sterols and suppresses them Interfere with signalling of plant's own cellular immune response	Nicholson *et al.* (2012)
Ficolin-3-like protein	*D. noxia*	32	Acts defensively by binding host-plant proteins and provides immunity to insects against fungal and bacterial contamination	Nicholson *et al.* (2012)
GTP-binding protein Di-Ras2-like	*D. noxia*	53	May act as phytotoxin by interacting with RAS (reticular activating system) Rho proteins of plants and vacuolization of host cells	Nicholson *et al.* (2012)
Putative cofilin/actin depolymerizing factor-like protein	*D. noxia*	53	Alters plant cellular organization by promoting actin disassembly of plant tissue by binding and depolymerizing	Nicholson *et al.* (2012)
Hydroxymethylglutaryl-CoA lyase, mitochondrial-like isoform 2	*D. noxia*	75	EC 4.1 Carbon–carbon lyases EC 4.1.3 Oxo-acid-lyases Degrades plant protein and interferes with lipid signalling of plant Alters defence metabolite of plant Could play a role as a phytotoxin	Nicholson *et al.* (2012)
Nuclear lamin L1 alpha	*D. noxia*	121	Alters plant-defence mechanism	Nicholson *et al.* (2012)

Lva protein	*D. noxia*	403	Likely inhibits golgi related process of protein secretion and glycosylation in phloem companion cells and surrounding plant tissues and therefore can act as phytotoxins in companion cells	Nicholson *et al.* (2012)
Chitooligosaccharidolytic α-N-acetylglucosaminidase (NAGase)	*D. noxia*	403	EC 3.2 Glycosylases EC 3.2.1.14 Chitinase Increases aphid fecundity by its overexpression in plant May inhibit fungal growth in stylet-probed tissue Inhibit NAGase activity of plant tissue	Nicholson *et al.* (2012)
MAP1	*D. noxia*	484	Acts as plant analog of MAP and negatively affect signalling and cellular organization of plant	Nicholson *et al.* (2012)

EC – Enzyme Commission number [Nomenclature Committee of the International Union of Biochemistry and Molecular Biology (NC-IUBMB)].
[1] Activity of enzyme is reported.
[2] Adapted molecular weight.

vinifera (Vitaceae) and the vector's foregut. β-glucosidase is considered the carrier of bacterial cells egested into the plant, thus initiating the infective process of *X. fastidiosa* leading to Pierce's disease in *Vitis* (Backus *et al.*, 2012).

Among the stylet-sheath forming Hemiptera, the Aphididae are the most investigated. The gelly and watery saliva in the Aphididae include a variety of proteins: phenol oxidases, peroxidases, pectinases, amylases in the watery saliva; polyphenol oxidase, peroxidases and 1,4-glucosidases in the gel saliva, which perform a variety of functions. While tracking phloem cell in the host plant, taxa of the Aphididae injure many mesophyll-parenchyma cells activating wound-signalling pathways (Martinez de Ilarduya *et al.*, 2003), whereas those of the Aleyrodoidea 'tactically' avoid apoplastic plant-defence compounds in host-cell vacuoles (Walling, 2008). The saliva of these insects, while interacting with plants, either transmits microbial pathogens or induces galls. Reactive sites are vital for gall induction; salivary enzymes play a role in stimulating appropriate host physiology resulting in gall induction (Raman, 2010). Among gall-inducing Phlaeothripidae, salivary proteins play a critical role in gall induction. The saliva of the gravid females of *Arrhenothrips ramakrishnae* includes greater quantities of proteases, amylases and lipases than that of the adult males. This is significant because only adult gravid females induce galls on the leaves of *Mimusops elengi* (Sapotaceae); the saliva of the first and second larvae includes maximal levels of amylases, which contribute to gall growth in *M. elengi* (Raman *et al.*, 1999).

To the best of our knowledge, no consolidated discussion on the functions of salivary proteins of phytophagous sap-sucking hemipteroids on the levels of physiological changes in plants exists. In such a context, this article discusses salivary proteins of the hemipteroids (oxidoreductases, hydrolases, transferases, lyases, Ca^{++}-binding proteins, the effector proteins and the newly found salivary proteins such as lamin 1, ficolins) and their role in phytophagy.

Salivary proteins and functions

Amylases, proteases, phenol oxidases, α-glucosidases, catechol-oxidases and pectinases are the most studied enzymes in hemipteroid saliva (Miles, 1999; Hori, 2000). Trehalases, esterases, lipases, acid and alkaline phosphotases, α-galactosidases and peptidases are equally well known (Miles, 1999; Hori, 2000). Whereas the salivary proteins of a majority of the Sternorrhyncha have been implicated in stressing host-plant tissues, a minority has been shown to play a role in modifying host-plant defences (Kaloshian & Walling, 2005). Detoxification of plant-defence compounds is a critical function of both the gel and watery saliva. Polyphenol oxidase and peroxidases in the gel saliva polymerize phenolics of the plant-cell apoplast as an induced-defence mechanism (Miles, 1999). The level of volatiles emitted is low in plants attacked by phloem-feeding Hemiptera and this could be due to salivary enzymes and proteins that can inhibit synthesis of volatiles (Walling, 2008). Activity of esterases, glutathione transferases and cytochrome P-450-dependent mono-oxygenases is known in the saliva of the polyphagous *F. occidentalis*is responsible for the detoxification of different plant allelochemicals, such as organic cyanides, terpenoids and alkaloids (Feyereisen, 1999; Jensen, 2000; Li *et al.*, 2002).

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Oxidoreductases

Catalases, catechol oxidases, superoxide dismutases, ascorbate oxidases, peroxidases, cytochromes and glucose oxidases are present in the hemipteran saliva (Miles, 1999; Hori, 2000; Ni *et al.*, 2000; DeLay *et al.*, 2012). By altering the redox balance, these proteins detoxify phenolic compounds in plant-defence reactions (Miles & Oertli, 1993). Alterations to the redox balance are responsible for tissue damage (Miles, 1999; Ni *et al.*, 2000; Sarker & Mukhopadhyay, 2006). For example, glutathione peroxidase in the saliva of *A. pisum* degrades reactive-oxygen species (ROS) generated in *V. faba* to achieve redox balance; in addition, glutathione peroxidase also reduces lipidhydroperoxides to their corresponding alcohols and also reduces the free H_2O_2 to H_2O (Carolan *et al.*, 2011). Oxidases in the hemipteran saliva act on the aglycones, produced through hydrolase action on glycosides, converting them into non-toxic compounds (Miles, 1999).

Other flavin-adenine dinucleotide-dependent oxidoreductases such as glucose–methanol choline (GMC) as shown in the saliva of *A. pisum* mediate the oxidative detoxification of allelochemicals such as lactic, benzoic, *p*-hydroxybenzoic, vanillic, adipic, succinic, malic, glycolic and *p*-hydroxyphenylacetic acids in *V. faba* (Asaduzzaman & Toshiki, 2012) thus suppressing plant-defence mechanisms (Carolan *et al.*, 2009). This action is similar to that of the salivary glucose oxidase (which is also a GMC oxidoreductase) in *Helicoverpa zea* (Lepidoptera: Noctuidae) feeding on *Nicotiana tabacum* (Solanaceae) reducing the nicotine-defence pathways (Eichenseer *et al.*, 1999). Glucose oxidase in the saliva of *M. persicae* induces weak wound responses in *V. faba* by suppressing defence mechanisms (Harmel *et al.*, 2008). Synthesis of glucose oxidases could be a dominant strategy in plant-feeding hemipteroids, because it affects jasmonic-acid-biosynthesis-regulating genes in plants, when attacked by different species of Aphididae (Harmel *et al.*, 2008).

Dehydrogenases elicit plant-signalling responses to feeding by different Aphididae (Couldridge *et al.*, 2007). For example, *M. persicae* while feeding on the leaves of *Solanum tuberosum* (Solanaceae) rapidly enhances activities of glutamine synthase and glutamate dehydrogenase at the feeding site and an elevated activity of glutamine synthase at distant leaves (Giordanengo *et al.*, 2010), reinforcing the involvement of multiple genes in NO_3 and sugar remobilization (Divol *et al.*, 2005). Glucose dehydrogenase functions similarly to glucose oxidase in suppressing plant defences (Cox-Foster & Stehr, 1994). However, it is unclear whether it alters the redox balance in plants. Glucose dehydrogenase occurs in the saliva of *A. pisum*, *D. noxia* (Aphididae) and *M. persicae* (Harmel *et al.*, 2008; Carolan *et al.*, 2009; Cooper *et al.*, 2010). Zn-binding dehydrogenases from the saliva of *M. persicae* (Cooper *et al.*, 2010) detoxify plant allelochemicals, especially the alcohols. Alcohol $NADP^+$ oxidoreductases reduced aldehydes to alcohol and triggered salicylic-acid, methyl-jasmonate and ethylene biosynthesis pathways in tested plants (Somssich *et al.*, 1996; Montesano *et al.*, 2003).

Phenol oxidases cause browning of individual plant cells by accumulating *o*-quinones and by triggering hydroxylation of monophenols to *o*-diphenols and oxidation of *o*-diphenols to quinines (Urbanska *et al.*, 1998). Phenol oxidases are vital for the detoxification of phenolic compounds; salivary phenol oxidases from *Aphis gossypii*, *Macrosiphum euphorbiae*, *Macrosiphum rosae*, *Sitobion avenae*, *M. persicae* (Aphididae) and some taxa of the Miridae (Hori, 2000; Sarker & Mukhopadhyay, 2006). Phenol-oxidase activity is also known from the salivary sheaths of different aphids and in halos around the sheaths on artificial diets (Urbanska *et al.*, 1994). Phenol oxidases, in high likelihood, oxidize the plant polyphenols to *o*-quinones. During penetration by stylets, the host plant produces phenolics as a defence reaction and phenol oxidases detoxify them by hydrolysation (Miles, 1999).

Ascorbate oxidase – a phenol oxidase – occurs in *D. noxia* and *R. padi* and detoxifies plant phenolics (Ni *et al.*, 2000). Laccase and catechol oxidase have been shown in *N. cincticeps*, while feeding on *Oryza sativa* (Poaceae) (Hattori *et al.*, 2005), where catechol oxidase is indicated to play a role in overcoming plant defences (Miles, 1999). Catechol oxidase in the saliva of *N. cincticeps* oxidizes and polymerizes phenolic compounds that accumulate around the salivary sheath. Monolignols in *O. sativa* produce quinine methides, when plant cells are ruptured by stylet action of *N. cincticeps*, and these quinine methides are protein-alkylating agents, which harm *N. cincticeps* (quinines acts on proteins and diminishes dietary protein value for insects by alkylation; Duffey & Stout, 1996) (Hattori *et al.*, 2005). Laccase oxidizes monolignols to lignin in *O. sativa* and is responsible for making the host-plant consumable.

Peroxidases dehydrogenate phenolic substances (e.g., chlorophenols) and produce phenoxy radicals in the presence of H_2O_2 to form phenolic polymers. Different peroxidases occur in *A. gossypii*, *Therioaphis trifolii maculata*, *M. euphorbiae*, *M. rosae*, *R. padi*, *S. avenae* and *M. persicae*, which appear to mimic phenol oxidases by acting on host-plant phenolics, particularly on alkaloids (e.g., DIMBOA [2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one], gramine) on which phenol oxidase cannot act. H_2O_2 is critical for peroxidase activity; phenol oxidase releases H_2O_2 acting on plant phenolics. Hence, the activity of phenol oxidase and peroxidase is possibly synergistic (Miles, 1999; Cherqui & Tjallingii, 2000; Ni *et al.*, 2000). While feeding on *Camellia sinensis* (Theaceae), these enzymes in the saliva of *Helopeltis theivora* (Miridae) induce necrosis in growing shoots (Sarker & Mukhopadhyay, 2006). Oxidation of phenols is necessary for insect survival on plants, but this process also produces H_2O_2, which can damage plant cells. The concurrent presence of peroxidase in insect saliva may act on the synthesized H_2O_2 and reduce it, thus preventing a hypersensitive response of the plant and enabling the insect to consume the plant without interruption. Catalases and superoxide dismutase act on H_2O_2 and convert it into H_2O and O_2. Catalase is reported from the salivary secretions of *D. noxia* and is responsible for leaf chlorosis in susceptible wheat plants either by reducing chlorophyll synthesis or by degrading chlorophyll and indirectly affecting the redox balance of the plant (Ni *et al.*, 2000).

Cytochrome P-450 (Cyt P-450) is a major enzyme class in the saliva of almost all insects. They act as mixed-function oxidases and mono-oxygenases. Cyt P-450 is critical for defending insects against plant chemicals. Adaptation of insects to a particular host plant also depends on plant-chemical break down using Cyt P-450 (Feyereisen, 1999). Salivary Cyt P-450 in *D. noxia*, while feeding on *T. aestivum*, detoxifies allelochemicals, such as *p*-hydroxybenzoic, *trans*-*p*-coumaric, *cis*-*p*-coumaric, syringic, vanillic, *trans*-ferulic and *cis*-ferulic acids, DIMBOA (Wu *et al.*, 2000; Nicholson *et al.*, 2012). Cyt P-450 sequences are vital in mediating isoprenoid biosynthesis; isoprenoids function in plant–arthropod signalling as herbivore repellents and as attractants of arthropod

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parasitoids (Boyko *et al*., 2006), although this aspect has not yet been demonstrated in plant-feeding hemipteroids.

Hydrolases

Hydrolases induce phytotoxicosis, such as wilting and necrosis of plant tissues, as shown in *Eucalyptus regnans* and *Eucalyptus nitans* (Myrtaceae) consequent to feeding by *Amorbus obscuricornis* (Coreidae) (Steinbauer *et al*., 1997) and browning of cells in *S. tuberosum* following feeding by *S. avenae* (Urbanska *et al*., 1998). Pectinase, cellulase and amylase soften the tissue facilitating stylet entry and its movement in host tissue. Simultaneously, pectinases provide gustatory clues and render the plant amenable to feeding. To elicit the gustatory clue, the aphids initially taste cell contents. For example, *M. persicae* feeds on artificial diets that include 2, 3-diacetyl pectin, a component in its preferred host *Beta vulgaris* (Amaranthaceae). Monophagous (e.g., *B. brassicae*) and oligophagous aphids (e.g., *Melanocallis caryaefoliae*) show greater gustatory sensitivity for plant polysaccharides compared with polyphagous aphids (e.g., *M. persicae*). Aphids with a lesser capability to discriminate between different polysaccharides usually remain polyphagous (Campbell *et al*., 1986). While degrading plant tissue, damage due to hydrolases varies according to feeding sites: when species of *Lygus* feed on mesophyll tissue they induce simple lesions, but when they feed on meristematic tissue, they inflict severe damage resulting in tissue malformation (Hori, 2000).

Pectinase degrade pectin, one of the principal components of the middle lamella of plant cells. As part of the watery saliva, pectinases induce degenerative changes in host cells, as shown in the saliva of *Lygus hesperus* (Miridae) in disintegrating parenchyma cells (Strong & Kruitwagen, 1968) and in pre-empting a wound response by producing pectin fragments (Miles, 1999; Hori, 2000). Activity of pectinase is reported from different aphids and the Heteroptera (table 1).

Cellulase activity is known from *S. graminum* enabling the depolymerization of xylans and arabinogalactans of cell walls, which on secretion into plant tissue render cellulose ingestible. Hydrolysis of cell-wall polysaccharides by salivary cellulase facilitates stylet penetration, although the mechanical properties of the cell wall regulate its movement within, as shown in *Acrosternum hilare* (Pentatomidae) in enabling stylet penetration in *Sorghum vulgare* (Poaceae), but due to degradation of cellulose, occurrence of wound responses due to cellulose action is a possiblity (Miles, 1999). β -1,4-glucanase (which is related to cellulase) in the saliva of *H. vitripennis* (Cicadellidae) hydrolyses hemicelluloses in cell walls, facilitating the sealing of the sheath-encased stylet tips into xylem elements. Enzymes in the saliva are also hypothesized to loosen populations of Pierce's-disease bacterium in the vector's foregut, allowing subsequent egestion to inoculate the bacteria into the xylem of *V. vinifera* (Backus *et al*., 2012).

Polygalacturonase is a pectin-hydrolysing enzyme that enables intercellular-stylet movement (Campbell & Dreyer, 1990). Endo- and exo-polygalacturonases are known from the hemipteran saliva (Laurema & Nuorteva, 1961; Miles, 1999; Celorio-Mancera *et al*., 2009). Activity of these enzymes is recorded for *Lygus rugulipennis*, *Lygus pratensis*, *Orthops kalmii* (Miridae), *Adelphocoris lineolatus* (Miridae) *Closterotomus norwegicus* (Miridae) (Frati *et al*., 2006), *S. graminum*, *A. pisum* and *M. persicae* (Miles, 1999; Cherqui & Tjallingii, 2000). Exo-polygalacturonase produces lesser quantities of galacturonides by acting on the oligouronides compared with other pectinases. Endo-polygalacturonases degrade pectin and generate oligosaccharides (Celorio-Mancera *et al*., 2009). Polygalacturonase activity is shown in the saliva as well as in other body parts of the Hemiptera, in halos of watery saliva restored in artificial diets and in salivary proteins (Miles, 1999; Frati *et al*., 2006).

Amylases are the most prevalent enzymes in the saliva of most of the phytophagous hemipteroids (Urbanska & Leszczynski, 1997; Hori, 2000; Harmel *et al*., 2008). α- and β-amylase and amyloglucosidase occur in the saliva of *Anoplocnemis curvipes*, *Clavigralla tomentosicollis*, *Clavigralla shadabi* (all Coreidae), *Riptortus dentipes* and *Mirperus jaculus* (both Alydidae) that feed on *Vigna unguiculata* (Fabaceae). Whereas the α-amylase and amyloglucosidase hydrolyse starch to release energy, β-amylase hydrolyses 1,4-α-d-glycosidic linkages of starch and releases β-maltose. Amyloglucosidase removes glucose units from amylopectin and hydrolyses a greater proportion of starch from *V. unguiculata* (Soyelu *et al*., 2007). α-amylase is also known to occur in *Eurygaster maura* (Scutelleridae), which feeds on wheat seeds (Mehrabadi & Bandani, 2009). Lower-molecular weight of salivary α-amylase suggests that salivary α-amylase is an isozyme (Zibaee *et al*., 2012). In the Heteroptera, amylase activity is known from different species of the Pentatomidae, Coreidae, Lygaeidae, Dinidoridae, Pyrrhocoridae, Miridae, Aradidae, Cydnidae, Largidae, Scutelleridae, Berytidae and Tingidae (Hori, 2000) (table 1). In the Sternorrhyncha, amylases have been recorded in *R. padi* and *S. avenae* (Miles, 1999). While feeding on *V. faba*, *S. avenae* releases α – 1,4-glucan-4-glucanohydrolase, which is an amylase, that metabolizes the carbohydrates in *V. faba*, but simultaneously stress*V. faba*. Salivary α-amylase in *M. persicae* catalyses the hydrolysis of oligosaccharides and polysaccharides and renders glucose to *M. persicae* (Harmel *et al*., 2008). Amylase activity has also been reported from *A. ramakrishnae* (Thysanoptera: Phlaeothripidae) and *B. tabaci* (Cohen & Hendrix, 1994; Raman *et al*., 1999).

Trehalase degrades trehalose to two molecules of glucose. Trehalose (1,1-α-D-glucopyranosyl α-D-glucopyranoside) has both protective and adverse effects on plants in that it is critical for the infectivity of pathogens and in eliciting defence responses to abiotic and biotic stresses, although its exact role and mechanism in biotic stress is being debated (Fernandez *et al*., 2010). Trehalose has been implicated for defence response in *Arabidopsis thaliana* against *M. persicae*. Trehalose-PO^4-synthase 11 (TPS11) is critical for antixenosis and antibiosis against *M. persicae* by promoting relocation of C into starch; TPS11 thus enhances accumulation of starch in plant tissue *in lieu* of sucrose. Trehalase occurs not only in the saliva of *A. pisum* but also in its midgut (Cristofoletti *et al*., 2003; Carolan *et al*., 2011; Nicholson *et al*., 2012). Degradative action of trehalase may affect trehalose-based plant defensive responses (trehalose delays programmed-cell death, elicits plant defence, promotes stress responses to proteins such as ϕ -glutathione S-transferase 2 [AtGSTF2], flavin mononucleotide-binding flavodoxin-like quinone reductase 1 [FQR1], cytosolic dehydroascorbate reductase 1 [DHAR1] and S-adenosylmethionine synthetase 2 [SAMS2]) (Baea *et al*., 2005), besides enabling insect survival on *V. faba* (Nicholson *et al*., 2012).

α-glucosidase, α – 1,4-glucosideglucohydrolase, amyloglucosidase, β-glucosidases (β – 1,4-glucoside glucohydrolase), 1,3-glucosidase and 1,4-glucosidase are known in the

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Hemiptera. These enzymes mediate hydrolysis of glucose molecules and the 'toxic' phenolic glycosides in plants, which are released during stylet insertion in mesophyll tissues. Glucosidases convert phenolic glycosides into aglycones. Glucosidases have been isolated from the salivary-gland homogenates of *S. avenae* and *R. padi* and from gut extract and watery saliva of *M. profana* (Miles, 1999; Hori, 2000). Amyloglucosidase in the saliva of *A. curvipes*, *C. tomentosicollis*, *C. shadabi*, *R. dentipes* and *M. jaculus* hydrolyse greater quantities of starch as shown in *V. unguiculata* compared with other salivary amylases in providing energy to these Coreidae (Soyelu *et al.*, 2007). 1,3-glucosidases break pectin contents of plant tissue and may also act on the callose on sieve plates (Miles, 1999). α- and β-galactosidase, are also carbohydrate digesting enzymes, whose weak activity is reported from saliva of *Palomena angulosa* (Pentatomidae), *Coreus marginatus* (Coreidae) and *Orthocephalus funestus* (Miridae).

β-D-fructofuranosidase and α-D-glucohydrolase are sucrose, maltose and trehalose hydrolysers. Urbanska & Leszczynski (1997) confirmed that probing by *S. avenae* and *R. padi* into substrates containing sucrose releases glucose by the activity of β-D-fructofuranosidase, which is available as a carbon source for the feeding insects. In the saliva of *M. profana* (Coreideae), β-D-fructofuranosidase enables degradation of sucrose to glucose and fructose and enhancing apoplast osmotic pressure and helps *M. profana* to feed from apoplast (Miles & Taylor, 1994; Taylor & Miles, 1994). α-dihydroxy-glucohydrolase is known in the saliva of *R. padi* and *S. avenae*; however, its role is confusing because the usual function of this enzyme is to unload the phloem content; yet this function is not required by these aphids. However, gall-inducing aphids may use this enzyme for feeding indirectly from sieve-tube elements (Miles, 1999). Sucrase in the saliva of *A. obscuricornis* and *Gelonus tasmanicus* (Coreidae) possibly enables the insects to feed on phloem and in consequence, induces wilting and necrosis in the leaves of *Eucalyptus regans* and *Eucalyptus obliqua* (Steinbauer *et al.*, 1997).

Another less frequently occurring hydrolase is chito-oligosaccharidolytic β-N-acetylglucosaminidase (NAGase) from the saliva of *D. noxia* feeding on *T. aestivum* (Poaceae). NAGase is a chitinase protein and is involved principally in the regeneration of the exoskeleton of *D. noxia*. It is also known to enhance fecundity in *M. persicae*, when overexpressed in *S. tuberosum* (Saguez *et al.*, 2005) and functions as an antifungal compound in other plants by hydrolysing N-glycans of polysaccharides and glycoproteins (Altmann *et al.*, 1999). Because of such a role, in the saliva of *D. noxia*, it possibly inhibits fungal infection in the probed-plant tissues; it appears that NAGase-s act in concert with chitinase and chitin synthase providing opportunity for controlled lysis and synthesis of chitin is known (Horsch *et al.*, 1997). In plants, NAGase functions as a defence protein against fungal pathogens therefore NAGase in the aphid saliva possibly protects the stylet from the host plant's NAGase activity (Nicholson *et al.*, 2012).

Peptidase (protease, proteinase) are the protein-hydrolysing enzymes, reported from a range of hemipteroids. Proteases are important for initiating gall induction in *M. elengi* by *A. ramakrishnae*. In pod-sucking Coreidae, protease occur abundantly in saliva and are responsible for characteristic symptoms such as shrivelling of young pods, partially filled older pods and dimpled seeds in mature pods (Soyelu *et al.*, 2007).

CLIP-domain serine protease (clip-SP, paper-clip-like domain) occurs in the saliva of *A. pisum*, where it inhibits phenol oxidase-based innate defences of *V. faba* (Carolan *et al.*, 2011). M2 metalloprotease (angiotensin-converting enzyme) and M1 zinc metalloprotease are also known from the saliva of *A. pisum*, where these enzymes destroy plant-defence proteins and improve food quality for phloem-feeding insects by increasing the level of free-amino acids in phloem. Although the exact mechanism is unclear, M2 metalloprotease degenerates signalling peptides, such as hormones and neuropeptides (Carolan *et al.*, 2011).

Phosphatases are responsible for dephosphorylation of proteins. Alkaline phosphatase (ALP) is recorded from the saliva of *B. tabaci* and *B. argentifolii* (Aleyrodidae). ALP in other tissues plays a secondary role in the production of sheath and glue from colleterial glands for the attachment of eggs to foliage (Funk, 2001; Cooper *et al.*, 2010; Yan *et al.*, 2011). It is also reported from salivary glands of other Hemiptera such as one species of *Lygaeus*, *Dysdercus koenigii* and *Coridius janus* (Dinidoridae; Hori, 2000). Acid phosphatase is reported from *Oncopeltus fasciatus*, *C. janus*, *D. koenigii*, *L. rugulipennis*, and *Cletus signatus*, but not in any taxon of the Aphididae (Hori, 2000).

Lipase, esterase and pectin-methylesterase (pectinesterase) form another group of hemipteran salivary enzymes which act on lipids. Lipase activity is shown in the salivary glands of *A. ramakrishnae* (Raman *et al.*, 1999), and *Trioza jambolanae* (Triozidae) (Rajadurai *et al.*, 1990) and a few taxa of the Lygaeidae and Miridae (Hori, 2000; Sarker & Mukhopadhyay, 2006). Pectinesterase is important in intercellular-stylet penetration by dissolving the middle lamellae (Campbell & Dreyer, 1990) and reported in *A. pisum*, *D. noxia*, *M. persicae*, *R. padi* and *S. graminum* (Ma *et al.*, 1990; Cherqui & Tjallingii, 2000; Ni *et al.*, 2000) and carboxylesterhydrolases in *O. fasciatus* (Hori, 2000). Presence of pectinesterase in *Phenacoccus manihoti* (Pseudococcidae) is shown to be responsible for degrading middle lamellae of *Manihot esculenta* (Malpighiales: Euphorbiaceae) (Calatayud *et al.*, 1996).

Transferases and lyases

Information on transferases in insect saliva is limited, although the role of glutathione S-transferase in insects is established for inducing resistance against insecticides (Kostaropoulos *et al.*, 2001). Activity of cell-degrading phosphorylase is known in *Pyrrhocoris apterus* (Pyrrhocoridae) (Hori, 2000). The function of phosphorylase, in general is to confer or add a phosphate group to a protein or a compound. They hydrolyse starch into glucose through a cascade of events (Rathore *et al.*, 2009) and also phosphorylate proteins (Giordanengo *et al.*, 2010) or possibly facilitate the generation of ROS (Manda *et al.*, 2009) thereby stressing the host plant. Lyases degrade the substrate without hydrolysis and oxidation. In hemipteroid saliva, lyase activity has not been much explored but the role of hydroperoxide lyase is demonstrated in hemipteroids, such as in *Sogatella furcifera*. Hydroperoxide lyase plays a role in inducing resistance in *O. sativa* to bacterial blight, *Xanthomonas oryzae* (Gomi *et al.*, 2010). Hydroxymethylglutaryl-CoA lyase has been detected in salivary constituents of *D. noxia*. This is an enzyme of mitochondrial origin and primarily helps in ketone-body production. It seems to degrade plant proteins and interfere in lipid signalling and hence may alter host-plant physiology (Nicholson *et al.*, 2012).

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Ca^{++}-binding proteins

Ca^{++}-binding protein (Calmoludin) are recorded in the saliva of many aphids. After puncturing sieve-tube elements, aphids feed passively with phloem flowing into their stylet canals enabled by a turgor-pressure gradient. Innate plant-defence mechanisms enable occlusion of sieve-tube elements by callose, a high-molecular weight β-(1,3)-glucan polymer, in response to the wound inflicted by insertion of the stylets. Callose formation is preceded by the formation of proteinaceous materials (Furch *et al*., 2009), such as the forisomes (the contractile protein bodies that can modify their structures from crystalloid to sphaeroid formations) shown in Fabaceae, the parietal-phloem proteins (e.g., GFP–SEO proteins) in Cucurbitaceae, and the phloem-protein network in Brassicaceae (Sjölund, 1997). However, what is common among the three studied plant families is that the occlusion of sieve elements is Ca^{++}ion dependent (Knoblauch & van Bel, 1998). To prevent sieve-tube occlusion, the Hemiptera use salivary Ca^{++}-binding proteins such as calmodulin, calreticulin, C002 protein, angiotensin and PR1-like protein SMP-30 (regucalcin), NcSP84 and Calreticulin-like isoform 1, which bind with Ca^{++} influx in the phloem restricting sieve-tube occlusion. The presence of these proteins was detected in saliva of *A. pisum*, *Megoura viciae*, *D. noxia*, *Aphis fabae*, *M. euphorbiae*, *S. graminum* and *N. cincticeps* (Carolan *et al*., 2009, 2011; Will *et al*., 2009; Hattori *et al*., 2012; Nicholson *et al*., 2012). This is also coincide with study of feeding behaviour by electrical penetration graph (EPG) (Prado & Tjallingii, 1994; Tjallingii, 2006). EPG study of *A. pisum*, *M. viciae*, *M. euphorbiae*, *B. brassicae*, *A. gossypii* and *M. persicae* shows that while continuously ingesting phloem sap, aphids switch from ingestion to secretion of watery saliva. Wounding triggers the plant for Ca^{++} influx, enabling sieve-tube occlusion, which, in turn, enables a drop in sieve-tube pressure stimulating the aphids to secrete Ca^{++} including watery-saliva (Will *et al*., 2009). The acrostyle on the maxillary stylets of *A. pisum* is believed to be responsible for releasing Ca^{++}-binding proteins with watery saliva (Uzest *et al*., 2010).

Calreticulin interferes with Ca^{++} influx in probed plant cells through chelation and may circumvent Ca^{++}-mediated wound responses of the host plant (Carolan *et al*., 2011). Calreticulin-like isoform-1 enables *A. pisum* to ingest phloem sap. It alters the mechanism of blocking the sieve-tube element, which usually eventuates as a plant response to insect attack (Nicholson *et al*., 2012). C002 protein helps the insect to feed on phloem sap of the plant by altering the blocking mechanism, which is induced due to plant response to insect attack. In addition, it is also implicated in converting forisomes of the sieve element to contract, preventing blockage of sieve elements (Mutti *et al*., 2008). PR1-like proteins of insect saliva, which are a homologue of the PR1 protein of plants, can interfere with the function of PR1 in plants. PR1 are considered lipid-transfer proteins that mediate the signalling of systemic defence responses in plants, thereby altering defence mechanisms (van Loon *et al*., 2006; Carolan *et al*., 2009). SMP-30 (Regucalcin) is a Ca^{++}-binding protein reported from *A. pisum* feeding on *V. faba*. This protein is also known to have a suppressive effect on intracellular calcium ion homoeostasis and thus regulate intracellular signalling (Carolan *et al*., 2009). Other than aphids, recently Ca^{++}-binding proteins (NcSP84) are reported from *N. cincticeps*, which feeds on phloem and xylem of *O. sativa* (Youn, 1998; Hattori *et al*., 2012).

Effector proteins

In insect–plant interactions, an induced plant-defence mechanism is critical. This mechanism is a part of the plant's innate immune system and works in two phases, as shown in microbial pathogenesis (Hogenhout & Bos, 2011). The first phase depends on the recognition of microbial-associated molecular patterns of pathogens, such as 'flagellin' (flg), a protein, which is recognized by the host plant's pattern-recognition receptors. This recognition induces a 'microbial-associated molecular pattern-triggered immunity' (Jones & Dangl, 2006). The microbial pathogens counter the host-plant's triggered immunity by generating effector molecules, which could be proteins suppressing such a first-phase immunity. These effectors induce an effector-triggered immunity, which is associated with plant disease resistance genes (e.g., R genes) as the second phase. Similar effectors, e.g., Mp10, Mp42 and MpC002 have been reported in the saliva of *M. persicae* (Mp), feeding on *Nicotiana benthamiana* (Bos *et al*., 2010). These effector proteins inflict chlorosis in *N. benthamiana*, when overexpressed. Mp-10 effector causes chlorosis and local cell death; however, it does not show response in other plants on which it was tested, viz., *N. tabacum* and *Solanum lycopersicum*. Mp10 suppresses flg22-induced oxidative burst responses of the plant-defence mechanism, but does not suppress any chitin-induced oxidative burst response, which could be caused by the stylet action. Moreover, overexpression of Mp10 also causes reduced fecundity of aphids. Similarly, Mp 42 also reduces fecundity of aphids but MpC002 increases fecundity of aphids (Bos *et al*., 2010).

Non-enzymatic proteins

A putative ficolin-3-like protein is known in *D. noxia*. This protein contributes to the innate immunity of animals. Ficolins, powerful molecules in host defence (Endo *et al*., 2011), can recognize N-acetyl compounds such as lipopolysaccharides of bacterial and fungal cell walls. Ficolins can activate the associated complementary compounds such as lectins enabling phagocytosis and the breakdown of pathogenic microbes. In sap-sucking insects ficolins prevent secondary infection of the host plant during stylet insertion. Moreover, cellular Ca^{++} influxes during aphid feeding may provide suitable conditions for ficolin activity as Ca^{++} is required as a cofactor for ficolin activity (Nicholson *et al*., 2012). Nuclear lamin-like protein (L1 alpha) is also known from *D. noxia*. It functions as intermediate filaments (IF) proteins. IF-proteins are, however, capable of modifying their configuration and adapt to performing new functions. Elasticity is another property of this protein. IF-proteins are capable of cushioning cellular mechanical stress. Presence of exoskeleton in insects is explained as a reason behind the absence of cytoplasmic IF in insects, and the IF-proteins can be compensated by other proteins in insects (Herrmann & Strelkov, 2011). However, their exact role is not known yet but, L1 alpha may function in reducing mechanical stress during stylet insertion by aphids into plant tissue (Nicholson *et al*., 2012).

Vesicular-fusion protein, N-ethylmaleimide-sensitive factor 1 (Nsf1) is an ATPase. ATPases occur in all eukaryotic cells. Nsf-s are concerned with membrane fusion and can regulate neurotransmission. Expression of one of the negative mutants of Nsf inflicts cell death (Zhao *et al*., 2008). In plants after wounding, sieve plates occlusion occurs, preventing

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phloem-sap flow. In the saliva of *D. noxia*, the presence of Nsf1 may hinder vesicle formation, which is necessary for sieve-tube element fusion (Nicholson *et al.*, 2012).

Actin, a multifunctional protein, occurs in all eukaryotes, and is an integral component of cytoskeleton. In *D. noxia* saliva, three putative actin-binding and depolymerizing proteins are known. Actin-depolymerizing factors are essential for *Meloidogyne incognita* (Nematoda: Heteroderidae) infestation (Clément *et al.*, 2009). Stretchin–myosin light chain kinase protein that enables the assembly of actin filaments in its host-plant tissue is known in *D. noxia*. Putative cofilin–actin depolymerizing factor-like protein facilitates actin depolymerization. Hence, these proteins may prevent activation of defence responses of plants to insect feeding, which depends on actin polymerization (Nicholson *et al.*, 2012).

Microtubule-associated protein futsch (MAP1) known in the nerve signalling and microtubulular organization in *Drosophila melanogaster* (Diptera: Drosophilidae) (Bettencourt da Cruz *et al.*, 2005), is also known from plants, although their role in plants is not yet established in microtubular organization (Gardiner & Marc, 2011). MAP1 in the saliva of *D. noxia* is therefore inferred to act similarly to plant MAP proteins, obstructing cell signals and thus facilitating the feeding action of insects (Nicholson *et al.*, 2012). Lava lamp (Lva), a golgin protein, in *D. noxia* is implicated in cellularization, which is the separation of a multi-nucleate cell into several uninucleate cells. The Lva domains have been demonstrated to bind the microtubule-dependent motility factors and inhibit Golgi movement leading to cellularization in *Drosophila melanogaster*. It is proposed that Lva may interfere with the Golgi particle-related process of protein synthesis in companion cells of the phloem and surrounding plant tissues and thus can be toxic in companion cells (Nicholson *et al.*, 2012).

Guanosine triphosphate (GTP)-binding Di-Ras2-like protein is a GTPase and can hydrolyse GTP. Whereas the 'Ras' proteins activate nerve-tissue formation (Hall & Lalli, 2010), overexpression of Di-Ras2-like protein inhibits cell growth and cell survival as shown in human tissue (Gasper *et al.*, 2010). Di-Ras2-like protein, shown in *D. noxia* saliva, may inflict damage through vacuolization in host-plant cells (Nicholson *et al.*, 2012).

Lipases catalyse either formation or cleavage of fats. In insect saliva, the only lipase known is apolipophorin from *A. pisum* (Carolan *et al.*, 2009) and *D. noxia* (Nicholson *et al.*, 2012). In many other insects including *Manduca sexta* (Lepidoptera: Sphingidae) and *Schistocerca gregaria* (Orthoptera: Acrididae) apolipophorin is implicated in lipid transportation (Wang *et al.*, 2002; van der Horst & Rodenburg, 2010). Apolipophorin is abundant in insect haemolymph and participates in the insect's immune system. It has the capacity to interact and alter the plant-defensive sterols, fatty acids and carotenoids (Ma *et al.*, 2006; Zdybicka-Barabas & Cytryńska, 2011). Secreted apolipophorins could interfere with signalling of a plant's cellular immune response, apolipophorins after binding to lipid elicitor molecule undergoes a confirmational change and induces plant-immune response.

Conclusion

Feeding behaviours among the hemipteroids vary widely as indicated by EPG studies on *R. padi* (Prado & Tjallingii, 1994), *Diaphorina citri* (Psyllidae; Bonani *et al.*, 2010), *Phenacoccus solenopsis* (Pseudococcidae) (Huang *et al.*, 2012), *H. vitripennis* (Backus *et al.*, 2005*a*), *Orosius orientalis* (Cicadellidae) (Trebicki *et al.*, 2012) and *F. occidentalis* (Kindt *et al.*, 2003). Feeding guilds, too, in the hemipteroids vary equally in magnitude.

Thysanoptera, with their relatively short, characteristically asymmetrical mouth parts damage multiple host cells (e.g., epidermal and upper mesophyll cells) during feeding (Moritz, 1995; Kirk, 1997). Among those belonging to the gall-inducing guild, e.g., many phlaeothripids, one gravid female triggers gall development, although the final gall shape is realized only by the collective feeding impact of all of her offspring (Raman *et al.*, 1978; Raman, 2003). Unfortunately, not much is known on the salivary composition of the Thysanoptera other than amylases, proteases and lipases are implicated in damaging epidermal cells (Raman *et al.*, 1999). Pectinases, known in the saliva of Heteroptera, e.g., *L. hesperus* (Hori, 2000) have not yet been demonstrated in the Thysanoptera leaving the question open whether the amylases, proteases and lipases can by themselves perform the function of host-cell degradation. Evolution of thrips from a plesiotypic life style (Mound & Morris, 2005) to feeding on leaves (e.g., *A. ramakrishnae* on *M. elengi*) and fruits (e.g., *Scirtothrips citri*; Thripidae, on fruits of different species of *Citrus* (Rutaceae) on the one hand, and on fungal mycelia and spores (e.g., *Allothrips bournieri*; Phlaeothripidae), pollen (e.g., *Thrips fuscipennis*; Thripidae on *Rosa* sp.; Rosaceae) on the other, and their capability to induce complex galls by modifying the vegetative terminal meristems to develop into large enclosing pouches (e.g., *Austrothrips cochinchinensis*; Phlaeothripidae on *Calycopteris floribundus*; Combretaceae) indicate that the enzyme machinery in thrips saliva – details still to be determined – is highly varied. What can be determined is that the feeding action of the Thysanoptera is unwieldy compared with that of the Sternorrhyncha, but is vaguely similar to the majority of the Auchenorrhyncha.

Both Auchenorrhyncha and Sternnorrhyncha are phytophagous. The Sternorhyncha feeds on plant sap, from leaves (e.g., *D. citri*), stems (e.g., *K. lacca*) and roots (e.g., *Pemphigus betae*; Aphididae). The adults of a majority of the Aphidoidea, which are obligate-phloem feeders, seldom rely on surface signals (Powell & Hardie, 2000; Powell *et al.*, 2006). Their stylet pathway is intercellular, but they puncture mesophyll cells randomly along the path during probing and tasting. Adults of the Aleyrodoidea, which essentially feed on phloem, occasionally ingest xylem sap and, contrary to that found in the Aphidoidea, make fewer attempts probing and tasting. They, thus, inflict fewer intracellular punctures in the mesophyll cells (Walling, 2008; Stafford *et al.*, 2012). A majority of enzymes characterized in the Sternorrhyncha is in different Aphidoidea and have been shown to perform varied functions such as degradation of cells by amylases and cellulases, detoxifying plant-defence compounds by peroxidases and phosphatases and the proteins responsible in plate formation during cell divisions (e.g., actin), and binding mannans during host-plant metabolism (e.g., ficolin), whereas in the Aleyrodoidea, the key enzymes are phosphatases (Funk, 2001). Other Sternorrhyncha insert their stylets intercellularly but, similar to the Aphidoidea probe and taste host parenchyma before accessing phloem (Raman & Takagi, 1992; Gullan *et al.*, 2005). The Psylloidea feed either on phloem (*D. citri;* Bonani *et al.*, 2010; *D. truncata*; Balakrishna & Raman, 1992) or on xylem (*Bactericera cockerelli;* Triozidae; Butler *et al.*, 2012).

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Compared with the probing—tasting and feeding behaviour of the Auchenorrhyncha and the Heteroptera, the Sternorrhyncha inflict less mechanical damage but, due to their innate salivary chemistry, they alter the physiology of the host plant, such as aggravated transcriptomic changes (De Vos *et al*., 2005) and gall induction (Raman, 2011). Presence of salivary sheath helps the sternorrhynchan insects to avoid apoplastic plant-defence compounds and enzymes such as peroxidases and phosphatases simultaneously enabling in detoxifying the encountered plant-defence compounds. Gall induction capability is an extreme capability in modifying the host-organ morphology among the Sternorrhyncha. This may be due to the occurrence of specific proteins such as α-dihydroxy-glucohydrolase (Miles, 1999) during feeding indirectly on phloem sap. Similarly the presence of Ca^{++}-binding proteins in the saliva of the Sternorrhyncha, could be a facility for their phloem feeding in reducing the occlusion of sieve-tube elements, which would occur as an induced defence response in plants.

The Auchenorrhyncha, on the other hand, feed on plant sap, but a few species belonging to the Cercopoidea, Membracoidea, Cicadoidea feed on fungal mycelia and moss thalli (Nickel, 2003). Nevertheless, the feeding process among the Auchenorrhyncha is not as subtly developed as it has in the Sternorrhyncha, because many of the adult Auchenorrhyncha damage phloem tissue by their stylet bundles of larger dimensions than those of the Sternorrhyncha. This habit – obviously – costs them immensely in terms of the energy spent, since the damaged phloem cannot respond to their feeding action with adequate subcellular pressure (Backus, 1985); consequently these Auchenorrhyncha have to spend more energy to extract the preferred quantities of phloem sap. While feeding on xylem against negative pressure, the cibarial muscles play a key role (Dugravot *et al*., 2008). Membracoidea and Fulgoroidea insert stylets intracellularly and feed on xylem (e.g., *P. spumarius*, Cercopidae) (Crews *et al*., 1998), mesophyll (e.g., *Empoasca fabae*; Cicadellidae) (Hunter & Backus, 1989), and phloem (e.g., *N. lugens*) (He *et al*., 2011). Activity of β-1, 4-endoglucanase in saliva of *H. vitripennis*, which is a cellulose-degrading enzyme, demonstrates the relevance of such proteins in pathogen transfer (Backus *et al*., 2012). However, the 'unique' gall-induction capability by the instar I nymphs of *Scenergates viridis* (Cicadellidae) on the leaves of *Alhagi maurorum* (Fabaceae) (Rakitov & Appel, 2012) illustrates the probability of specific salivary enzymes, not yet characterized. Not much is known about the salivary enzymes of the Auchenorrhyncha. However, the presence of most of cell-degrading enzymes, such as amylases, lipases and trypsin, with detoxifying enzymes such as superoxide dismutase is known from *E. fabae* (DeLay *et al*., 2012). With our current knowledge, we can only infer that similar to that in the Heteroptera, cell-degrading enzymes play a critical role in the feeding process of the Auchenorrhyncha.

Cell-rupturing feeding behaviour reinforces the plentiful occurrence of cell-degrading enzymes (amylases, proteases and pectinases) in the Heteroptera. Among these insects, the labium plays a key role in dabbing before site selection and stylet insertion. By secreting pectinases, the heteropterans (e.g., *Leptocorisa chinensis* Alydidae; Ishizaki *et al*., 2007) macerate the plant tissue. Heteropteran feeding substrates are staggeringly diverse: detritus (e.g., Corixidae), other arthropods (e.g., Anthocoridae) and blood of mammals, birds and reptiles (e.g., Reduviidae), and this renders a generalization difficult. Facultatively carnivorous heteropterans (e.g., Pentatomidae, Miridae) feed on nitrogen-rich plants parts, such as fruits and seeds, as well as on animals (Schaefer, 1997; Schaefer & Panizzi, 2000). In comparison with the saliva of the Culicidae (Diptera) that includes trypsin active at an alkaline pH, the blood-feeding Heteroptera include cathepsin-like proteinases active at acidic pH. This argument illustrates that the salivary physiology varies with insect groups although their feeding guilds are similar, which possibly has been driven by different evolutionary pathways (Lehane, 2005). Extending on this, the incidence of hydrolases in the Heteroptera stands as a useful example: in a majority of the plant-feeding heteropterans, hydrolases occur as the predominant enzyme machinery, whereas in the in the blood-feeding heteropterans, hydrolases occur negligibly (see table 1). While feeding on leaves (e.g., *Anasa tristis*; Coreidae, on *Citrullus lanatus*; Cucurbitaceae), fruits (e.g., *Campylomma verbasci*; Miridae, on *Malus domestica*; Rosaceae) and seeds (e.g., *O. fasciatus*; Lygaeidae on *Asclepias* sp. Asclepiadaceae), these Heteroptera employ cell-rupturing mechanism, thus acquiring greater energy levels quickly (Hori, 1992). Due to a higher degree of mechanical damage and different salivary elicitors, *L. hesperus* and *Nezara viridula* (Pentatomidae) influence plant-volatile production through damage to *Gossypium hirsutum* (Malvaceae) and *Zea mays* (Poaceae), respectively (Williams *et al*., 2005).

The ability of the hemipteroids to transmit pathogens is closely linked to the feeding strategy and the nature of the target tissue. Sternorrhyncha and Auchenorrhyncha are the more efficient vectors of microbial pathogens than the Heteroptera (Mitchell, 2004). Enzyme 'weaponry' decides the transmission modes of microbial pathogens (Hogenhout *et al*., 2008*b*); they also act as elicitors for induced-plant responses. For instance, glucosidase known in *Pieris brassicae* (Tumlinson & Lait, 2005) and glucose oxidase known in *Heliothis zea* (Lepidoptera: Noctuidae) (Morkunas *et al*., 2011) trigger emission of volatiles (e.g., volicitin: *N*-(17-hydroxylinolenoyl)-L-glutamine) in their respective host plants. Given that glucosidases and glucose oxidase are known in the saliva of different hemipteroids, their role in eliciting plant volatiles cannot be overlooked. Induction of plant volatiles due to the feeding effect of *L. hesperus* and *N. viridula* could be the starting point of our need to understand the importance of elicitors in hemipteroid saliva (Williams *et al*., 2005). Feeding behaviour of the hemipteroids immensely influences the nature and chemistry of enzymes of the salivary glands and gut. A majority of hydrolyses are known from the Heteroptera and they are generally known for their function in cell degradation; but their incidence appears to trigger gall induction (e.g., amylases and lipases; Raman *et al*., 1999; Miles, 1999), in manipulating the plants osmotic pressure to elicit mobilization of compounds (e.g., sucrases; Miles & Taylor; Taylor & Miles, 1994), and in detoxifying plant-defence compounds (e.g., catalases; Miles, 1999; Ni *et al*., 2000).

This review has attempted to consolidate the available information on the salivary enzymology of the hemipteroids. Hemipteroids, among Insecta, are a complex group showing a range of adaptations to different habitats and with an equally complex feeding guilds and behaviours. A better understanding of enzymatic proteins and effectors should shed better light on the interrelationship between different hemipteroid groups, their feeding behaviour and various other aspects of insect–plant interaction.

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