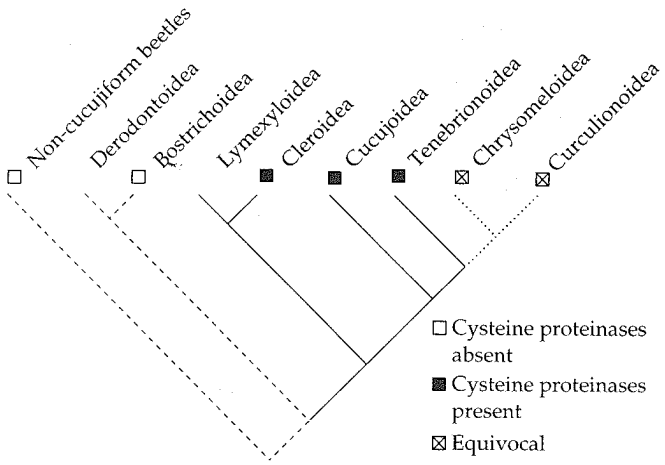

Figure 2.5 Hypothesized cladogram showing the distribution of cysteine proteinases in the major superfamilies of Coleoptera.

Note: The cladogram is based on data for 52 species representing 17 families. Some secondary loss of cysteine proteinases has occurred in the more derived and phytophagous superfamilies.

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ancestor of the series Cucujiformia (Fig. 2.5), perhaps in response to a seed diet rich in trypsin inhibitors, and in total occur in five related superfamilies (Johnson and Rabosky 2000). Cysteine proteinases have been secondarily lost in some Cerambycidae (superfamily Chrysomeloidea), suggesting reversion to a digestive strategy utilizing serine proteinases. Although polymer digestion is considered unnecessary in aphids, Cristofoletti *et al.* (2003) have recently demonstrated substantial cysteine proteinase activity in the midgut of the pea aphid, *A. pisum*.

Carbohydrases fall into two broad categories according to whether they are active on polysaccharides or on smaller fragments. Amylases (active on starch or glycogen) and cellulases (see Section 2.4.1) cleave internal bonds in polysaccharides. Lysozyme is involved in the digestion of bacterial cell walls in the midgut of cyclorrhaphan Diptera. The second category includes glucosidases and galactosidases, which hydrolyse oligosaccharides and disaccharides. Use of the term 'sucrase' does not differentiate between sucrose hydrolysis by α-glucosidases or less common β-fructosidases. Trehalase, which hydrolyses trehalose into glucose, is widespread in insect tissues and, in the midgut, may counteract back-diffusion of trehalose into the lumen (first suggested by Wyatt 1967).

Insect lipases are less easily studied than proteases and carbohydrases because of their lower activities. Moreover, reaction between the enzymes, which are water soluble, and their substrates, which are not, requires a suitable emulsion. These are difficult to prepare experimentally (Applebaum 1985). Phospholipases act on membrane lipids and cause cell lysis. Triacylglycerols are major lipid components of the diet and are hydrolysed to fatty acids and glycerol. In general, lipid digestion is poorly understood in insects (Arrese *et al.* 2001).

Regulation of enzyme levels

Do the levels of digestive enzymes vary according to the quantity or quality of food? Continuous and discontinuous feeders will obviously have different requirements regarding control of digestive enzyme secretion. Ultrastructural evidence indicates that secretion usually follows soon after synthesis, even in discontinuous feeders, although there are examples of storage of enzymes in the latter group (Lehane and Billingsley 1996). Synthesis and secretion are controlled in two ways: 'secretagogue' stimulation according to the amount of relevant substrate in the gut, or hormonal regulation. These