Eighth Edition

ANIMAL NUTRITION

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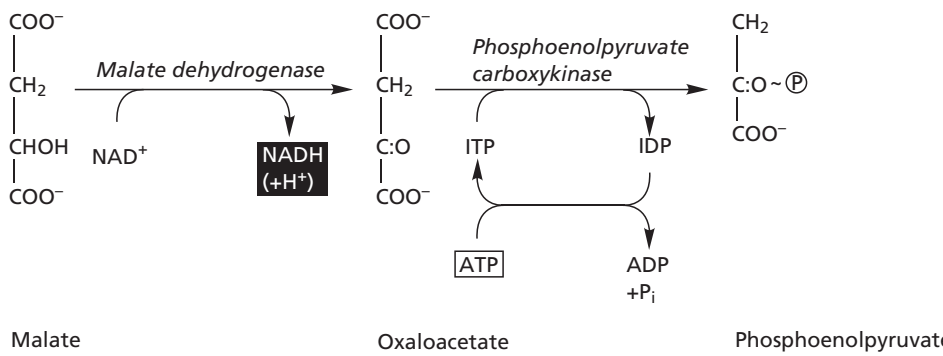
ANIMAL NUTRITION

of energy from glycogen requires its breakdown to glucose, which is then metabolised as described previously. The breakdown of glycogen within cells takes place through the action of inorganic phosphate and glycogen phosphorylase. This enzyme catalyses the hydrolysis of the 1:4-glycosidic bonds of glycogen (see Chapter 2), beginning at the non-reducing end of the chain. Glucose-1-phosphate molecules are successively released until a branch point is reached. A rearrangement of the molecule then takes place in the presence of oligotransferase, which exposes a terminal 1:6-linked glucose unit. Cleavage of the 1:6 linkage by an amylo-α1:6-glucosidase (de-branching enzyme) releases free glucose, with further glucose-1-phosphate being produced by glycogen phosphorylase. The net result of glycogen breakdown is the production of glucose-1-phosphate and a little glucose. Glucose-1-phosphate is then converted to glucose-6-phosphate by phosphoglucomutase, which is then metabolised through glycolysis or the pentose phosphate pathway, with the residual glucose. The production of glucose-6-phosphate from the breakdown of glycogen does not require ATP, except that used to convert residual glucose to glucose-6-phosphate. Energy production from glycogen is therefore slightly more efficient than it is from glucose.

Propionic acid as an energy source

In ruminants, propionic acid is produced as an end product of carbohydrate fermentation in the rumen. The acid is absorbed through the rumen wall, where a small proportion is converted to lactate. The remainder is transported to the liver, where it is converted into glucose by gluconeogenesis. The first stage of this process is the conversion of propionic acid to succinyl-coenzyme A (Fig. 9.7).

The succinyl-coenzyme A then enters the tricarboxylic acid cycle and is converted to malate (see Fig. 9.5), where the equivalent of 2.5 moles of ATP are produced. The malate is transported into the cytosol, where it is converted to oxaloacetate and then phosphoenolpyruvate:



The phosphoenolpyruvate is then converted to fructose diphosphate by reversal of reactions 10, 9, 8, 7 and 5 in the glycolysis pathway shown in Fig. 9.4. This is then converted to fructose-6-phosphate by hexose diphosphatase and then to glucose-6-phosphate. The glucose produced may then be used for component synthesis or to provide energy. The balance sheet is presented in Table 9.2.

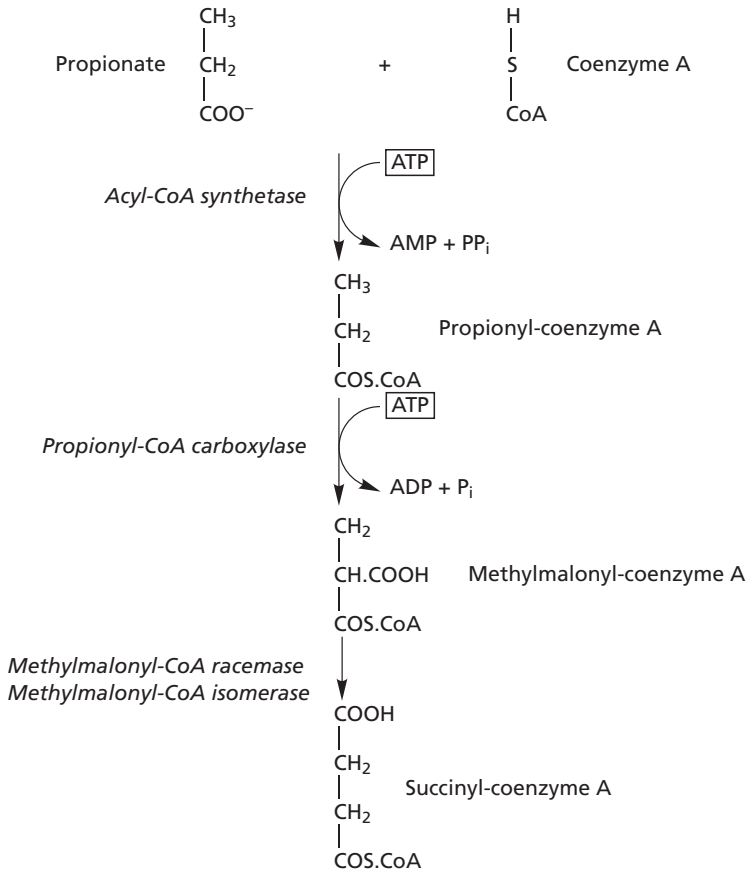


Fig. 9.7 Conversion of propionate to succinyl-coenzyme A.

Table 9.2 ATP yield from propionic acid as an energy source (via glucose)

	ATP gained	ATP used
2 moles propionate to 2 moles succinyl-CoA		6
2 moles succinyl-CoA to 2 moles malate	5	
2 moles malate to 2 moles phosphoenolpyruvate	5	2
2 moles phosphoenolpyruvate to 1 mole glucose		5
1 mole glucose to CO_2 + H_2O	30	
Total	40	13
Net gain of ATP	**27**	
Net gain per mole propionate	**13.5**	

Table 9.3 ATP yield from propionic acid as an energy source (via pyruvate)

	ATP gained	ATP used
1 mole propionate to 1 mole succinyl-CoA		3
1 mole succinyl-CoA to 1 mole malate	2.5	
1 mole malate to 1 mole phosphoenolpyruvate	2.5	1
1 mole phosphoenolpyruvate to 1 mole acetyl-CoA	3.5	
1 mole acetyl CoA to CO_2 + H_2O	10	
Total	18.5	4
Net gain of ATP per mole propionate	**14.5**	

Small amounts of propionic acid in the blood stream could arise due to incomplete removal by the liver, or from the oxidation of odd-chain fatty acids. Such propionic acid could conceivably be used directly for ATP production. The pathway would be the same as previously described as far as phosphoenolpyruvate. The phosphoenolpyruvate would then follow glycolysis via pyruvate, acetyl-coenzyme A and the tricarboxylic acid cycle. The balance sheet is presented in Table 9.3 and the pathway is marginally more efficient than that via glucose.

Butyric acid as an energy source

Butyric acid is also produced in the rumen as an end product of carbohydrate fermentation. During absorption through the walls of the rumen and omasum, butyric acid is converted to β-hydroxybuyrate (D-3-hydroxybutyrate), as shown in Fig. 9.8. The β-hydroxybutyrate may be used as a source of energy by a number of tissues, notably skeletal and heart muscle. In non-ruminants (but not ruminants) utilisation by the brain increases markedly when glucose is in short supply. The reactions involved in energy production are shown in Figure 9.9.

If the acetyl-coenzyme A produced is metabolised in the tricarboxylic acid cycle, the balance sheet is as presented in Table 9.4.

Table 9.4 ATP yield from butyric acid as an energy source

	ATP gained	ATP used
1 mole butyrate to 1 mole D-3-hydroxybutyrate	4	4.5
1 mole D-3-hydroxybutyrate to 2 moles acetyl-CoA	2.5	2.0
2 moles acetyl-CoA to CO_2 + H_2O	20	
Total	26.5	6.5
Net gain of ATP per mole butyrate	**20**	

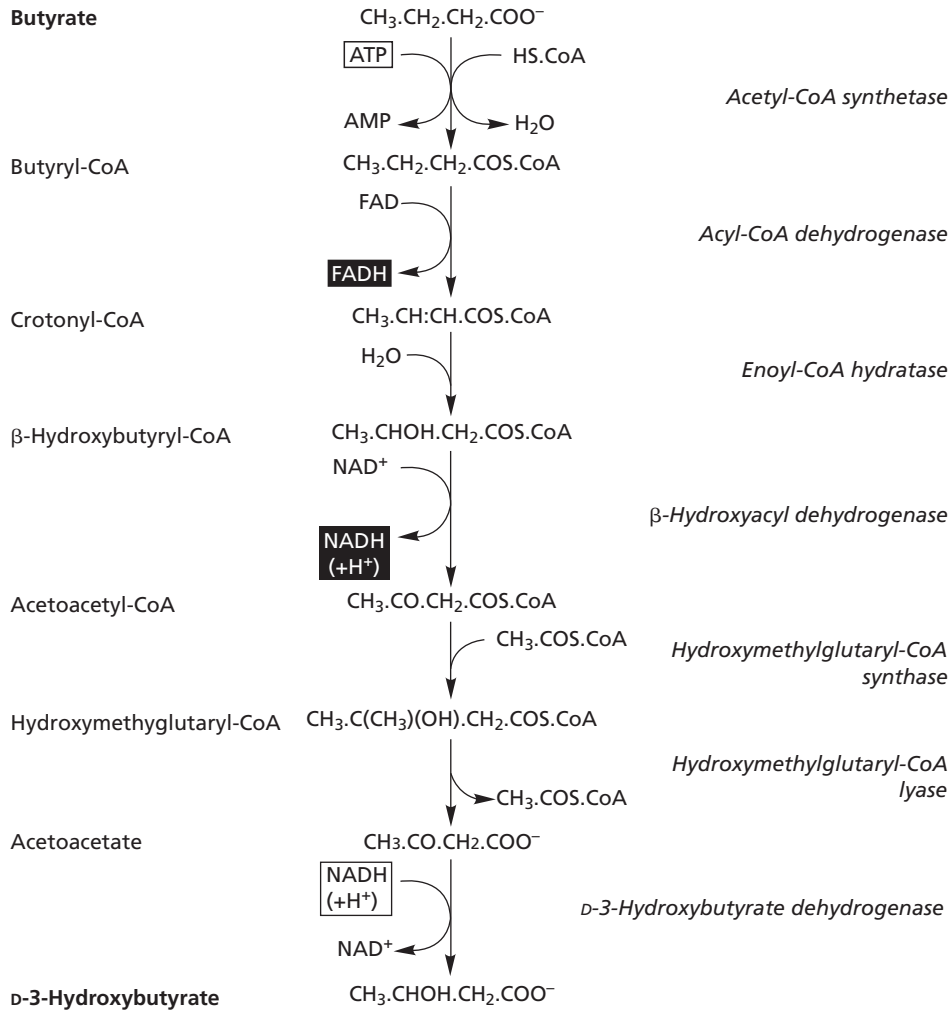


Fig. 9.8 Production of D-3-hydroxybutyrate from butyrate.

If the conversion of acetoacetate to acetoacetyl-coenzyme A takes place via the succinyl-coenzyme A pathway, there is a saving of two moles of ATP and the net yield would be 22 moles of ATP. However, the energy cost of producing succinyl-coenzyme A would have to be accounted for, and this pathway would then be slightly less efficient than the other.

Acetic acid as an energy source

Acetic acid is the main end product of carbohydrate fermentation in the rumen and the only volatile fatty acid present in peripheral blood in significant amounts. It is used by a wide variety of tissues as an energy source. The initial reaction is the

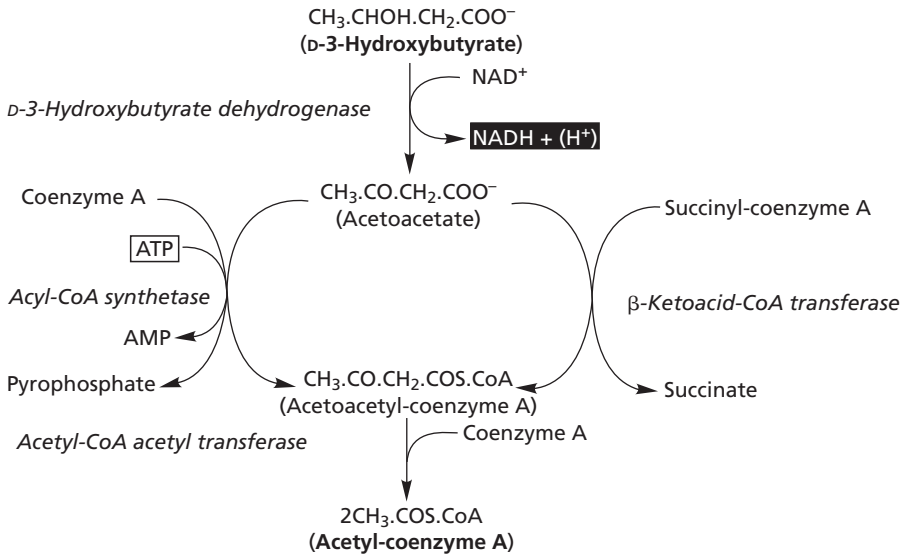
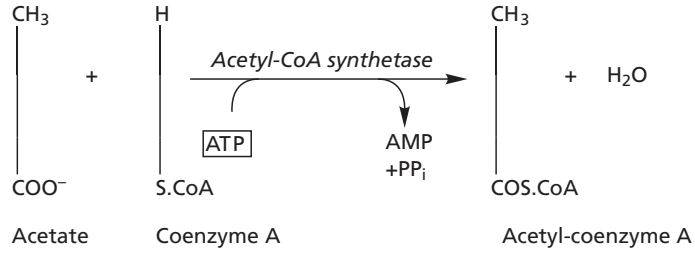


Fig. 9.9 Formation of actyl-coenzyme A from D-3-hydroxybutryrate.

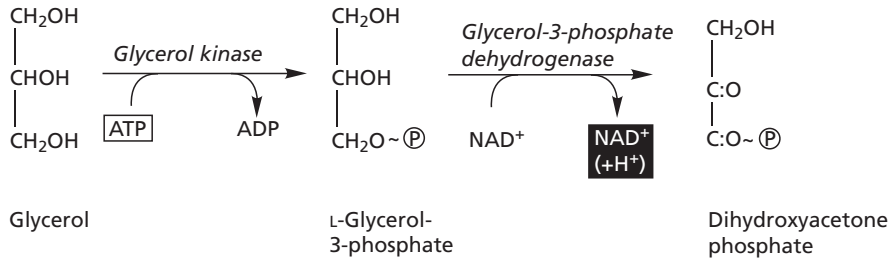
conversion of acetate to acetyl-coenzyme A in the presence of the enzyme acetyl-coenzyme A synthetase:



The formation of acetyl-coenzyme A takes place in the cell cytoplasm, whereas its oxidation in the tricarboxylic acid cycle takes place in the mitochondrial matrix. The acetyl-coenzyme A is unable to cross the mitochondrial wall and has to be complexed with carnitine. Within the mitochondrial matrix, the complex is broken down releasing acetyl-coenzyme A, which then enters the tricarboxylic acid cycle and is oxidised to yield 10 moles of ATP per mole. Since two moles of ATP were used in the initial synthetase mediated reaction, the net ATP yield is 8 moles per mole acetate.

Fat as an energy source

The triacylglycerols that makes up body fat are mobilised to provide energy by the action of lipases, which catalyse the production of glycerol and fatty acids. The glycerol is glycogenic and enters the glycolytic pathway (see Fig. 9.4) as dihydroxyacetone phosphate, as shown in the following reaction:



Glucose may then be produced by the reverse of the aldolase reaction to give fructose-1,6-diphosphate, which is then converted to glucose by the action of hexose diphosphate, glucose-6-phosphate isomerase and glucose-6-phosphatase. If the glucose is used to produce energy, we can assess the efficiency of glycerol as an energy source, as shown in Table 9.5.

Alternatively, the dihydroxyacetone phosphate may enter the glycolytic pathway and be metabolised via pyruvate and the tricarboxylic acid cycle to carbon dioxide and water. Under these circumstances, the efficiency of glycerol as an energy source is presented in Table 9.6.

By far the most important source of energy provided by triacylglycerols is derived from the fatty acids, and the major pathway associated with fatty acid degradation is β-oxidation. This results in shortening of the carbon chain by the progressive removal of two carbon atoms at a time. The first stage of β-oxidation is the reaction

Table 9.5 ATP yield from glycerol as an energy source

	ATP gained	ATP used
2 moles glycerol to 2 moles dihydroxyacetone phosphate	5	2
2 moles dihydroxyacetone phosphate to 1 mole glucose		
1 mole glucose to CO_2 + H^2O	30	
Total	35	2
Net gain of ATP per mole glycerol	**16.5**	

Table 9.6 ATP yield from glycerol (via pyruvate)

	ATP gained	ATP used
1 mole glycerol to 1 mole dihydroxyacetone phosphate	2.5	1
1 mole dihydroxyacetone phosphate to 1 mole pyruvate	4.5	
1 mole pyruvate to CO_2 + H_2O	12.5	
Total	19.5	1
Net gain of ATP per mole glycerol	**18.5**	