of food (Dow 1981), and it is considered unlikely in continuously feeding caterpillars (Dow 1986; Woods and Kingsolver 1999). Terra and colleagues argue that phylogeny is more important than feeding habits in determining the enzymes present and the organization of digestion, and it is possible that most insect species possess a full complement of digestive enzymes, although the relative amounts vary with diet (Terra *et al.* 1996*a*). The fast gut passage rates of many insects suggest potential costs in terms of digestive enzyme loss, but countercurrent fluxes may displace enzymes anteriorly and aid in their recycling (Terra *et al.* 1996*b*).

2.3.2 Gut physicochemistry of caterpillars

Conditions in the gut lumen can vary dramatically among insect herbivores (Appel 1994). The most extreme conditions (and most expensive to maintain) are found in caterpillars. Dow (1984) recorded pH values over 12, the highest known in any biological system, in the anterior and middle regions of caterpillar midgut (Fig. 2.6). The large volume of the midgut compartment suggests substantial acid–base transport to regulate this extreme pH. Ion transport in the midgut of *M. sexta* has been studied intensively using electrophysiological techniques, initially because of its potent K^+-transporting ability (Klein *et al.* 1996). *Manduca* midgut is a model tissue (the frog skin of invertebrates), possessing the advantages of large size, commercial availability of insects and synthetic diet, and ease of making *in vitro* preparations. Caterpillar midgut was also the first animal tissue in which proton pumps were identified and found to energize secondary active transport (Wieczorek *et al.* 1991). Vacuolar-type proton ATPases (V-ATPases) are highly conserved enzymes located in bacterial, yeast, and plant plasma membranes but are now also known to occur in many animal plasma membranes (Harvey *et al.* 1998; Wieczorek *et al.* 1999). They are coupled to antiporters: in caterpillar midgut the V-ATPase is coupled to a $K^+/2H^+$ antiporter to produce what was long assumed to be a primary K^+ pump (Harvey *et al.* 1998). The V-ATPase is confined to the apical membrane of the goblet cells (shown by

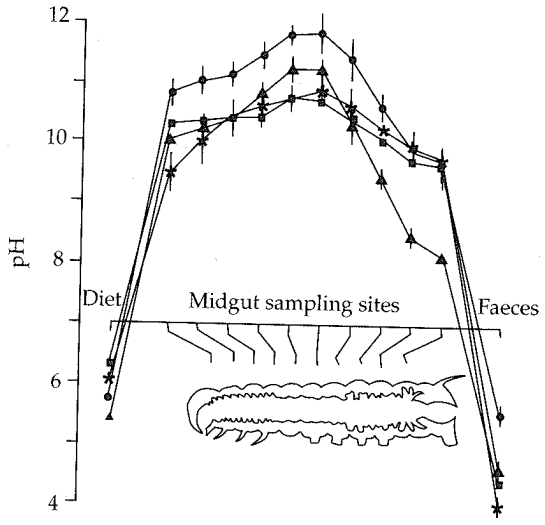

Figure 2.6 Midgut pH profile for four larval lepidopterans, with values for food and faeces shown for comparison.

Note: In all cases, haemolymph pH was 6.7. Species: circles, *Acherontia atropos* (Sphingidae); triangles, *Manduca sexta* (Sphingidae); squares, *Lichnoptera felina* (Noctuidae); and asterisks, *Lasiocampa quercus callunae* (Lasiocampidae). Mean ± SE, $n = 4$.

Source: Dow (1984).

immunohistochemistry using plasma membrane fractions) and is responsible for a large lumen-positive apical voltage in excess of 150 mV. It serves to alkalinize the midgut lumen, maintaining favourable pH conditions for enzyme activity, and energizes amino acid uptake via K^+-amino acid symport (see below). Alkalinization results from the stoichiometry of the $K^+/2H^+$ antiporter and the high voltage generated by the V-ATPase, the result being net K^+ secretion and net H^+ absorption (Wieczorek *et al.* 1999). A model of midgut transport processes is presented in Fig. 2.7.

Leaf-eating caterpillars have a diet very low in Na^+, and their low haemolymph Na^+ concentration precludes use of a sodium pump as primary energizer (goblet cells lack any detectable Na^+/K^+-ATPase). However, carnivorous and some herbivorous insects may use the Na^+/K^+-ATPase to drive absorption of fluid and organic solutes, as vertebrates do (Klein *et al.* 1996). In both cases secondary processes are coupled to a primary ion transport ATPase, but the V-ATPase and