

succinate lyase is inhibited by an increase in the level of aldosterone. Hormonal regulation of the osmoregulatory process has also been shown for *Rana temporaria*, but the exact mechanism is not known.

The South African tree frog *Chiromantis xerampelina* (Racophoridae) and the South American species *Phyllomedusa sauvagii* (Hyllidae) possess a uricotelic mechanism which protects against dehydration. Uric acid, as a proportion of the total nitrogen excreted, is 50–57% in *C. xerampelina*, about 80% in *P. sauvagii*, but only 24–25% in the related species *P. pailona*, *P. iherengi* and *P. hypochondrialis*; in other genera of the Hyllidae, such as *Agalychnia*, *Pachymedusa* or *Hyla*, it is in fact always less than 3.5%. In the liver of the uricotelic species, the activities of the enzymes of urea synthesis (arginase) and uricolysis (uricase) are relatively low, and those of the enzymes of uric acid synthesis (xanthine dehydrogenase) are relatively high. *Hyperolius viridiflavus* (Hyperoliidae) produces mainly guanine and hypoxanthine, which are deposited in iridophores. Thus, the osmotic problems accompanying water loss are solved and, at the same time, the high reflectance of these cells reduces heat absorption [218]. *H. nasutus*, which is also very resistant to dehydration, is, in contrast, purely ureotelic.

Amongst the **reptiles**, the snakes and lizards are all uricotelic, and the crocodile excretes mainly urea but also ammonia. Turtles and tortoises may be ammoniotelic, ureotelic or uricotelic, depending on their habitat. In addition to these species-specific differences there is also variation in the regulatory mechanisms. Aquatic and semi-aquatic species excrete ammonia and urea in about equal proportions; terrestrial species from wet biotopes produce much more urea than ammonia; and species from dry biotopes produce about 60% uric acid and 40% urea. Transfer of the turtle *Trionyx spiniferus* from freshwater to brackish water with 0.7% salt results in an accumulation of urea in the tissues.

The urine of **birds** consists almost entirely of ammonium urate, i.e. it contains uric acid nitrogen and ammonia nitrogen in the ratio 4:1. Needham (1931) in his pioneering work *Chemical Embryology* described how, during chick development, ammonia is excreted initially (maximum at day 3), then urea (days 5–9) and, finally, uric acid; he cited this as an example of the biogenetic rule also being valid in biochemistry. However, already by 1935, he found that the urea in fact originated from preformed arginine. Today, it is

quite clear that in the chicken, as in other birds, there is no functioning urea cycle.

Mammals are ureotelic. In addition to urea, their urine always contains uric acid or allantoin, as an end product of purine metabolism, and many other nitrogenous compounds. Hippuric acid, which is a product of the detoxification of benzoic acid, is found at high concentration in the urine of herbivores but only in trace amounts in the carnivores and omnivores.

12.4 Nitrogen Metabolism of the Amino Acids

The degradation of most amino acids begins with the cleavage of the amino group and formation of the corresponding keto acid. The L-amino acid oxidases that may be present in tissues are not significantly involved in this process; the usual situation in animals is that **deamination of amino acids** occurs by one of two more indirect pathways, one via glutamate dehydrogenase (GDH) and the other via the purine nucleotide cycle. In both pathways, the amino groups of different amino acids are initially transferred to a common intermediate (glutamic or aspartic acid), and only in a second step, if at all, are they released as ammonia. The **GDH pathway** occurs typically in vertebrate liver. Here, the glutamic acid intermediate is oxidatively deaminated by mitochondrial glutamate dehydrogenase. The fate of the ammonia released in the liver mitochondria differs markedly in different species. In ureotelic animals, it is bound to carbamylphosphate synthetase I and then incorporated into citrulline, which is released into the cytosol and there used for urea synthesis. The second amino group required comes from aspartic acid. In uricotelic animals, the ammonia is converted to glutamine by mitochondrial glutamine synthase and is then used in the cytosol for uric acid synthesis. The **purine nucleotide cycle** (Fig. 12.3) is typical of vertebrate muscle, which contains only low GDH activity. The product of the transamination is aspartic acid and its nitrogen then serves in the conversion of IMP to AMP; ammonia is released from the AMP by an AMP deaminase, giving again IMP.

Little is known of the relative importance of these two pathways of amino acid deamination in different invertebrate animals. Apart from in birds and mammals, the complete enzyme system of the purine nucleotide cycle has been found only in the goldfish and in the hepatopancreas of