carbon by increased CO_2 output, that is, 'wastage' respiration (Zanotto *et al.* 1993, 1997). Use of chemically defined diets with sucrose radiolabelled in either the glucose or fructose moiety has shown that the pea aphid, *Acyrthosiphon pisum*, preferentially assimilates and respires the fructose from ingested sucrose, while converting the glucose into oligosaccharides which are excreted in the honeydew (Ashford *et al.* 2000).

2.3 Digestion and absorption of nutrients

Some digestion may occur in the crop, as a result of salivary enzymes or midgut enzymes moving anteriorly (as in beetles, Terra 1990), but most biochemical transformation occurs in the midgut. Occasionally the midgut has a storage function, like the anterior midgut of *Rhodnius prolixus* (Hemiptera, Reduviidae) (exploited by researchers wishing to obtain blood non-invasively from bats, Helverson *et al.* 1986). Dow's (1986) review brought together information on ultrastucture, ion transport, enzymes, and detoxification for midguts from all main insect feeding types shown in Fig. 2.1. In addition to the hindgut (Section 4.1.3), the midgut is a major site of ion regulation (which is fundamental to nutrient absorption) and the best understood transport epithelium in insects.

The midgut, as a primary interface between insect and environment, is a target for insect control. Insecticides based on Bt toxin from the soil bacterium *Bacillus thuringiensis* are highly effective against certain pests, particularly larvae of Lepidoptera, Coleoptera, and Diptera, and transgenic crops expressing Bt genes are now in widespread use. The toxin, which is activated by midgut proteases, is thought to bind to receptor proteins on the columnar cell microvilli; it then undergoes a conformational change and inserts into the membrane in aggregates, forming pores that result in osmotic lysis and disintegration of the epithelium (Pietrantonio and Gill 1996). Assays of osmotic swelling in membrane vesicles from the midguts of target insects can be used to measure susceptibility to the toxins produced by different strains of Bt (Escriche *et al.* 1998). Young, actively feeding larvae are most affected, and the success of Bt products as microbial insecticides is due to their specificity to the target insects. Possible harmful effects on non-target species, including natural enemies, are the focus of active research (Zangerl *et al.* 2001; Dutton *et al.* 2002).

2.3.1 Digestive enzymes and the organization of digestion

Digestive enzymes

Insect digestive enzymes are all hydrolases, show general similarities to mammalian enzymes and are classified using standard nomenclature based on the reactions they catalyse (Applebaum 1985; Terra and Ferreira 1994; Terra *et al.* 1996*a*). The biochemistry and molecular biology of purified enzymes is currently an active field. Molecular biology is now used as an alternative to exhaustive protein purification, especially for the large arrays of serine proteinase genes present in disease vectors and other insects (Muharsini *et al.* 2001). For example, there are about 200 genes encoding serine proteinases in the genome sequence of *D. melanogaster* (Rubin *et al.* 2000).

Serine proteinases (of which the trypsins and chymotrypsins are well characterized) hydrolyse internal peptide bonds, while carboxypeptidases and aminopeptidases remove terminal amino acids. The term protease, thus, includes both proteinases (endopeptidases) and exopeptidases. Serine proteinases of blood-sucking insects are important in vector-parasite relationships: infection requires that the parasite survive protease activity in the midgut. For phytophages, naturally occurring proteinase inhibitors are important secondary plant compounds (Section 2.4.3), and when chewing breaks up plant cell walls some of the plant enzymes released are also active in the gut lumen (Appel 1994). In bruchid beetle larvae, which specialize on a diet of legume seeds, reduced levels of proteases are complemented by additional enzymes obtained from the seeds (Applebaum 1964). The main digestive proteinases of Bruchidae are not serine but cysteine proteinases, which require a lower pH and are common in the midguts of Hemiptera and some Coleoptera. The distribution of cysteine proteinases in beetles has a phylogenetic basis. These enzymes first appeared in an