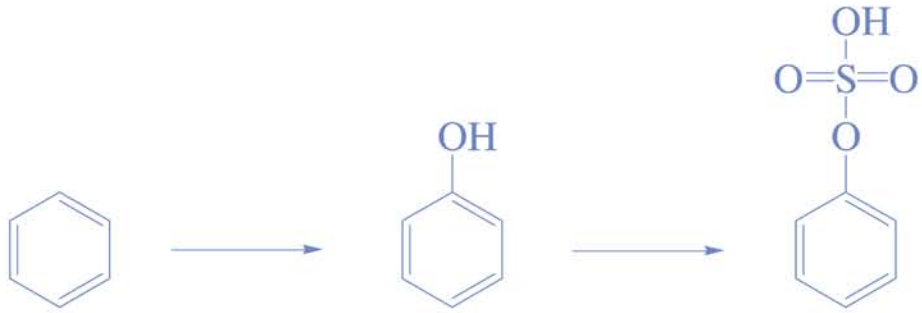
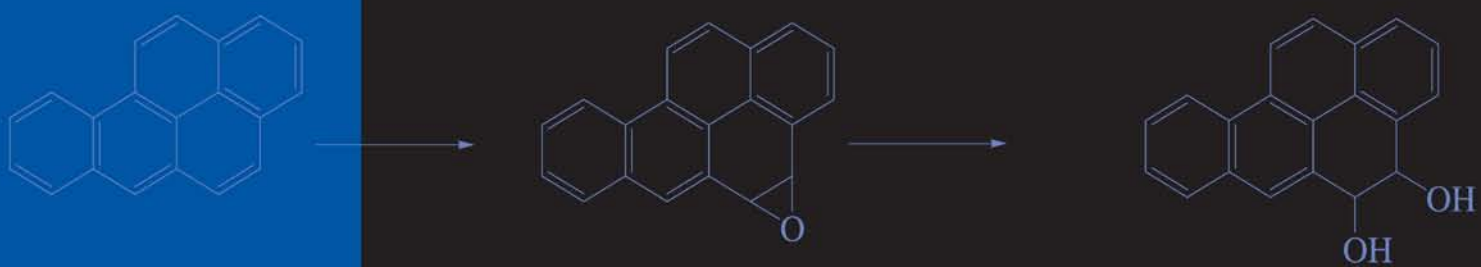


Handbook of

BIOTRANSFORMATIONS OF AROMATIC COMPOUNDS



B.L. Goodwin

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Contents

Author Biography

Brian Goodwin, D.Phil., is retired. He received his M.A. in natural sciences from Cambridge University, England and his D.Phil., from Oxford University, England. He worked as a researcher in the pharmaceutical industry (1958–1961), research worker in the Department of the Regius Professor of Medicine, Oxford University (1961–1967), visiting research worker, Fels Research Institute, Yellow Springs, Ohio (1967–1969), Principal Biochemist, Queen Charlotte's Maternity Hospital, London (1969–1991), Research scientist, Royal Botanic Gardens, Kew, London (1991–1993) and Senior Research Fellow, King's College London (1994–1997). He is also a qualified horticulturist and preacher.

Dr Goodwin's main research interests have been the metabolism of aromatic amino acids and amines and their connection with disease, the metabolic pathways of aromatics and the development of potential drugs.

Dr Goodwin is a Member of the Biochemical Society and a Fellow of the Royal Society of Medicine.

Introduction

Since the earlier work on this subject was published (Goodwin, B.L. [1976] *Handbook of Intermediary Metabolism of Aromatic Compounds*, London: Chapman & Hall), which covered research until about 1972, a great deal of new work has been published, mainly on new compounds, and the need of a new reference work has become apparent, covering research published since then.

Most of the literature cited is found in journals written in English, as most information finds its way into such research journals. However, information quoted in Chemical Abstracts is used when non-English sources are important, for instance Chinese and Japanese literature. In general, reviews and symposia have been excluded as source material; Federation Proceedings is an exception. Since the information in Chemical Abstracts is necessarily incomplete, it is inevitable that much important information is lost when this has been the only available source material.

The aromatic compounds listed in this work are those that contain at least one aromatic C_6 ring, which may be fused with other ring systems. Other aromatic systems (such as pyridine) are excluded; quinoline with benzene fused with pyridine is included. Other ring systems with some aromatic properties with ring systems that do not contain six carbon atoms are also excluded.

It has not been possible to include structural formulae, pharmacological properties, toxicology or medicinal use of the compounds listed in this index. Although structures are not always shown in the original papers, structural formulae of many of the compounds are found in *The Merck Index* Whitehouse Station, N.J.: Merck & Co, Inc, and *Dictionary of Organic Compounds, 6th edition* (1996), London: Chapman & Hall. Almost all of the remainder can be deciphered with the help of Chemical Abstracts.

The data are divided into two sections: Part I Reactions of Individual Compounds, and Part II Enzymes and Reactions, with extensive indexing of Part II. A full bibliography is supplied.

The structure of each compound entry in Part I is:

A[a]
Formed from: B[b]
Formed from C in R[c] W321
Probably formed from: D[d]
→ E[e]
In: S W123
T W456
With H W135[f]
See also: W789[g]
Contrast (in U) W987[h]
→ F[e]
Probably in: V W234[j]
Does not yield G in X W345[k]

[a]The name of the compound listed. Most of these are aromatic compounds, but some are closely related to aromatic compounds that are aromatized by a simple reaction. Acids are named as acids and not as their salts, although the reactions may occur with the ionized forms.

[b]Under the entry for compound B a reaction is shown which forms compound A.

[c]Compound A is formed from compound C in species R; C is usually a simple aliphatic compound, such as acetic acid that is not listed in its own right. The information is quoted from reference W321 (all the W123-type entries illustrate references found in the bibliography).

[d]Under the entry for compound D a reaction is shown which forms compound A, but the evidence is not strong enough to be included under the 'Formed from' heading.

[e]Compound E is formed from compound A.

[f]This reaction has been reported to occur in species S and T in publications W123 and W456 respectively. There is a corresponding entry under compound E of 'Formed from: A'. 'In' indicates that the studies have been carried out in whole organisms, tissue extracts or with purified enzymes obtained from that species. In cases where the source of the enzyme specified has been difficult to establish the alternative form of entry illustrated by 'With H W135' is used, where H is the name of the enzyme. If the identity of the species and enzyme are both unclear, the species name is replaced by 'species unclear'.

[g]Publication W789 reports evidence supporting this reaction, but is not in itself adequate to be quoted as definite evidence. The two main reasons for this are that the identity of the starting compound or the product has not been adequately determined. A second situation is where the reaction A → E is one in a reaction sequence, and either the starting compound studied is not A, or the product detected is not E, but A → E is implicit. This reaction may be one of a network of possible reactions; parallel reactions in such networks are not usually recorded other than under one of the possible reactions. Where structural constraints on compound E require that it originates from compound A, although compound A was not the compound under test, such as benzene → phenyl sulphate where phenol is the necessary intermediate, the published data are counted as definitive evidence and are not included under this heading. This may also apply where the time of appearance and disappearance of compounds in a reaction sequence indicates that A → E is an established reaction.

[h]This heading is rarely used, and is generally reserved for situations where either the reaction is observed in some species but not in others, or when the validity of the reaction has been challenged, such as the biotransformation of saccharin, where the observed reaction in early studies may have been due to the presence of impurities, or where the product has been mis-identified.

[j]This entry is used with the same force as the entries described under the footnote[g], but where there is no literature for a fully authenticated reaction. There is a corresponding entry under compound F of 'Probably formed from: A'.

[k]This is a rarely used entry, where conversion to G in species X has been sought unsuccessfully.

The compound name listed has been chosen primarily for utility; it is more important that the compound can be recognized by the reader than that an accurate systematic name is used. In general, it has been considered that the Chemical Abstracts names are too unwieldy or too unfamiliar for routine use. With lead compounds, a systematic name is also listed (except for those that are too long to be considered useful), as are common alternatives for any compound. In cases where alternatives are relatively simple or are in regular use they are listed in their own right with a reference to the compound name where the data are listed. This arrangement has inevitably led to some inconsistencies of naming. Very occasionally, there is a small discrepancy between the name used at[a] and the product entry when there are some ambiguities, particularly between publications, such as stereochemistry. A similar discrepancy often occurs in the alternative names of compounds listed under trivial names and those used for metabolites; the former are often based on Chemical Abstracts naming which may differ from the names used in the publications reporting the metabolism. Because of these variations in naming in the literature, it is probable that some compounds have been listed under more than one name, although extensive steps have been taken to prevent duplicate entries.

In the previous book it was assumed that conjugation in animals was the final stage of a metabolic sequence prior to excretion, and conjugation reactions were automatically given a definitive reaction step status; since it is no longer certain that this is so, many references to conjugation are now given no more than a 'See also' status.

Some compounds are used routinely in probing the status of P450 systems; when they are used just as probes the literature cited is usually not used unless the data cited in Part 1 are considered to be otherwise inadequate.

Mercapturates are listed as N-Acetyl-S-(L-cysteinyl)-.

'Desmethyl' in a compound name has generally been replaced by 'Demethyl'; 'Desethyl' has been left unaltered. In many instances 'Nor' (when referring to the loss of a methyl group) has been replaced by 'Demethyl'; catecholamines and their analogues such as noradrenaline are exceptions.

'Acetamido' is preferred to 'Acetylamino', and 'Formyl' is used for many aldehydes.

Unless otherwise stated, compound moieties such as 'Phenylpropionic', 'Phenyloctane', 'Phenyloctyl' are straight chain compounds with a terminal phenyl moiety and any side-chain functional group at the other terminal. In general the prefix *n*- is not used for these compounds.

In general, entries such as Hydroxy-demethyl- are preferred to Demethyl-hydroxy; whereas Bisnor-tetrahydro- is used rather than Tetrahydro-bisnor-, particularly with cannabinoids.

Esters may be listed under the name of either the parent acid or parent alcohol.

Plant glucosides are usually β-glucosides; this information is often omitted from the publications cited. Such conjugates are generally named as glucoside, glucuronide etc. without stating the full systematic name.

Certain classes of compounds are named on the basis of alternative numbering systems. As far as possible, this has been rationalized, for instance, cannabinoids, but areas of ambiguity may have led to inadvertent duplication of entries. Stereoisomers are often not listed separately, especially where they are converted into the same product (possibly at different rates). In some cases the research literature cites, for instance, optical isomers that yield a named product, but without sufficient information to identify the stereochemistry. When there is an entry for the product, possibly formed additionally from some other compound, a blurring of the stereochemistry may have been applied to the entries, to avoid misleading the reader. This problem is particularly acute when different systems for describing stereochemistry are used, such as D and L, *d* and *l*, (*R*) and (*S*), + and −, where the information on their interconversion is often not available, with consequent uncertainties.

In these entries the species name is usually either a trivial name like Rat, or the Genus name, without reference to the species name. This is a compromise adopted not only for the sake of consistency and compactness, but also because many studies, especially with microorganisms, either do not identify the microorganisms involved at all, or are identified as a genus with, perhaps a reference number but no species name. In Part 2 the organisms are more fully identified. In work on recombinant organisms, where possible, the organism from which the original genetic material was obtained is quoted.

Little effort has been exerted in rationalizing species and genus names, except where duplication in an entry has become apparent. For instance, Daucus and carrot are used as alternatives, based largely on the preference of the researchers. In general, the name Pseudomonas has not been replaced by Burkholderia, but Corn has been replaced by Zea, since this avoids confusion between corn (Zea) and wheat (Triticum).

Part 1
Reactions of Individual Compounds

Part 2
Enzymes and Reactions

Prior to 1972 many of the key enzyme systems described here were extensively studied, and were reviewed in my previous volume. Many of these systems have been further studied since 1972, and the new material is reviewed here. However, in some cases the newly published material is no more than a tidying-up of loose ends; no attempt has been made to re-introduce material published prior to 1972, except for enzymes given an E.C. number that would not otherwise be listed; these are listed with minimal data.

The policy for reviewing reactions and enzymes has been, not to write exhaustive reviews on each reaction type, but to give a representative set of data for those that have received extensive experimental study, and to concentrate relatively more effort on those that have not been extensively studied or are novel. Where extensive studies have been carried out in several species, the results for each species (and in some cases, each specific organs in that species) have been grouped together in a single paragraph; occasionally results are grouped according to substrate.

The molecular weights quoted are in Daltons, and temperature in degrees Celsius; the units are not mentioned in the text.

P450 Enzymes

Many microsomal reactions are catalyzed by enzymes of the P450 group (E.C. 1.14.14.1), particularly where xenobiotics are involved. Although most P450 studies have been carried out with liver microsomes, P450-containing microsomes are obtained from many tissues, and also from plants. The name P450 refers to Pigment with maximal optical absorption at 450 nm, observed with the carbon monoxide complex formed from the reduced enzyme; this binding inhibits the enzyme. The haem moiety binds molecular oxygen, which hydroxylates the substrate with the additional formation of water. Electron transport into the system is usually mediated by the flavin moiety of NADPH: cytochrome P450 reductase.

In this review no attempt has been made to rationalize isozyme names; over the years numerous isozymes have been detected and improved methods have been developed for distinguishing between isozymes, resulting in improved systems of naming (see below).

Some compounds have been found to be specific substrates for individual isozymes, and these have been used as probes for their identification. Studies for isozyme identification have been so repetitive that in general they have not been reported in the compound section of this book.

Some commonly used P450 probes

Isozyme	*Probe*	*Reaction*
CYP1A2	Phenacetin	de-ethylation
	7-Ethoxyresorufin	de-ethylation
CYP1A/12	7-Ethoxyresorufin	de-ethylation

Table (*Continued*)

Isozyme	*Probe*	*Reaction*
CYP2A6	Coumarin	7-hydroxylation
CYP2B6	Bupropion	*t*-butyl hydroxylation
	(*S*)-Mephenytoin	N-demethylation
	7-Ethoxy-4-trifluoromethylcoumarin	de-ethylation
CYP2C8	Taxol	6α-hydroxylation
CYP2C9	Tolbutamide	methyl hydroxylation
	Diclofenac	4′-hydroxylation
CYP2C18	2-(2,3-Dichloro-4-(4-hydroxybutoxy)benzoyl)thiophene	5-hydroxylation
CYP2C19	(*S*)-Mephenytoin	4′-hydroxylation
CYP2D6	Dextromethorphan	demethylation
	Bufuralol	1′-hydroxylation
CYP2E1	*p*-Nitrophenol	*o*-hydroxylation
	Chlorzoxazone	6-hydroxylation
CYP3A4	Testosterone	6β-hydroxylation
	Medazolam	α-hydroxylation
CYP3A5	Testosterone	6β-hydroxylation
CYP4A9	Lauric acid	12-hydroxylation
CYP 4A11	Lauric acid	12-hydroxylation

Monoclonal antibody studies are also used for the identification of several isozymes, for instance, CYP2C8, CYP3A5 and CYP4A11.

The major isozymes are 1A2, 2C9, 2C19, 2D6 and 3A4. Structural variants have been detected in these groups, such as 2C9 with a difference involving an arginyl/cysteinyl residue and 2D6 with a methionyl/valyl difference.

The reactions carried out by P450 enzymes are listed under the relevant reactions in the Reactions section of this book. However, the following publications are illustrative, particularly of earlier naming systems.

A naming system for rabbit liver microsomal isozymes was introduced with LM designations, followed by a subscript numbering scheme. LM_1, molecular weight 47 000 and LM_7, molecular weight 60 000, were not induced by phenobarbital or by β-naphthoflavone. LM_2, molecular weight 50 000, was induced by phenobarbital, and LM_4 by β-naphthoflavone. The substrates studied showed relatively poor discrimination between isozymes [A2147]. The isozymes show quantitatively different reaction rates for the formation of 4 tetrahydrotetraols formed from *trans*-benzpyrene-7,8-dihydrodiol, via the two corresponding 9, 10-oxides. The P450 types were then (1978) designated LM_1, LM_2, LM_{3b}, $LM_{4(BNF)}$, $LM_{4(PB)}$ and LM_7 [A3605]. This redundant system was also used with monohydroxylation of benzpyrene [A2327].

Rat microsomal enzyme is induced by phenobarbital and 3-methylcholanthrene; the induced enzymes differ slightly in the absorption maxima of the carbon monoxide adducts (450 and 448 nm respectively) [A734]. Multiple forms with molecular weights of about 50 000 were separated [A3028]. In one study (1978) with solubilized enzyme from male rat, four fractions were obtained by an initial separation, each of which could be separated into eight haem-containing bands [A3447]. Another study detected 21 fractions. Benzpyrene hydroxylase was associated with P448 isozymes, pI 6.83, 6.55 and 6.36; the second of these fractions also exhibited 7-ethoxycoumarin de-ethylase activity [D740]. One publication designated two of these as P-448_{MC} and P-448_{HCB}; they catalyse hydroxylation at different positions on 2-acetamidofluorene [D269]. Isozymes designated as A, B and D N-hydroxylate 2-acetamidofluorene [D142]. The primary structures of male rat isozymes f, g and h, molecular weights

51 000, 50 000 and 51 000 respectively differ from one another and from isozymes a-e, and this is confirmed by antibody studies. Isozymes f and g showed a low activity towards all the substrates tested; h N-demethylated benzphetamine and hydroxylated zoxazolamine and 17β-oestradiol [D39]. These naming systems are also redundant.

Liver microsomes from phenobarbital-treated mice yield 4 P450 fractions with marginally different absorption spectra [A1699].

A monkey liver P450, molecular weight 50 000, catalyzes oxidations on a series of substrates, in the presence of a hydrogen transport system [D510].

Guinea pig isozymes, designated as the IIB family, molecular weight 52 000, hydroxylate Δ^9-tetrahydrocannabinol and aniline, and demethylate *p*-nitroanisole [F819].

A mathematical analysis based on potential energy profiles during the reaction, based on arene oxide ring opening, gave a close approximation to the extent that the NIH shift (the migration of a substituent to a position *ortho* to its original position at the hydroxylation site) was observed for *para* hydroxylation, in agreement with the hypothesis that there is a *p*-quinoid intermediate. The data also support the hypothesis that there may be a pathway involving initial formation of a tetrahedral intermediate in the absence of epoxide formation [E284].

A full assessment of P450 enzymes is found in David Lewis "Guide to Cytochromes P450", Taylor & Francis, London (2001).

1. Reactions involving the formation and degradation of the aromatic nucleus

1.1 *Aromatization of 6-membered carbon and heterocyclic rings.*

Prephenate dehydrogenase (E.C. 1.3.1.12)

Prephenate → *p*-hydroxyphenylpyruvate

The amino acid composition of A. aerogenes enzyme, molecular weight 76 000, has been determined; it is involved in the biosynthesis of tyrosine [K873].

Prephenate dehydrogenase ($NADP^+$) (E.C. 1.3.1.13)

The mung bean (Vigna radiata) enzyme, molecular weight 52 000, requires NADPH; it may be identical with pretyrosine dehydrogenase [B290]

Prephenate dehydratase (E.C. 4.2.1.51)

Salmonella typhimurium enzyme, optimum pH 8.5, is part of a complex with chorismate mutase (E.C. 5.4.99.5). The reaction product, phenylpyruvate, is further converted into phenylalanine [K859].

Arogenate (pretyrosine) dehydrogenase (E.C. 1.3.1.43)

Arogenate + NAD(P) → L-tyrosine + NAD(P)H

Vigna radiata (mung bean) enzyme, molecular weight 52 000, may be identical with prephenate dehydrogenase [B290].

Nicotiana silvestris enzyme is inhibited by L-tyrosine and substituted tyrosines [C501].

Corynebacterium glutamicum and Brevibacterium flavum enzymes have molecular weights of 158 000, and B. ammoniagenes 68 000. They are not inhibited by tyrosine, and *p*-chloromercuribenzoate inhibition is reversed by thiols. Contrary to some earlier reports, these organisms lack the *p*-hydroxyphenylpyruvate pathway for the formation of tyrosine [B47].

Actinoplanes missouriensis enzyme, molecular weight 68 000, has an optimum at pH 9.5 [F277].

Streptomyces phaeochromogenes enzyme is a dimer with subunit molecular weight 28 100 and pI 4.45 [D880].

This reaction has also been observed in Microtetraspora glauca [F222], Claviceps [E234], Streptomycetes [C695] and Flavobacterium devorans [C115].

Phenylalanine formation from arogenate

This reaction has been detected in Claviceps [E234].

Anthranilate synthase; (E.C. 4.1.3.27)

Chorismate + glutamine or NH_3 → anthranilate

Saccharomyces cerevisiae enzyme is dimeric, molecular weight 130 000, and subunit molecular weight 64 000 [D512]. Enterobacter liquefaciens and Erwinia carotavora enzymes have molecular weights of 140 000, and Aeromonas formicans

220 000 [A1481]. Claviceps enzyme has an optimum pH of 7.8 or 8.6 using glutamine as co-substrate. It requires Mg^{2+}, partly replaceable by Mn^{2+} or Co^{2+}, is stimulated by K^+, Na^+ or NH_3^+ and is inhibited by tryptophan, chanoclavine, elymoclavine, indoleacrylate and prephenate [A2552].

Shikimate forms phenazine-1-carboxylate in Pseudomonas aureofaciens [A958]; earlier publications suggest that the pathway is via chorismate and anthranilate.

p-Aminobenzoate formation from chorismate

Streptomyces coelicolor catalyzes this reaction, but isochorismate is not a substrate; however, both compounds are precursors of *p*-aminobenzoate in S. aminophilus and Enterobacter aerogenes; isochorismate may initially be converted into chorismate [F111]. S. griseus enzyme, molecular weight 50 000 uses ammonia or glutamine as the source of the amino group [D734].

p-Aminophenylalanine formation from chorismate

In Streptomyces this reaction is an initial step in the formation of chloamphenicol. Its formation is considered to be a four-stage biosynthesis including a transamination, and the reaction is stimulated by an aminotransferase from the crude extract, as well as by several other enzymes present [A2461, B158].

Benzoate formation from shikimate

This reaction has been observed in rat [A2706].

p-Hydroxybenzoate formation from shikimate

This reaction occurs in Lithospermum erythrorhizon as an early step in the formation of the naphthoquinone shikonin and γ-glutaminyl-4-hydroxybenzene [A3763, B810].

Phenylalanine formation from shikimate

Phenylalanine and tyrosine are formed from shikimate in Reseda lutea, R. odorata and Iris. Previous publications indicate an involvement of prephenate [A1601].

3-Carboxyphenylalanines formed from shikimate

3-Carboxyphenylalanine and 3-carboxytyrosine are formed from shikimate in Reseda lutea, R. odorata and Iris, as well as phenylalanine and tyrosine. The carboxyl group arises from shikimate; it is not considered that carboxylation of the parent amino acid is involved [A1601].

Phenazine-1-carboxylate and iodinin formation from shikimate

These reactions involve the formation of a phenazine ring system, apparently incorporating two shikimate molecules, probably with anthranilate as an early intermediate.

The formation of phenazine-1-carboxylate has been observed in Pseudomonas aureofaciens [A958].

The formation of iodinin has been observed in Brevibacterium/Chromobacterium iodinum [A958, A2941].

Menaquinone MK-9(II-H_2) formation from shikimate

This reaction, which involves the formation of a naphthoquinone, has been observed in Mycobacterium phlei [A691].

Catechol formation from shikimate and dehydroshikimate

The first reaction has been observed in rat, [A2706] and the second in E. coli, where it is a major pathway for the anaerobic utilization of glucose [G366].

o-Succinylbenzoate formation from isochorismate

E. coli and Aerobacter aerogenes enzymes catalyze this reaction, with α-oxoglutarate as co-substrate. It appears that earlier claims that chorismate is the substrate were incorrect. The enzyme, optimum pH 8.3, requires thiamine pyrophosphate as coenzyme, and it may be a Mn^{2+}-containing enzyme [D682, E430, E457]. The reaction product is the starting point for the formation of a range of substituted naphthalene natural products.

3-Amino-5-hydroxybenzoate formation from 5-deoxy-5-amino-3-dehydroshikimate

This reaction has been detected in Amycolatopsis mediterranei. The enzyme, which contains bound pyridoxal phosphate, catalyzes both an α,β-dehydration and a stereospecific 1,4-enolisation during the reaction sequence. The product is a key intermediate in the formation of rifamycin [J643].

cis-Dihydrobenzene-1,2-diol dehydrogenase; (E.C. 1.3.1.19)

cis-1, 2-Dihydroxycyclohexa-3, 5-diene → catechol

Mouse kidney contains four soluble (three minor) isozymes. Two minor ones are immunologically identical with aldehyde reductase (E.C. 1.2.1 class) and 3α-hydroxysteroid dehydrogenase (E.C. 1.1.1.213). The other two, molecular weight 39 000, require $NAD(P)^+$ as coenzyme. Both *cis* and *trans* isomers are substrates, as well as other dihydrodiols; *p*-nitrobenzaldehyde and quinones are also reduced [F377].

An enzyme in Bacterium acts only on *cis*-isomers [B871]. Pseudomonas putida enzyme, a homotetramer, molecular weight 102 000, acts on a range of aromatic hydrocarbon *cis*-dihydrodiols except those substituted on K-regions [A1298, A1591].

Pseudomonas putida *cis*-naphthalene-1,2-dihydrodiol dehydrogenase (E.C. 1.3.1.29) and *cis*-biphenyl-2,3-dihydrodiol dehydrogenase both oxidize *cis*-naphthalene-1,2-dihydrodiol and *cis*-biphenyl-2,3-dihydrodiol as well as *cis*-2,2′,5,5′-tetrachlorobiphenyl-3,4-dihydrodiol. They both require NAD^+ [K196].

Pseudomonas *cis*-chlorobenzene dihydrodiol dehydrogenase acts on *cis*-(1*R*,2*S*)-indan-1,2-diol, but not on *cis*-(1*S*,2*R*)-indan-1,2-diol. Some enantiomeric selectivity is observed with *p*-halotoluene-2,3-dihydrodiols, *cis*-1,2-dihydroxytetralin and *cis*-naphthalene-1,2-dihydrodiol [K348].

Xanthobacter flavus enzyme is a homotetramer, monomeric molecular weight 26 500 and pI 5.4. It requires $NADP^+$ (NAD^+ is less effective) and acts on *cis*-3,6-dichlorobenzene-1,2-dihydrodiol and benzene-1,2-dihydrodiol [J186].

Bacillus enzyme is a homohexamer, monomeric molecular weight 29 500, pI 6.4 and optimum pH 9.8. It oxidizes *cis*-toluene-2,3-dihydrodiol, and is stable up to 80° [E368].

trans-Dihydrobenzene-1,2-diol dehydrogenase; (E.C. 1.3.1.20)

trans-1, 2-Dihydroxycyclohexa-3, 5-diene → catechol

This and similar enzymes aromatize *trans*-dihydrodiols formed from benzene and a range of analogues formed from polynuclear hydrocarbons, including those that are carcinogenic. This reaction is one step in the potential degradation of these hydrocarbons; the catechols so formed could undergo ring fission, at least in microorganisms.

An enzyme in pig lens oxidizes this and other similar substrates, utilising $NADP^+$. Quinones and nitrobenzaldehydes are also substrates for the reverse reaction [F389].

Monkey liver cytosol contains four isozymes, molecular weights in the range 36 000–39 000, each with a similar range of specificities, and optima at pH 5.8, 6.2, 7.9 and 8.7. One isozyme was formerly known as indanol dehydrogenase (E.C. 1.1.1.112) [F388]. One at least is a dimer that is inactive towards *cis*- isomers [F391].

Hamster liver cytosol contains five isozymes with a broad specificity, molecular weight about 35 000 [F153].

Guinea pig liver contains four major and four minor isozymes, molecular weights about 34 000, except for two minor ones, molecular weights 26 500 and 14 500. The specificity is broad [E67].

Rat liver cytosolic enzyme requires NADP as co-substrate, and acts on *trans*-naphthalene-1,2-dihydrodiol and *trans*-benzpyrene-7,8-dihydrodiol [E583].

Mouse liver enzyme has been separated into four isozymes that require NADP. Two are monomers, molecular weights 30 000 and 34 000, and two dimers, molecular weights 64 000 and 65 000, pI 8.1, 6.2, 5.5 and 5.4, respectively [C712]. Another study found two cytosolic forms that were identified as 17β-hydroxysteroid dehydrogenase (major; E.C. 1.1.1.63 and 1.1.1.64) and aldehyde reductase. The major one also oxidizes a range of alcohols and reduces a range of aldehydes and ketones [E821].

Beef liver cytosolic enzyme contains three enzymes that are active towards *trans*-benzene dihydrodiol. One is 3α-hydroxysteroid dehydrogenase and a second is a high K_m aldehyde reductase. The third also acts on other dihydrodiols including *trans*-naphthalene dihydrodiol; it is a distinctly different activity [G750].

1,6-Dihydroxycyclohexa-2,4-diene-1-carboxylate dehydrogenase (E.C. 1.3.1.25)

Alcaligenes eutropus enzyme, molecular weight 95 000 and optimum pH 8.0 may be a homotetramer. It forms catechol and CO_2, and requires NAD^+; $NADP^+$ is ineffective, and no other cofactors are required [K944].

***cis*-1,2-dihydroxycyclohexa-3,5-diene-1-carboxylate dehydrogenase** (E.C. 1.3.1.55)

Pseudomonas putida and Acinetobacter calcoaceticus enzymes, molecular weight 28 000 form catechol from the substrate [K763].

2,3-Dihydro-2,3-dihydroxybenzoate dehydrogenase; (E.C. 1.3.1.28)

Aerobacter aerogenes and E. coli enzymes require NAD^+ as co-substrate [K876].

***o*-Succinylbenzoate synthase**

Amycolaptosis enzyme acts on 2-hydroxy-6-succcinyl-2,5-cyclohexadienecarboxylate as substrate [K68].

Kynurenate-7.8-dihydrodiol dehydrogenase (E.C. 1.3.1.18)

Pseudomonas fluorescens enzyme requires NAD^+ for the formation of 7,8-dihydroxykynurenate [K874].

***trans*-Acenaphthene-1,2-dihydrodiol dehydrogenase** (E.C. 1.10.1.1)

Rat liver cytosolic enzyme acts on the (−), but not on the (+) isomer (an inhibitor), with $NADP^+$ as co-substrate, whereas NAD^+ is inactive. A further substrate is (−)-1-phenylethanol. Activity is also found in mouse, guinea pig, rabbit, hamster, dog, cat and pig liver. Some of these can accept NAD^+ as co-substrate; it has been suggested that more than one enzyme may be involved [K817].

Aromatization of dihydropyridines

Nilvadipine, a 1,4-dihydro-4-phenylpyridine is aromatized in rat liver microsomes, and utilises NADPH. The reaction is inhibited by P450 inhibitors [E847]. Many metabolic studies on calcium channel blockers with similar structures to nilvadipine have demonstrated that a major proportion of each drug is similarly aromatized.

A large number of studies with the neurotoxin 1,2,3,6-tetrahydro-1-methyl-4-phenylpyridine (MPTP), which causes a drug-induced parkinsonism, have demonstrated that the proximal

toxin is 1-methyl-4-phenylpyridinium (MPP^+). Metabolic studies have detected the formation of MPP^+ in mouse, monkey, rat, man and beef (e.g. [E3, D222, D141, E3, F458] respectively). The formation of 2,3-dihydro-1-methyl-4-phenylpyridinium has also been observed, and this in turn is converted into MPP^+, at least in mouse [E684]. A major study with human placental MAOA and beef liver MAOB found that a large range of MPTP analogues, particularly those with substituents on the aryl moiety are substrates. Although the products were not identified, it was assumed that they were MPP^+ analogues [F395].

Tetrahydroprotoberberine aromatization

Berberis wilsonae enzyme is a flavoprotein, molecular weight 100 000 and optimum pH 8.9. Tetrahydroprotoberberine yields protoberberine, presumably via the 7,14-dehydroberbinium analogue; canadine and tetrahydrojatrorrhizine are also substrates. The reaction requires oxygen and forms peroxide as the second product. The enzyme is specific for (*S*)- isomers [D145].

Corydalis cava bulb protoberberine reductase, optimum pH 7.5, requires NADH for the reduction of protoberberines to (14*R*)-tetrahydroberberines, apparently in two stages. For instance, both berberine and 7,8-dihydroberberine are reduced to canadine. The reaction, which dearomatizes the heterocyclic ring, is reversible; both 7,8-dihydroberberine and (*R*)-canadine are oxidized to berberine, with $NADP^+$ as coenzyme. Palmatine, dehydrosinactine, coptisine, columbamine, jatrorrhizine and dehydroscoulerine are also substrates [G136].

Tetrahydroberberine (canadine) aromatization

Thalictrum minus tetrahydroberberine oxidase is composed of 3 isozymes, two of which are specific. All have an optimum at pH 9.0. The molecular weight of one of the specific enzymes is more than 200 000, and the other, a trimer, is 145 000 [H401].

Coptis japonica (*S*)-tetrahydroberberine oxidase (E.C. 1.3.3.8) is a dimer, molecular weight 58 000, and requires oxygen and Fe; it is highly specific. It aromatizes one of the heterocyclic rings [E678, E732].

Berberis aggregata aromatizes tetrahydroberberine, tetrahydrocolumbamine and tetrahydropalmatine, with the formation of a quaternary amino moiety [K947].

Aromatization of dihydromacarpine

Eschscholtzia californica enzyme, molecular weight 56 000, pI 8.8 and optimum pH 7.0, requires oxygen to oxidize dihydromacarpine to macarpine. This completes the aromatization of the ring system, including the formation of a quaternary nitrogen [E604].

Dihydrobenzophenanthridine oxidase
(E.C. 1.5.3.12)

Sanguinaria canadensis enzyme is composed of three isozymes, molecular weights 77 000, 67 000 and 59 000 and optimum pH 7.0. It converts dihydrosanguinarine into sanguinarine and dihydrochelerythrine into chelerythrine, aromatizing the heterocyclic ring [G723]. Eschscholtzia californica enzyme, molecular weight 56 000, pI 8.8 and optimum pH 7.0, requires oxygen to convert dihydromacarpine into macarpine [E604]. In all of these a quaternary base is formed.

Many plant alkaloids contain an aromatic heterocyclic ring moiety. There may be an aromatizing step similar to this one, but in most cases the enzymology has not been studied.

D-Dopachrome tautomerase

Human enzyme is found in erythrocytes and other blood cells, but not in plasma, with 5,6-dihydroxyindole as the product [H872].

The enzyme that enolizes indole-3-pyruvate and *p*-hydroxyphenylpyruvate converts

D-dopachrome into 5,6-dihydroxyindole. The enzyme source is not clear from Chemical Abstracts; it is claimed to be a rat enzyme, but it may be the same as that described in another publication, found in human lymphocytes. The latter is a macrophage migration inhibition factor in addition to its tautomerase activity [J475, J514].

L-Dopachrome tautomerase (E.C. 5.3.3.12)

Mouse melanoma enzyme forms 5,6-dihydroxyindole-2-carboxylate as the initial product. The apoenzyme is activated by Zn^{2+}, but not by Fe^{2+} or Cu^{2+} [H338].

Locusta migratoria enzyme, dopachrome conversion factor, (dopachrome Δ-isomerase, E.C. 5.3.3.12), molecular weight 85 000, forms 5,6-dihydroxyindole from L-dopachrome; it also acts on L-dopachrome methyl ester and methyldopachrome, but not on their D-isomers or dopaminechrome [J842].

Bombyx mori dopa quinone imine conversion factor, optimum pH 7.5–9, forms 5,6-dihydroxyindole from L- (but not D-) dopachrome [H429].

Aromatization of lindane

Lindane (the isomer used is not clear, but is presumed to be the active γ-isomer) is converted into 1,2,4-trichlorobenzene in bean, and into 1,2,3- and 1,2,4-trichlorobenzene in Zea mays [A766].

1.2 *Formation of carbon ring systems*

Naphthalene derivatives formed from *o*-succinylbenzoate

a. Naphthoate synthetase (E.C. 4.1.3.36)

E. coli enzyme, molecular weight 45 000, requires acetyl CoA, ATP and Mg^{2+} to form 1,4-dihydroxy-2-naphthoate. In crude extracts, the addition of farnesyl pyrophosphate results in the formation of menaquinone-3 at the expense of 1,4-dihydroxy-2-naphthoate [A2774]. Studies with Mycobacterium phlei, E. coli and Galium mollugo have found that *o*-succinylbenzoyl CoA is formed as an intermediate [C337, E594]. M. phlei enzyme has a molecular weight of 44 000 and optimum pH 6.9. The succinyl carboxyl is retained as the carboxyl group in 1,4-dihydroxy-2-naphthoate [A2943].

b. Phylloquinone formation

In Zea mays phylloquinone is formed from *o*-succinylbenzoate, retaining its structural integrity [A175, A3973].

c. 1,4-Naphthoquinone formation

Juglans regia catalyzes the formation of 1,4-naphthoquinone and juglone (5-hydroxy-1,4-naphthoquinone) [A3470]. 1,4-Dihydroxy-2-naphthoate is an intermediate in juglone formation as well as in lawsone (2-hydroxy-1,4-naphthoquinone) formation [A1639].

Cannabidiolate synthetase

Cannabis sativa enzyme, molecular weight 74 000 and pI 6.1, catalyzes the ring closure of cannabigerolate and cannabinerolate into cannabidiolate. The enzyme is not an oxygenase or peroxidase; presumably it is a dehydrogenase, which forms a cyclohexene ring system [J205].

Pinosylvin (3,5-dihydroxystilbene) synthase (E.C. 2.3.1.146)

Pine (Pinus sylvestris) enzyme catalyzes the condensation of cinnamoyl CoA with malonyl CoA to form a second aromatic ring. With *p*-coumaroyl CoA the hydroxylated analogue, resveratrol is formed [B313].

Dioscorea shows similar metabolic reactions with cinnamoyl CoA, *m*-hydroxyphenylpropionyl

CoA and analogues; the products, such as resveratrol and pinosylvin are intermediates in the formation of hircinol and batatasins [D136].

This reaction occurs poorly in Barlia longibracteata with cinnamoyl CoA, *m*-coumaroyl CoA and *p*-coumaroyl CoA as substrates. The corresponding dihydro substrates form the analogous bibenzyls, but more effectively [C734].

Epipactis palustris enzyme, molecular weight 85 000, shows a similar specificity and co-substrate requirement to those for the above enzymes [G138].

Bibenzyl synthase

Barlia longibracteata enzyme acts on CoA conjugates of 3-phenylpropionic acid; the *m*- and *p*-hydroxy analogues also form the corresponding bibenzyls [C734].

Bletilla striata enzyme is a dimer, monomeric molecular weight 46 000, which condenses *m*-hydroxyphenylpropionyl CoA with malonyl CoA to form 3,3′,5-trihydroxybibenzyl [H101].

Epipactis palustris enzyme, molecular weight 85 000 acts on *m*-hydroxyphenylpropionyl CoA; a good additional substrate is phenylpropionyl CoA, which yields dihydropinosylvin, but the corresponding cinnamoyl CoAs are poor substrates [G138]. This distinguishes the enzyme from stilbene synthase, which it closely resembles.

Chalcone synthase (E.C. 2.3.1.74)

This reaction is the first step in the reaction sequence that leads to the formation of polycyclic flavonoid plant pigments from cinnamates, forming a second aromatic ring.

Buckwheat enzyme is a homodimer, molecular weight 83 000, pI 5.2 and optimum pH 8.0. It condenses malonyl CoA with *p*-coumaroyl CoA, feruloyl CoA and caffeoyl CoA [E180].

Cephalocereus enzyme converts cinnamoyl CoA into 2′,4′,6′-trihydroxychalcone [H633].

Daucus carota enzyme exhibits optima at pH 7.9 and 6.8 with *p*-coumaroyl CoA and caffeoyl CoA, respectively [D698].

Dianthus caryophyllus enzyme exhibits pH optima of 8.0 and 7.0 with *p*-coumaroyl CoA and caffeoyl CoA, respectively [C392].

Glycine max enzyme, molecular weight 75 000, is composed of three isozymes, pI 5.45 (main), 5.35 and 5.5, and pH optima of 7.5 and 6.5 with *p*-coumaroyl CoA and caffeoyl CoA, respectively [E579]. A reductase is involved in the reaction sequence [E661].

Glycyrriza echinata enzyme acts on *p*-coumaroyl CoA, malonyl CoA and NADPH [E619].

Parsley enzyme, molecular weight 77 000 appears to be a dimer (monomeric molecular weight 42 000) with *p*-coumaroyl CoA and malonyl CoA as substrates [B352, K808].

Phaseolus vulgaris enzyme, molecular weight 77 000 and optimum pH 8.0, acts on malonyl CoA and *p*-coumaroyl CoA [C813].

Rye enzyme requires malonyl CoA as co-substrate, and acts on *p*-coumaroyl CoA (optimum pH 8) and caffeoyl CoA (optimum pH 6.5) to form 2′,4,4′,6-tetrahydroxy- and 2′,3,4,4′,6′-pentahydroxychalcones (precursors of naringenin and eriodictyol), respectively [E662].

Spinach enzyme is composed of two isozymes, pH optimum 7.5–8, with *p*-coumaroyl CoA, feruloyl CoA and caffeoyl CoA as substrates [D596].

A tulip anther enzyme, molecular weight 55 000 and optimum pH 8.0 acts on *p*-coumaroyl CoA, feruloyl CoA and caffeoyl CoA to form naringenin, homoeriodictyol and eriodictyol respectively; it is inhibited by CoA, flavanones and thiols. The preparation was claimed to be free from chalcone-flavanone isomerase activity; the expected chalcone intermediates were not detected [A3792]. A similar enzyme found in Haplopappus gracilis, optimum pH about 8 for *p*-coumaroyl CoA, and 6.5–7 for caffeoyl CoA was called flavanone synthase. The reaction was not stoichiometric, with small amounts of by-products such as benzalacetones being formed [A3362]; a similar series of reactions was found in Petroselinum crispum [A2618]. These publications all come from early studies on the enzyme system, and despite the claims that chalcone-flavanone isomerase activity was

absent, there must be a suspicion that the preparations were all contaminated with this enzyme.

Benzophenone synthase (E.C. 2.3.1.151)

Centaurium erythraea enzyme, optimum pH 7.5, acts on *m*-hydroxybenzoyl CoA and malonyl CoA to form 2,3′,4,6-tetrahydroxybenzophenone [J35].

Norsolorinate synthase

Aspergillus parasiticus converts hexanoate or pentanoate into norsolorinate, a polyphenolic anthraquinone, which is a postulated precursor of aflatoxin B_1. With pentanoate, an additional reaction product with a 5-oxopentane side-chain, instead of a 6-oxohexane side-chain, has been detected; if 6-fluorhexanoate is used, 6′-fluoronorsolorinate is formed [H675].

Phloroisovalerophenone synthase

Humulus lupulus enzyme, found in cone glandular hairs, is a homodimer, monomeric molecular weight 45 000 and pI 6.1; the amino acid sequence has been determined. It utilizes one mol of isovaleryl CoA, and three mol of malonyl CoA to form the aromatic nucleus. Replacement of the former with isobutyryl CoA yields the corresponding isobutyrophenone [K175].

6-Methylsalicylate synthase

Penicillium patulum enzyme is a tetramer, molecular weight 750 000. It condenses acetyl CoA, and requires NADPH [G751].

Benzoates from pyrones

Macrophoma commelinae converts a series of 2-pyrones into the corresponding benzoates, usually in good yield. The carbonyl group becomes the benzoate carboxyl, and the 3, 4, 5 and 6-substituents on the pyrone become the 2, 3, 4 and 5-substituents on the benzoate [E766].

Purpurogallin formation

Pyrogallol → purpurogallin

This reaction is catalyzed by peroxidases (E.C. 1.11.1.7) from peanut, with peroxide as co-substrate. Four isozymes are found with pH optima at 6, 6.4, 8 and 8 [A2519].

Salutaridine synthase (E.C. 1.1.3.35)

Papaver somniferum enzyme, probably a P450 that requires oxygen and NADPH, is found in root, shoot and capsules, but not in latex. The enzyme acts on (*R*)- (but not (*S*)-) reticuline, and the reaction involves the formation of a 6-membered carbon ring by linkage between the two aromatic nuclei, one of which is converted into a cyclohexadienone system [K759].

4,5-Methylenechrysene formation

This reaction has been detected in rat liver cytosol, with 5-methychrysene as substrate [G118].

1.3 *Formation of heterocyclic ring systems*

Indole-3-glycerol-phosphate synthase; (E.C. 4.1.1.48)

1-(*o*-Carboxyphenylamino)-1-deoxyribulose-5-phosphate → indole-3-glycerolphosphate

The Bacillus subtilis enzyme, molecular weight 23 500, differs from N-(5′-phosphoribosyl) anthranilate isomerase (E.C. 5.3.1.24) [B97].

Hordenine cyclization

Mushroom tyrosinase, with peroxide, acts on hordenine with an optimum at pH 6.7 to form a compound whose spectra indicates that the product is N,N-dimethylindoliumolate, presumably via a quinone [K374].

Chalcone-flavanone isomerase (chalcone isomerase; E.C. 5.5.1.6)

Grapefruit enzyme acts on chalcone-4′-neohesperosides with a free, unhindered 4-hydroxyl group. Other structural features required for substrate activity are the presence of either 2,6-dihydroxy or 2-hydroxy-4-methoxy groups. It is reversibly inhibited by cyanide but not by azide, EDTA, Hg^{2+} or *p*-chloromercuribenzoate [A2518]. Tulipa petal enzyme is cytosolic [A2523].

There are many publications on chalcone synthase in which this activity is part of the reaction system, and its requirement is implicit in the formation of all flavonoids.

Riboflavin formation

This involves two enzymes in the later part of the reaction sequence, 6,7-dimethyl-8-ribityllumazine synthase and riboflavin synthase (E.C. 2.5.1.9):

5-Amino-6-ribitylamino-2,4(1*H*,3*H*)-pyrimidinedione + (3*S*)-3,4-dihydroxy-2-butanone-4-phosphate → 6,7-dimethyl-8-ribityllumazine

6,7-Dimethyl-8-ribityllumazine → riboflavin + 5-amino-6-ribitylamino-2,4(1*H*,3*H*)-pyrimidinedione

Two synthases in Bacillus subtilis have molecular weights of 70 000 and 1 000 000. The smaller (more active) molecule appears to be a homotrimer; the larger molecule is composed of one of the above molecules as well as about 60, possibly identical, polypeptide chains of a different type [B315]. Further studies on the larger molecule have shown that it is a complex of an icosahedral capsid of 60 β units surrounding a core of three α units. The β units catalyze the first reaction, and the α units the second reaction. In the first reaction the natural (*S*)-butanone can be replaced by the (*R*)-isomer; the latter reacts at 1/6 of the rate for the (*R*)-isomer. The second reaction involves a dismutation, which forms both riboflavin and the substrate for the first reaction [H398].

Formyltetrafolate cyclo-ligase (E.C. 6.3.3.2)

Sheep liver enzyme, optimum pH about 4.8, forms $N^{5,10}$-methenyltetrahydrofolate with hydrolysis of the ATP co-substrate to ADP. It is inhibited by thiol-binding reagents [K826].

5,10-Methylenetetrahydrofolate reductase (E.C. 1.7.99.5; formerly 1.1.1.68)

E. coli enzyme, optimum pH 6.3–6.4, requires $FADH_2$ to form 5-methyltetrahydrofolate [K851].

Methylenetetrafolate dehydrogenase ($NADP^+$) (E.C. 1.5.1.5)

Calf thymus enzyme, optimum pH 6.5 is very unstable, and it is protected by thiols and glycerol. The reaction is reversible, forming $N^{5,10}$-methenyltetrahydrofolate preferentially [K935].

Methylenetetrafolate dehydrogenase (NAD^+) (E.C. 1.5.1.15)

Clostridium formicoaceticum enzyme is a homodimer, molecular weight 60 000 and Stokes radius 3.32nm. The reaction forms 5,10-methenyltetrahodrofolate, activation energy 8.5 kcal/mol; $NADP^+$ is not an alternative co-substrate [K928].

Formiminotetrafolate cyclodeaminase (E.C. 4.3.1.4)

Pig liver enzyme forms 5,10-methenyltetrahydrofolate and ammonia as reaction products [K937].

Tetrahydroisoquinoline and tetrahydro-β-carboline formation

A large number of plant alkaloids contain a ring system based on the formation of 1,2,3,4-tetrahydroisoquinolines (THIQ). This reaction can occur spontaneously (Pictet-Spengler reaction); for instance, under physiological conditions dopamine condenses with acetaldehyde to form salsolinol (6,7-dihydroxy) and small amounts of its isomer isosalsolinol (7,8-dihydroxy). In principle, any aldehyde or ketone may react with any phenethylamine analogue activated in the *meta* position. The small amounts of salsolinol found in man are probably formed mainly spontaneously.

In rat brain, a mitochondrial enzyme catalyzes the formation of 1-methylTHIQ from phenethylamine and pyruvate [J360]. Tryptamine forms 1,2,3,4-tetrahydro-β-carboline [A2285]. The enzyme requires 5-methyltetrahydrofolate as methyl donor; it also acts on N-methyltryptamine to form 1,2,3,4-tetrahydro-2-methyl-β-carboline. It is inhibited by dopac and by other catecholamine and indoleamine metabolites [A104]. In brain stem, serotonin and acetaldehyde form 1-methyl-1,2,3,4-tetrahydro-6-hydroxy-β-carboline [A908].

Rat brain and rabbit lung form 1,2,3,4-tetrahydro-β-carboline from tryptamine, 1,2,3,4-tetrahydro-2-methyl-β-carboline from N-methyltryptamine, 1,2,3,4-tetrahydro-6-hydroxy-β-carboline from serotonin and 1,2,3,4-tetrahydro-6-hydroxy-2-methyl-β-carboline from N-methylserotonin [A111].

In pig liver, 5,10-methylenetetrahydrofolate reductase oxidizes N^5-methyltetrahydrofolate to 5,10-methylenetetrahydrofolate, which (presumably non-enzymatically) forms norsalsolinol from dopamine with formaldehyde from 5,10-methylenetetrahydrofolate [A2346].

Eschscholtzia tenuifolia (*S*)-norlaudanosoline synthase ((*S*)-norcoclaurine synthase, E.C. 4.2.1.78), molecular weight 15 500 and optimum pH 7.5 or 7.8, is composed of four isozymes, with dopamine and 3,4-dihydroxyphenylacetaldehyde as substrates; the latter can be replaced by other phenylacetaldehydes, but not by pyruvates. The product is the L-(−) compound. Berberis regeliana, Corydalis sempervireus (misprint for sempervirens?), Dicentra spectabilis, E. pulchella, Fumaria officinalis, Glaucium rubrum, Meconopsis cambrica, Papaver somniferum, Ranunculus flammula and Thalictrum tuberosum also show this activity [B919, C859].

Berberis stolonifera also contains (*S*)-norlaudanosoline (norcoclaurine) synthase (E.C. 4.2.1.78) [K932, K933].

Strictosidine synthase (E.C. 4.3.3.2)

Rauwolfia serpentina enzyme, which is monomeric, molecular weight 30 000, pI 4.5 and optimum pH 6.5, contains 5.3% carbohydrate. It catalyzes the ring closure of tryptamine with the aldehyde group of secologanin, to form the tetrahydro-β-carboline strictosidine as the product [F63].

Catharanthus roseus enzyme, molecular weight 38 000, pI 4.6 and optimum pH 5.0–7.5 (or 6.8) forms strictosidine, but none of its epimer vincoside [B71, B265].

Chanoclavine 1 cyclase

Claviceps enzyme, which forms agroclavine, requires ATP and $NAD(P)^+$, but not FAD or oxygen. An aldehyde appears to be an intermediate. The enzyme develops rapidly in the transition from trophophase to idiophase, and decreases sharply after 9–10 days fermentation [A893].

Berberine bridge formation ((S)-Reticuline oxidoreductase E.C. 1.5.3.9)

Berberis beaniana enzyme, molecular weight 49 000 or 52 000, pI 4.9 and optimum pH 8.9 converts (*S*)-reticuline into (*S*)-scoulerine, involving ring closure with the N-methyl group. The reaction requires oxygen, and peroxide is the second product. (*S*)-Protosinomenine and (*S*)-laudanosoline also undergo a similar reaction. It is inhibited by *o*-phenanthroline and by reducing agents [D615, D878].

Eschscholtzia californica enzyme contains one mol of FAD, but no metal. The substrates are 1-benzyl-N-methyltetrahydroisoquinolines, with closure of the *ortho* position in the benzyl moiety to the N-methyl ring; several compounds with this structure are substrates [H680]. The putative molecular weight, based on gene sequence is 57 352 (excluding carbohydrate) [K705].

Macleaya microcarpa enzyme has an optimum pH of 7.5–8.2 [A1565].

This reaction has been observed in rat liver microsomes [B478] and in Papaver somniferum [A3141].

Cinnabarinate synthesis (phenoxazinone synthase, formerly E.C. 1.10.3.4)

$$\text{3-Hydroxyanthranilate} + O_2 \rightarrow \text{cinnabarinate}$$

In mouse, one enzyme appears to be catalase (E.C. 1.11.1.6), based on results from animals with an inborn metabolic error in which catalase is absent. The catalase and haemoglobin-catalysed reactions both require Cu^{2+} or Mn^{2+} [A3587]. Baboon and beef liver synthases require Mn^{2+}, these also appear to be catalase [A3083].

Goat bladder cinnabarinate synthase, molecular weight about 55 000 and optimum pH 7.2, is inhibited by divalent cations (except Mn^{2+}) and by chelating agents. The activation energy at 20° is 12.36 kcal/mol [K279].

Two Streptomyces antibioticus enzymes, molecular weights 900 000 and 200 000, appear to be monomeric and dimeric. They are not interconverted; the monomers are considered to be different [B924]. S. antibioticus enzyme acts on 3-hydroxy-4-methylanthranilate to form actinocin; this is a key reaction in the formation of actinomycin [E676]. A Drosophila melanogaster phenoxazine synthase appears to act by preventing the formation of an inhibitor rather than by directly catalyzing the formation of cinnabarinate (or xanthommatin from 3-hydroxykynurenine). It requires Mn^{2+} [A2574].

Formation of esculetin

Mushroom tyrosinase oxidizes *cis*-caffeic acid to esculetin [D598].

Dehydrodicinnamic acid dilactone formation

Inonotus (a mushroom) enzyme, molecular weight 39 000, optimum pH about 6 and stable up to about 60°, forms dehydrodicaffeic acid dilactone from caffeate. The reaction involves hydroxylation of caffeate at the β-position and dimer formation (with loss of the double bond) at the α-position and lactonization between the side chains. It is stimulated by a range of divalent cations, and inhibited or inactivated by cyanide, diethyldithiocarbamate and several physiological reducing agents. The reaction is also catalysed by peroxidase and peroxide, or by *o*-diphenol oxidase (E.C. 1.10.3.1) [A3016, A3019].

Sorghum bicolor enzyme, called ferulic dimerase, acts on ferulate [A1641].

Protoaphin dehydratase (cyclizing) (E.C. 4.2.1.73)

Woolly aphid (Eriosoma lanigerum) protoaphin dehydratase (E.C. 4.2.1.73), molecular weight 120 000 is a glycoprotein, which acts on protoaphin aglycone to form xanthoaphin. The enzyme is inhibited by naphthoresorcinol [A3112].

Pummerer's ketone formation

Pisum sativum ascorbate peroxidase (E.C. 1.11.1.11) acts on *p*-cresol to form

Pummerer's ketone, a tetrahydrodibenzofuran [K404].

Dihydrovindoline ether formation

Streptomyces griseus catalyzes the formation of an internal ether bond in vindoline between an existing hydroxyl group and a double bonded carbon, with loss of the double bond [A2984].

Methylenedioxy ring formation

Berberis stolonifera berberine synthase (columbamine oxidase, E.C. 1.1.3.26), molecular weight 32 000 and optimum pH 8.9, is a Fe^{2+}-containing enzyme which forms berberine from columbamine, by ring closure between adjacent hydroxyl and methoxy groups. Tetrahydrocolumbamine is not a substrate [D536].

Thalictrum tuberosum microsomal (*S*)-canadine synthase (E.C. 1.1.3.36, a P450), optimum pH 8.5 requires NADPH, forming a methylenedioxy bridge in (*S*)-tetrahydrocolumbamine to form (*S*)-canadine. The enzyme shows high selectivity [H301].

Eschscholtzia californica microsomes contain (*S*)-cheilanthifoline synthase (E.C. 1.1.3.33), optimum pH 7.9 and activation energy 54 kj/mol, and (*S*)-stylopine synthase (E.C. 1.1.3.32), optimum pH 8.0 and activation energy 25 kj/mol. Both are inducible P450 enzymes requiring oxygen and NADPH (NADH is inactive), but addition of NADH activates the reaction. Both are highly specific; the former acts on (*S*)-scoulerine and the latter on (*S*)-cheilanthifoline [K914].

6β-Hydroxyhyoscyamine epoxidase (E.C. 1.14.11.14)

Hyoscyamus niger enzyme requires α-oxoglutarate, ascorbate and Fe^{2+} in the formation of scopolamine [K887].

Pterocarpin synthase (E.C. 1.1.1.246)

Cicer arietinum culture enzyme, optimum pH 6.0, which requires NADPH (NADH is poor) acts on vestitone, forming a cyclic ether by reduction [K879].

Dioxin formation

Horseradish peroxidase catalyzes the oxidation of pentachlorophenol to form octachloro-*p*-dioxin [H837].

Dihydrogeodin oxidase

Aspergillus terreus enzyme, an intensely blue protein, molecular weight 153 000, is a homodimer containing eight Cu/subunit. It is inhibited by azide and ethylxanthate, but not by cyanide or diethyldithiocarbamate. It forms geodin, with the formation of an internal ether bond, and the oxidation of one of the aryl rings to a 4-oxo-2,5-diene ring to form a *spiro*-compound [E300]. Although it is highly specific, it has some activity towards sulochrin and griseophenone B [C556].

Catechol oxidase (dimerising) (E.C. 1.1.3.14)

This spinach leaf enzyme, optimum pH 7.4, forms diphenylenedioxide-2,3-quinone with oxygen (1.5 mol) as co-substrate. It is activated by FAD, and inhibited by cyanide; it is not a copper-containing polyphenol oxidase [K880].

Rifamycin B oxidase (E.C. 1.10.3.6)

Monocillium oxidizes rifamycin B to rifamycin O. The reaction involves the oxidation of a phenolic ring to a *gem*-diol monoether quinone analogue, followed by ring closure of the acetoxy group to form a *gem*-diol ester. Other substrates are rifamycin SV and simple catechols and quinols. In contrast, Pleurotus laccase scarcely acts on

rifamycin B [C519]. The same reaction is observed in Humicola [D922].

Phenanthridinone formation

Rat liver converts fluorenone oxime into phenanthridinone. The enzyme appears to be both mitochondrial and microsomal. It requires NADPH, but not oxygen; it is not inhibited by carbon monoxide. The reaction involves ring expansion, with the oxime moiety being converted into a heterocyclic nitrogen, apparently with migration of the hydroxyl group to the carbon adjacent to the nitrogen [A3230].

Stilbene oxidase

Botrytis cinerea enzyme is laccase-like (E.C. 1.10.3.2), molecular weight 32 000, with two isozymes, pI 4.3 and 4.35. Pterostilbene, 4,4′-dihydroxystilbene and resveratrol are substrates, the latter forming ε-viniferin. The reaction involves dimerization, with the formation of a benzofuran ring system [J823].

Strictosidine conversion into 10-deoxysarpagine

Rauwolfia serpentina P450 catalyzes this reaction; it utilizes NADPH and oxygen. The reaction involves a C–C ring closure [H676].

Phthalide formation

Pseudomonas putida and Aspergillus niger oxidize 2-ethylbenzoate to (*S*)-3-methylphthalide. 2-*n*-Pentyl- and 2-*n*-nonylbenzoates similarly form the corresponding butyl and octyl phthalides [J486].

Geotrichum candidum converts methyl *o*-acetylbenzoate into 3-methylphthalide; this reaction is also observed in Mucor javanicus, M. heimalis, Endomyces magnusii, E. resii and Saccharomyces [J486].

Aflatoxin B_1 formation

Aspergillus flavus enzyme, molecular weight 64 000–70 000 (by two methods) and optimum pH 8 forms aflatoxin B_1 from sterigmatocystin; the enzyme(s) is activated by Zn^{2+}, Co^{2+} and Mn^{2+}. The reaction involves the conversion of two 6-membered fused rings, one aromatic, into two fused 5-membered rings, one of which is a lactone. It has been suggested that O-methylsterigmatocystin is an intermediate; presumably a number of other compounds are also intermediates. Dihydrosterigmatocystin yields dihydroaflatoxin B_1 [E691, G154].

Aspergillus parasiticus enzyme has an optimum at pH 7.5–7.8 [A2594].

1.4 *Polymerization reactions*

Formation of biphenyl compounds and oligomers

L-Tyrosine, α-methyl-L-tyrosine and morphine are dimerized by rat gut peroxidase [G617]. Horseradish peroxidase dimerizes tyrosine [J401] and a range of tyrosine-containing peptides. With N-acetyltyrosine and some peptides the products include trimers and tetramers [J327]. The site of reaction appears to be *ortho* to the hydroxyl group, forming a carbon-carbon bond.

Lactoperoxidase oxidizes guaiacol to 4,4′-dihydroxy-3,3′-dimethoxybiphenyl and 3,3′-dimethoxy-4,4′-biphenylquinone, and a mixture of guaiacol and catechol forms 2′,3′,4-trihydroxy-3-methoxybiphenyl [J352].

Human neutrophil myeloperoxidase and horseradish peroxidase convert phenol into 4,4′-dihydroxybiphenyl [E297]. Horseradish peroxidase also converts phenol into 2,2′-dihydroxybiphenyl and polymers [C468, D433].

Silkmoth larva and locust convert a mixture of 4-substituted catechols and resorcinols into biphenyls. For instance, N-acetyldopamine and 4-ethylresorcinol form 6′-acetamidoethyl-3-ethyl-3′,4,4′,6-tetrahydroxybiphenyl [G346].

Pisum sativum ascorbate peroxidase forms a biphenyl from *p*-cresol [K404].

A laccase-like copper-containing phenol oxidase in Rhizoctonia praticola, optimum pH 6.7–6.9 and molecular weight 78 000, converts 2,6-dimethoxyphenol into 3,3′,5,5′-tetramethoxybiphenoquinone [A3836].

Formation of higher polyphenols

Bjerkandera adusta manganese peroxidase (E.C. 1.11.1.13) converts guaiacol into a mixture of polymers, molecular weights up to about 3200. A range of other phenols, syringic acid and *o*-anisidine are also substrates [K565].

Trimerisation of indole

Oak, horse chestnut and Rhus oxidize indole to 2,2′-bis(3-indolyl)indoxyl [A3125].

Pterostilbene dimerisation

Botrytis cinerea laccase-like stilbene oxidase converts pterostilbene into a dimer (3-(3,5-dimethoxyphenyl)-5-(2-(3,5-dimethoxyphenyl) ethenyl)-2-(*p*-hydroxyphenyl)benzofuran) [K147].

Coniferyl alcohol dehydrogenase (E.C. 1.1.1.194)

Prunus strobus, Abies balsama, Laryx laricina, Picea rubens and Pinus banksiana enzymes act on coniferyl alcohol to form dehydrodiconiferyl alcohol and pinoresinol. The reactions involve condensation of the side chain to the aryl nucleus to form dehydrodiconiferyl alcohol, and between two side chains of coniferyl alcohol to form pinoresinol. Several isozymes are involved, which are glycoproteins [G745].

Sitka spruce (Picea sitchensis) xylem contains two glycoprotein isozymes, molecular weights 62 000 or 80 000 (depending on method; the higher value may be a methodological artifact); it is not a peroxidase [J820].

Berbabamunine synthase (E.C. 1.1.3.34)

Berberis stolonifera enzyme is a P450, molecular weight 46 000, pI 6.05 and optimum pH 8–8.5 or 7.2–7.5, depending on conditions. Substrates include (*R*)- and (*S*)-N-methylcoclaurine, and (*S*)-coclaurine, which are dimerized by stereo-specific oxidative phenol coupling, without transfer of activated oxygen to the substrate molecules [G736].

Vindoline dimerisation

Streptomyces griseus catalyzes the formation of a complex dimer from vindoline, probably via dihydrovindoline ether that involves a head-to-head C-C bond formation adjacent to the non-indole nitrogen [A2984].

1.5 *Reactions involving carbon ring fission*

Catechol 1,2-dioxygenase (pyrocatechase; E.C. 1.13.11.1)

Catechol → *cis*, *cis*-muconate

Rhodococcus rhodochrous enzyme, a homodimer with optimum pH 9, acts on catechol, 3- and 4-methylcatechol. The molecular weight of the monomer, based on mass spectrometry and genetic coding is 31 558 or 31 539, respectively [J703]. R. erythropolis enzyme, monomeric molecular weight 36 000–37 000 contains 1.3 mol Fe/mol. Pyrogallol, as well as catechol, 3- and 4-methylcatechol are substrates, but protocatechuate is not. It is inactivated at 50°. Its amino acid composition has been determined [D247].

Acinetobacter radioresistens enzyme is a homodimer, molecular weight 78 000. It is unusual in that it dissociates into an active monomer in 0.5M sodium sulphate. It contains 0.96 mol Fe^{3+}/subunit. It is more highly specific than Rhodococcus rhodochrous enzyme; 3- and 4-methylcatechol are poor substrates [J390].

A. calcoaceticus enzyme, molecular weight 81 000–85 000 (using different measuring techniques), is composed of two monomers and contains two mol Fe/mol. Additional substrates (poor) are 3- and 4-methylcatechol and 3-isopropylcatechol, but a number of other catechols are not substrates. It has a broad optimum at pH 7–9, which coincides with its stability range. Its amino acid composition has been determined; methionine is the amino terminal residue [A2640].

Rhizobium leguminosarum enzyme is a homodimer, molecular weight 70 000 and optimum pH 9–9.5, which contains one mol Fe/mol [F647]. R. trifolii enzyme is also a dimer, molecular weight 107 000, containing 1 mol Fe^{3+}/mol monomer [D672].

Candida tropicalis enzyme, optimum pH 7.6–8.0, acts on catechol, 4-methylcatechol, 3-and 4-chlorocatechol but not on other catechols [E204].

Trichosporon cutaneum enzyme has molecular weight 105 000 and 35 000 for holoenzyme and monomer respectively. Its specificity is broad, acting on catechol, 4-methylcatechol, pyrogallol and hydroxyquinol [C84].

Pseudomonas pyrocatechase II acts on catechols substituted at positions 3 and 4 with methyl, chloro or fluoro groups [B754]. P. arvilla enzyme converts pyrogallol into both α-hydroxymuconic acid and 2-pyrone-6-carboxylic acid; the latter is formed by ring closure of the ring fission product, possibly without prior release from the enzyme [B547].

Brevibacterium enzyme contains Fe^{3+}, apparently sulphur-bound [A1231].

Enzyme from an unspecified bacterium has an optimum between pH 7 and 10 [B525].

Catechol 2,3-dioxygenase (metapyrocatechase; E.C. 1.13.11.2)

Catechol → 2-hydroxymuconic semialdehyde

A study carried out on extradiol dioxygenases from a series of 7 Pseudomonas strains demonstrated that each enzyme has its own quantitative specificity towards catechol, 3- and 4-methylcatechol, 4-chlorocatechol and 2,3-dihydroxybiphenyl, ranging from good activity for most of these substrates to good activity for only 2,3-dihydroxybiphenyl [H272]. One Pseudomonas enzyme is a homotetramer, with apparent molecular weight for monomer and tetramer of 33 000 and 110 000, respectively. Its optimum pH is 8–8.5 and is stable up to 70°. It acts on catechol, 3- and 4-methylcatechol; 3-fluorocatechol, and 4-chlorocatechol are poor substrates [J649]. Another study by the same research team confirmed many of these results, but gave a tetrameric molecular weight of 120 000 [G355]. P. putida enzyme is probably a homotetramer with subunit molecular weight 34 000 [K204].

P. arvilla enzyme oxidizes pyrogallol to α-hydroxymuconic acid [B547] and is inhibited competitively by *o*-nitrophenol or *m*-phenanthroline relative to catechol, but noncompetitively relative to oxygen [A1031]. It is not inhibited by superoxide dismutase (E.C. 1.15.1.1), hence, superoxide is not the oxidizing species, nor by compounds capable of trapping singlet oxygen [A1047]. P. aeruginosa enzyme is inhibited by ATP and Mg^{2+} [A2832].

Bacillus thermoleovorans enzyme is a homotetramer, subunit molecular weight 34 700, pI 4.8, optimum pH 7.2, and contains one Fe/monomer. It is inactivated rapidly at 70° [K228].

Enzyme from a thermophilic Bacillus is inactivated by high concentrations of oxygen [J834].

Hydroxyquinol 1,2-dioxygenase (E.C. 1.13.11.37)

Burkholderia cepacia enzyme is a dimer, molecular weight 68 000. It is highly specific, forming maleylacetate [J251].

Azotobacter enzyme is a dimer, monomeric molecular weight 34 000, which is activated by Fe^{2+}. An additional substrate is 6-chloro-1,2,4-trihydroxybenzene [H602].

Phanerochaete chrysosporium enzyme is a dimer, molecular weight 90 000. It incorporates molecular oxygen into the product. It is highly specific, but also oxidizes catechol [H284].

This reaction has also been observed in Pseudomonas [A2697], Sporotrichum [B124], Trichosporon [B368, D232], Arthrobacter [H270], Aspergillus [H236], Bradyrhizobium [J484] and Streptomyces [H347].

2,4,5-Trihydroxytoluene oxygenase

Burkholderia enzyme is apparently a dimer; the molecular weight was found to be 67 000 or 78 000 by different methods. It contains two Fe/mol and is stimulated by Fe^{2+} and ascorbate. The product is 2,4-dihydroxy-5-methyl-*cis, cis*-muconic semialdehyde. Other catechols are also substrates [J903].

3-Methylcatechol 1,2-dioxygenase

3-Methylcatechol → 2-methyl-*cis*, *cis*-muconate

This reaction has been observed with protocatechuate 3,4-dioxygenase (E.C. 1.13.11.3) from Hydrogenophaga palleroni [J218], catechol 1,2-dioxygenases (E.C. 1.13.11.1) from Pseudomonas, Alcaligenes eutrophus, Trichosporon cutaneum, Rhodococcus rhodochrous and R. erythropolis, as well as by activated sludge microorganisms [A3769, B754, C84, D247, E31, J703].

3-Methylcatechol 2,3-dioxygenase

3-Methylcatechol → 2-hydroxy-6-methyl-*cis*, *cis*-muconic semialdehyde

This reaction has been observed in several subspecies of Pseudomonas putida, in Burkholderia cepacia, Sphingomonas and Bacillus stearothermophilus, in activated sludge microorganisms [A2397, E31, J654, K5], as well as being catalysed by chlorocatechol 2,3-dioxygenase and 1,2-dihydroxynaphthalene oxygenase (see below).

4-Methylcatechol 2,3-dioxygenase

4-Methylcatechol → 2-hydroxy-5-methyl-*cis*, *cis*-muconic semialdehyde

Bacillus stearothermophilus catalyses this reaction [A2397], and many reports suggest that this reaction may be common in other microorganisms.

4-Methylcatechol 3,4-dioxygenase

4-Methylcatechol → 3-methyl-*cis*, *cis*-muconate

This reaction has been observed with protocatechuate 3,4-dioxygenase from Hydrogenophaga palleronii [J218], and catechol 1,2-dioxygenases from Pseudomonas, Alcaligenes eutrophus, Trichosporon cutaneum, Rhizobium trifolii, Aspergillus niger, Candida tropicalis, Rhodococcus rhodochrous and R. erythropolis [A3769, B754, C84, C342, D247, D672, E204, G647, J703].

4-Methylcatechol 4,5-dioxygenase

4-Methylcatechol → 2-hydroxy-4-methyl-*cis*, *cis*-muconic semialdehyde

Candida tropicalis catalyzes this reaction [A943], and many reports suggest that this reaction may be common in microorganisms.

2,3-Dihydroxybiphenyl 1,2-dioxygenase (E.C. 1.13.11.39)

Pseudomonas enzyme is an octamer, monomeric molecular weight 33 200. The product is 2-hydroxy-6-oxo-6-phenylhexa-2,4-dienoate. Catechol, 3- and 4-methylcatechol are poor substrates [G771]. P. pseudoalcaligenes and P. aeruginosa enzymes, molecular weights 250 000 and monomeric molecular weights 31 000, contain Fe^{2+}. They are specific for the 1,2-position of 2,3-dihydroxybiphenyl [E329].

Pyrocatechuate 2,3-dioxygenase (E.C. 1.13.11.28)

Tecoma stans enzyme is found both in the lamellar structure of chloroplasts and in the cytosol. The properties of both enzymes are similar, except that the particulate enzyme is somewhat more stable. Copper-chelating reagents are inhibitory, especially diethyldithiocarbamate. A range of heavy metal ions at mM concentration are inhibitory, with some quantitive differences between chloroplast and cytosolic enzymes; in particular, the former is totally inhibited by Cd^{2+}, whereas the latter is unaffected [A202]. It is very labile. Additional substrates include 2,3-dihydroxy-4-isopropylbenzoate and 2,3-dihydroxy-4-methylbenzoate, but not a range of other catechols. Thiols and thiol-binding reagents are inhibitory. Pre-incubation with substrate does not prevent this inhibition, although it protects against thermal inactivation [A2241].

2,3-Dihydroxybenzoate 3,4-dioxygenase (E.C. 1.13.11.14)

Pseudomonas fluorescens enzyme requires oxygen, and forms α-hydroxymuconic semialdehyde and CO_2; other catechols, including catechol, are not substrates [K945].

Protocatechuate 2,3-dioxygenase

Bacillus macerans acts on protocatechuate to form 5-carboxy-2-hydroxymuconic semialdehyde [A3887].

Protocatechuate 3,4-dioxygenase; (E.C. 1.13.11.3)

Protocatechuate → β-carboxymethyl-*cis*,*cis*-muconate

Tecoma stans enzyme, molecular weight 150 000 and optimum pH 5.2, requires Fe^{2+}. It is highly specific, and is not a monophenol monooxygenase. Thiol-binding reagents are inhibitory, and this is partially reversed by thiols [B223].

Acinetobacter calcoaceticus enzyme (electrophoretically homogeneous) is inhibited by many substrate analogues that do not undergo oxidation. Its optimum pH is 8.5–9, and is inactivated at 60°. Amino acid analyses demonstrate a quite different composition from Pseudomonas enzyme [A2407].

Azotobacter vinelandii enzyme, molecular weight variously estimated as 480 000 and 510 000, is composed of monomers, molecular weight 23 300 and 25 250. The native enzyme contains 10 mol of iron [B262].

Brevibacterium fuscum enzyme, molecular weight 315 000 may be a pentamer, and is composed of subunits, molecular weights 40 000 and 22 500. It contains essential Fe^{3+}. Amino acid and spectral analyses have been carried out [D86].

Hydrogenophaga palleronii enzyme not only acts on protocatechuate, but also on dopac, caffeate and some neutral catechols as well as 4-sulphocatechol. Its molecular weight is 97 000 and is composed of monomers, molecular weights 23 000 and 28 500. The specificity of Agrobacterium radiobacter is similar, except that 4-sulphocatechol is not a substrate [J218].

Moraxella isozymes have molecular weights of 220 000 and 158 000. These both appear to be polymers of structure $(\alpha\beta)_3$ and $(\alpha\beta)_4$ [F62].

Pseudomonas fluorescens enzyme is wine red in colour, molecular weight 409 000. Its amino acid composition has been determined [C729]. It is also found in P. aeruginosa [B547]. 3-Fluoro-4-hydroxybenzoate is strongly inhibitory [A1958]. The latter enzyme is thought to utilize superoxide as oxidant [B299]. It contains non-haem Fe^{3+}, removable by reduction and chelation [A152]. Protocatechualdehyde inhibits competitively relative to protocatechuate, and non-competitively relative to oxygen [A1031].

Rhizobium leguminosarum enzyme is induced by protocatechuate [F224].

Protocatechuate 4,5-dioxygenase; (E.C. 1.13.11.8)

Protocatechuate → γ-carboxy-α-hydroxymuconic semialdehyde

Rhizobium leguminosarum enzyme is a dimer, molecular weight 120 000 and optimum pH 9.5 [H127].

Gentisate 1,2-dioxygenase; (E.C. 1.13. 11.4)

Gentisate → 6-carboxy-4-hydroxy-*cis*, *cis*-muconic semialdehyde (maleylpyruvate)

Pseudomonas acidovorans and P. testosteroni enzymes differ in molecular weight (164 000 and 158 000, respectively) and amino acid composition. They are similar in requiring Fe^{2+}, and show a broad specificity toward substituted gentisates; 1,4-dihydroxy-2-naphthoate, an analogue of gentisate with a fused ring system, is also a substrate for the P. acidovorans enzyme [F649]. P. alcaligenes enzyme is a tetramer, molecular weight 154 000, optimum pH 8 and pI 4.8–5.0. P. putida enzyme is a dimer, molecular weight 82 000, optimum pH 8 and pI 4.6–4.8. Enzymes from both species are activated by Fe^{2+} [K4].

Klebsiella pneumoniae enzyme is a tetramer, molecular weight 159 000, optimum pH 8–9 and pI 4.7 [J246]. Bacillus stearothermophilis enzyme appears to be a hexamer, monomeric molecular weight 40 000 that requires Fe^{2+} [H893]. Rhodococcus erythropolis enzyme, a homooctamer, molecular weight 328 000, is activated by Fe^{2+}. Other substrates are gentisates substituted with methyl or halogen [H441].

2,3-Dihydroxy-*p*-cumate 3,4-dioxygenase

Bacillus enzyme has an optimum pH of 8.2. The reaction product is 3-carboxy-2-hydroxy-7-methyl-6-oxoocta-2,4-dienoate. Other substrates include pyrocatechuate, 3-methylcatechol, 3-isopropylcatechol and 2,3-dihydroxy-*p*-toluate, but not catechol or 4-substituted catechols. This distinguishes the enzyme from catechol 2,3-dioxygenase [G766, G768].

Homogentisicase (homogentisate 1,2-dioxygenase; E.C. 1.13.11.5)

Homogentisate + O_2 → maleylacetoacetate

Rat liver enzyme shows a diurnal rhythm, with a sharp decrease in activity at 1800–2100, immediately after light is withdrawn. This coincides with maximal activity in the diurnal rhythm for tyrosine transaminase (E.C. 2.6.1.5) [A1060].

Mouse liver enzyme appears to be a homotrimer, molecular weight 149 000, optimum pH 6.1 and pI about 8. It has an absolute requirement for Fe^{2+}; ascorbate is required, probably to keep Fe in the reduced form [H436].

Rabbit liver enzyme is a heterodimer monomeric molecular weight 230 000 and 200 000, and an optimum at about pH 5. It is also found in human embryo [H768].

A homogentisicase has been found in Drosophyllum lusitanicum [A1149].

Aspergillus enzyme requires Fe^{2+}; other cations such as Fe^{3+}, Cu^{2+}, Co^{2+} and Mn^{2+} cannot substitute for Fe^{2+}. This enzyme is very labile in the presence of oxygen [B848]. Another study found that A. nidulans enzyme is 'rather stable' and highly specific [H900].

3,4-Dihydroxyphenylacetate 2,3-dioxygenase (E.C. 1.13.11.15)

3, 4-Dihydroxyphenylacetate → δ-carboxymethyl-α-hydroxy-*cis*, *cis*-muconic semialdehyde

Bacillus brevis enzyme is a tetramer, molecular weight 140 000, with monomeric molecular weight 36 000. It is not activated by Fe^{2+} or inhibited by CN^- (atypical for this type of enzyme, which is usually activated by Fe^{2+}), peroxide or diethyldithiocarbamate. It contains two mol of Mn/mol, probably as Mn^{2+}; it is claimed to be the first Mn-containing oxygen-activating enzyme described [B947]. It may utilize superoxide as co-substrate [B299].

Bacillus stearothermophilus enzyme is a globular protein, molecular weight 106 000,

composed of monomers, molecular weight 33 000–35 000, and is stable up to 55°. It acts on 3,4-dihydroxyphenylacetate, 3,4-dihydroxymandelate and dihydrocaffeate with a similar V_{max}; protocatechuate is a poorer substrate. Catechol, 4-methylcatechol, L-dopa and dopamine are not substrates, indicating a narrower specificity than for enzyme from Pseudomonas ovalis. It shows a broad optimum about pH 8.4–8.7. Its amino acid composition has been determined [A2827].

Pseudomonas ovalis enzyme (colourless), is apparently a homopolymer, molecular weight 140 000 and monomeric molecular weight 35 000. It contains 4–5 mol of non-haem iron (Fe^{2+}). Its amino acid composition has been determined, and the carbonyl terminal amino acid is leucine. Many catechols are substrates, but often with a very low oxidation rate. It is inactivated by oxygen or by other oxidizing agents; reactivation is brought about by Fe^{2+} or reducing agents, suggesting that inactivation involves oxidation to Fe^{3+} [A1090, A1230].

Klebsiella pneumoniae enzyme, a homotetramer, molecular weight 102 000, requires four mol of Mg^{2+}/mol [H232].

Arthrobacter synephrinum enzyme, molecular weight 282 000, additionally acts on 3,4-dihydroxymandelate and dihydrocaffeate [A3279].

3-Carboxyethylcatechol 2,3-dioxygenase (E.C. 1.13.11.16)

Achromobacter enzyme requires Fe^{2+} [K819].

Caffeate 3,4-dioxygenase (E.C. 1.13.11.22)

This reaction in Hydrogenophaga palleronii is catalyzed by protocatechuate 3,4-dioxygenase (see above) [J218].

L-Dopa 4,5-dioxygenase

Amanita muscaria enzyme is a heteropolymer, monomeric molecular weight 22 000. The muconic semialdehyde formed is an intermediate in the formation of betalamic acid. Other catechols are also substrates [G119].

Questin monooxygenase (E.C. 1.14.13.43)

Aspergillus terreus enzyme is composed of two proteins, optimum pH 7.5, requires oxygen and NADPH and is very unstable. The reaction involves opening the quinone ring to form a carboxylic acid [K701].

3,4-Dihydroxyphenylalanine: oxygen 2,3-oxidoreductase (recyclizing) (stizolobinate synthase, E.C. 1.3.11.30)

Stizolobium hassjoo seedling enzyme, optimum pH 7.6 is highly specific. It requires Zn^{2+}, is unstable especially in air and is inhibited by thiol-binding compounds [K706, K708].

3,4-Dihydroxyphenylalanine: oxygen 4,5-oxidoreductase (recyclizing) (stizolobate synthase, E.C. 1.3.11.29)

Stizolobium hassjoo seedling enzyme, optimum pH 7.4 is highly specific. It requires Zn^{2+}, is unstable especially in air and is inhibited by thiol-binding compounds [K706, K708].

1,2-Dihydroxynaphthalene oxygenase

Pseudomonas putida enzyme, molecular weight in excess of 275 000, and subunit molecular weight 19 000, yields 2-hydroxychromene-2-carboxylate, presumably a secondary product from *cis*-4-(*o*-hydroxyphenyl)-2-oxobut-3-enoate, the fission product. It requires Fe^{2+}; iron-binding compounds are inhibitory, and this is reversed by Fe^{2+}. 3-Methylcatechol is also a substrate, but most other catechols are not [B527].

1-Hydroxy-2-naphthoate 1,2-dioxygenase (E.C. 1.13.11.38)

Nocardioides enzyme, monomeric molecular weight 45 000 and native molecular weight 270 000, contains one mol Fe^{2+}/mol, which is essential for activity. The product is 4-(*o*-carboxyphenyl)-2-oxobutyrate [J598].

Coccus enzyme requires oxygen and is activated by Fe^{2+} [E730].

Diphenyl ether fission

Rat liver converts thyroxine into diiodotyrosine; the reaction requires oxygen [C809]. It is also catalyzed by human thyroid peroxidase [D553].

Pseudomonas cruciviae degrades diphenyl ether to phenol, probably with 2-phenoxymuconate as an intermediate [E41].

***o*-Aminophenol 1,6-dioxygenase**

Pseudomonas arvilla pyrocatechase oxidizes the substrate to 2-aminomuconic semialdehyde [A3636]. P. pseudoalcaligenes enzyme, molecular weight 140 000 and monomeric molecular weights 35 000 and 39 000, requires oxygen , with an apparent requirement for Fe^{2+}. It also acts on catechol, 6-amino-3-methylphenol, 2-amino-3-methylphenol and 2-amino-4-chlorophenol, but other catechols and quinols are not substrates [J255, J329].

A bacterial enzyme, molecular weight 140 000 and optimum pH 7.5 is stable between pH 7.5 and 9 [H915].

3-Hydroxyanthranilate 3,4-dioxygenase (E.C. 1.13.11.6)

3-Hydroxyanthranilate+O_2 → α-amino-β-carboxymuconic semialdehyde

The rat brain and liver enzymes, molecular weight 37 000–38 000, appear to be identical. It has a broad optimum at about pH 6–5 [E472]. Baboon liver enzyme has a similar molecular weight, optimum pH 7.4–7.6. It requires Fe^{2+} for activity [A2280] as do the vervet monkey and rat liver enzymes [A912, E114]. The latter enzyme exists as several isozymes. Beef kidney enzyme has a molecular weight of 34 000, and readily polymerizes to an inactive form [A2430].

4-Sulphocatechol 3,4-dioxygenase

Hydrogenophaga palleronii protocatechuate 3,4-dioxygenase acts on 4-sulphocatechol as well as on protocatechuate, dopac, caffeate and some neutral catechols. Its molecular weight is 97 000 and is composed of monomers, molecular weights 23 000 and 28 500. The product is 3-sulphomuconate [J218].

Chlorocatechol 2,3-dioxygenase (catechol 1,6-dioxygenase)

3-Chlorocatechol → 2-hydroxymuconic acid

Pseudomonas putida enzyme is a tetramer, monomeric molecular weight 33 400 and pI 7.1. Other substrates include catechol, and catechols substituted with methyl or halogen. Although the product formed from 3-chlorocatechol is 2-hydroxymuconic acid indicating the formation of the acid chloride by proximal fission, the product formed from 3,5-dichlorocatechol indicates distal (1,6) fission. This enzyme is atypical for extradiol dioxygenases in that it is rapidly inactivated above 40° [J515].

Chlordiazon catechol dioxygenase (E.C. 1.13.11.36)

Phenylobacterium immobilis enzyme, pI 4.5, contains one Fe/subunit, and has been crystallized. The product is a hydroxymuconic semialdehyde [C332].

Cyclopropane ring fission

Rat liver microsomes act on 1,1-dichloro-*cis*-diphenylcyclopropane to form several products such as 2-chloro-3-oxo-1,3-diphenyl-1-propene. This involves an unusual type of ring fission which is considered to form 2,3-dichloro-1,3-diphenyl-1-propene as the initial product [F573].

Methylococcus capsulatus soluble methane monooxygenase (E.C. 1.14.13.25) converts cyclopropylbenzene into benzyl alcohol. 3-Phenylprop-2-en-1-ol is also formed, and this may be an intermediate [F278].

1.6 *Reactions involving heterocyclic ring fission*

D-Tryptophan 2,3-dioxygenase (D-tryptophan pyrrolase)

$$\text{D-Tryptophan} + O_2 \rightarrow \text{D-kynurenine}$$

The properties of rat liver enzyme are very similar to those of L-tryptophan 2,3-dioxygenase, and it is readily induced by cortisone, D- or L-tryptophan. An intestinal mucosal enzyme that is less readily induced acts on both isomers of tryptophan [A598].

Wheat germ enzyme acts on both D- and L-tryptophan, and substituted analogues. The enzyme is found as 3 molecular forms [E24].

L-Tryptophan 2,3-dioxygenase (L-tryptophan pyrrolase; E.C. 1.13.11.11)

$$\text{L-Tryptophan} + O_2 \rightarrow \text{L-formylkynurenine}$$

This enzyme in vertebrates is the first in the sequence for the oxidation of dietary tryptophan ingested in excess of requirements for protein synthesis and hormone formation.

The enzyme is found (in decreasing order of activity) in mammalian liver, lung and brain from rat, gerbil and mouse. In rabbit, lung shows the highest activity [J830].

Rats receiving an I.P. dose of ethanol four hours prior to death showed a twofold increase in both enzyme quantity and total enzyme activity. This is caused by an increase in the half-life of the enzyme from 2.3 to 3.9 h. [A2059]. In contrast, treatment with sucrose or ethanol for two days resulted in no change in the amount of 'holoenzyme', but a 30 per cent decrease in 'total enzyme'. The effect of cortisol in conjunction with sucrose appears to result entirely from decreased 'holoenzyme', but with no effect on 'total enzyme'. On its own, cortisol markedly increases both enzyme forms and eliminates the effects of ethanol. In this study it appears that the two forms were distinguished by measuring activity with and without added haematin [A2062]. Rat cerebral activity is increased by administration of L-tryptophan [A1289].

Drosophila melanogaster eye enzyme is mainly cytosolic, but a small proportion is insoluble [A1194].

Wheat germ enzyme acts on both D- and L-tryptophan, and on a range of tryptophan containing peptides, as well as on tryptophan analogues substituted on both ionic groups or the 5- position, all with similar activity. The enzyme is found as three molecular forms [C559, E24].

Bacillus brevis (a thermophile) enzyme is a haemoprotein, which appears to be a homotetramer, molecular weight 110 000. The enzyme is stabilized by L-tryptophan [F737]. Pseudomonas acidovorans enzyme is a tetramer, containing two moles both of haem and copper (Cu^+ is the active form) per mole. Tryptophan interacts with both haem and copper, and molecular oxygen binds to the enzyme-tryptophan complex, possibly to the copper. Studies with chelating agents demonstrate that although Cu^{2+}-binding agents do not inhibit, Cu^+-binding agents are inhibitory. After oxidation diethyldithiocarbamate prevents reactivation by ascorbate [A792, A1426]. P. fluorescens enzyme does not contain copper; inhibition by copper-binding reagents appears to be by other mechanisms [A1096]. Streptomyces parvulis enzyme (optimum pH 8.3) requires ascorbate, and can utilize 5-methyl-, 5-fluoro- and α-methyl-L-tryptophan as additional substrates; D- isomers are not substrates. It is probably a haemoprotein, molecular weight 88 000 [E588, E589].

Peptide tryptophan 2,3-dioxygenase (E.C. 1.13.11.26)

Wheat germ (optimum pH about 8) and rat liver enzymes act on tryptophan residues in polypeptides such as pepsin and trypsin, converting them into kynurenine residues [K823].

Indole 2,3-dioxygenase; (E.C. 1.13.11.17)

$$\text{Indole} + O_2 \rightarrow \text{anthranilate}$$

In rat, indole is converted into N-formylanthranilate, which is the expected initial product of indole ring fission, as well as anthranilate [D158].

Jasminum grandiflorum leaf enzyme, optimum pH 4.8, forms anthranilate from the substrate. Other substrates are 5-hydroxy- and 5-bromoindole. FAD is co-substrate and Cu^{2+} is also required; Cu^{2+}-chelating reagents are inhibitory [B70].

Tecoma stans leaf enzyme, optimum pH 5.2, utilizes two molecules of oxygen. Other substrates are 5-hydroxyindole, 5-bromoindole and 5-methylindole. It is not inhibited by thiols or by thiol-binding reagents, copper or non-haem iron chelators, nor by atebrin, which suggests that it is not a flavoprotein. It is inactivated by dialysis, but the cofactor has not been identified [C170].

Zea mays leaf enzyme, molecular weight 98 000, exhibits an optimum at pH 5.0. The initial product appears to be 2-formamidobenzaldehyde, although the products detected are anthranil and anthranilate; their formation requires four oxygen atoms. Copper-binding reagents are inhibitors, reversible by Cu^{2+}, which also activates dialyzed enzyme [D334].

Aspergillus niger forms both N-formylanthranilate and anthranilate, and enzymes for both reactions were found [F417].

A similar reaction occurs in wheat seedling, converting skatole into *o*-formamidoacetophenone. The enzyme, which is composed of two isozymes, is different from tryptophan 2,3-dioxygenase [C559].

Indoleamine 2,3-dioxygenase (E.C. 1.13.11.42)

Mouse liver indoleamine 2,3-dioxygenase is totally different from rat liver tryptophan 2,3-dioxygenase, although tryptophan is the substrate. It is induced by lipopolysaccharide (which suppresses tryptophan 2,3-dioxygenase) and is found in almost all tissues examined, except trachea, bladder and spleen. In most tissues the activity is low, but good activity is found in lung, colon, liver, caecum, seminal vesicle and especially in epididymis [E30].

2,3-Dihydroxyindole 2,3-dioxygenase (E.C. 1.13.11.23)

A microorganism enzyme, optimum pH 8.0 and stable at pH 7–9, requires oxygen. Analogues of the substrate are not oxidized [K821].

Quinaldate 4-oxidoreductase (E.C. 1.3.99.18)

Alcaligenes enzyme, molecular weight 155 000, requires oxygen and NADH, and is activated by Fe^{2+}. The reaction product is kynurenate [J32].

Pseudomonas enzyme, optimum pH 8.0, pI 4.6 and molecular weight 300 000, is composed of subunits, molecular weights 90 000, 34 000 and 20 000 (consistent with a $\alpha_2\beta_2\gamma_2$ structure), contains molybdenum, iron, acid labile sulphur and FAD. It forms kynurenic acid from quinaldate. Heavy metals are inhibitory [K768].

Serratia marcescens enzyme (inducible), molecular weight 95 000–100 000 is a heterodimer, monomeric molecular weights 75 000–80 000 and 18 000–19 000; it contains Fe and Mo [K770].

7,8-Dihydroxykynurenate 8,8a-dioxygenase (E.C. 1.13.11.10)

This reaction forms 5-(3-carboxy-3-oxopropenyl)-4,6-dihydroxypyridine-2-carboxylate. The enzyme (source unstated) requires oxygen and NAD(P)H [K853].

Coumarin 3,4-oxide fission

This compound rapidly degrades to *o*-hydroxyphenylacetaldehyde in aqueous solution; it is postulated that this is an integral step in the route by which coumarin is degraded by mouse liver microsomes [H807].

Quercetin 2,3-dioxygenase (E.C. 1.13.11.24)

Aspergillus flavus enzyme contains copper but not iron. The products are 2-protocatechuoylphloroglucinolcarboxylic acid and carbon monoxide [K820].

Catechin oxygenase

Chaetomium cupreum enzyme, molecular weight 40 000, optimum pH 7.0 and pI 9.1, is a glycoprotein and is specific for catechin. The reaction products are catechol, protocatechuate and phloroglucinolcarboxylate [G814].

2-Hydroxychromene-2-carboxylate isomerase

Pseudomonas enzyme, molecular weight 25 000–27 000 and optimum pH about 8, is stable at pH 3–10. Glutathione appears to be both cofactor and stabiliser (at 50°). The reaction product is *o*-hydroxybenzylidenepyruvate, and lies on the degradation pathway of Tobias acid to salicylate [J711].

Maackiain fission

Stemphylium botryosum reductively opens the furan ring to form 2′,7-dihydroxy-4′,5′-methylenedioxyisoflavan [A2283].

Flavonol 2,4-dioxygenase

Aspergillus niger enzyme grown on rutin is a trimer, molecular weight 130 000–170 000 (clearly a mixture), monomeric molecular weights about 65 000, 55 000 and 33 000. It is a copper-containing glycoprotein composed of about 50 per cent N-linked oligomannose-type glycan chains. The products from quercetin are carbon monoxide and protocatechuoylphloroglucinol-carboxylate. It is potently inhibited by ethylxanthate, which specifically reduces Cu^{2+}. It is inhibited by diethyldithiocarbamate without loss of copper [K214].

(+)-Pinoresinol/(+)-lariciresinol reductase

Forsythia intermedia enzyme is composed of two isozymes, molecular weight 35 000, separable by anion-exchange chromatography. The reaction involves the successive fission of both ether rings in pinoresinol to larisiresinol and (−)-secoisolarisiresinol [H883].

Usnic acid dehydrogenases ((*S*)-usnate reductase, E.C. 1.1.1.199)

Evernia prunastri enzyme, molecular weight 450 000, requires NADH for the reduction of L-usnic acid. D-Usnic acid dehydrogenase is composed of two isozymes. The reaction results in the opening of the ether ring [B774, E126].

Phosphoribosyl isomerisation

Phosphoribosylanthranilate isomerase cleaves the ribosyl ether bond to form *o*-carboxyphenylaminodeoxyribulose-5-phosphate. The molecular weight of the enzymes from Enterobacter hafniae, Aeromonas formicans and Proteus is 67 000. This is a key reaction step in the formation of tryptophan; the next step is the formation of indole-3-glycerol phosphate, which either forms tryptophan directly, or forms indole as an intermediate [A1481].

(−)-Epigallocatechin ether fission

Musa accuminata forms 2-hydroxy-3-(2,4,6-trihydroxyphenyl)-1-(3,4,5-trihydroxyphenyl)-1-propanone from (−)-epigallocatechin; this presumably is an oxidative fission [K423].

3,4-Dihydroxyquinoline 2,4-dioxygenase (E.C. 1.13.99.5)

Arthrobacter and Pseudomonas putida enzymes form N-acetyl- and N-formylanthranilic acids, respectively, from 1*H*-3,4-dihydroxyquinaldine and 1*H*-3,4-dihydroxyquinoline, respectively, with release of carbon monoxide. Two oxygen atoms are incorporated, indicating oxygenolytic attack at C-2 and C-4 of both substrates [K774].

5,10-Methylenetetrahydrofolate dehydrogenase (E.C. 1.5.1.5 and 1.5.1.15; $NADP^+$ and NAD^+-requiring, respectively)

5, 10-Methylenetetrahydrofolate → 10-formyltetrahydrofolate

Pig liver enzyme appears to be a complex with 5,10-methenyltetrahydrofolate cyclohydrolase and 10-formyltetrahydrofolate synthetase (E.C. 6.3.4.3) [A2844].

In dihydrofolate-deficient immature domestic poultry chicks, activity is reduced by 25 per cent by folate or oestradiol, and these effects are additive [A1680].

Pisum sativum enzyme appears to be identical with 5,10-methenyltetrahydrofolate cyclohydrolase, but is separable from 10-formyltetrahydrofolate synthetase. Its molecular weight is 38 500, and it requires NADP [H619], with optimum pH 7.8 [A1429].

Saccharomyces cerevisiae enzyme is composed of two cytosolic isozymes; one requires NADPH and the other NADH [H794].

Peptostreptococcus productus 5,10-methylenetetrahydrofolate dehydrogenase, molecular weight 66 000 is a dimer. The product is said to be 5,10-methenyltetrahydrofolate, which makes it a different enzyme from others listed under this heading [F869].

5,10-Methylenetetrahydrofolate reductase (E.C. 1.1.1.68)

5, 10-Methylenetetrahydrofolate ↔ 5-methyltetrahydrofolate.

Pig liver enzyme, molecular weight 77 300, contains one mol of FAD [C85].

Rat liver and brain enzymes are cytosolic, optimum pH 6.6 [A1586, A2502]. The reverse reaction requires FAD as hydrogen acceptor. An additional substrate for the reverse reaction is 5-methyltetrahydropteroylpentaglutamate [A2502].

Human platelet enzyme releases formaldehyde from 5-methyltetrahydrofolate [A2446].

Clostridium formicoaceticum enzyme is an octomer composed of two different monomers, molecular weights 26 000 and 35 000, and contains iron and zinc, acid-labile sulphur and FAD. It is inactivated by oxygen. For the reverse reaction, methylene blue, menadione, benzyl viologen or FAD can be used as oxidant [D260].

Peptostreptococcus productus enzyme is a dimer, molecular weight 66 000 [F869].

5,10-Methenyltetrafolate cyclohydrolase (E.C. 3.5.4.9)

Pisum sativum enzyme, molecular weight 38 500, which requires NADP, could not be separated from 5,10-methylenetetrafolate dehydrogenase (E.C. 1.5.1.5 and 1.5.1.15). It is inhibited by dihydrofolates [H619].

Pig liver enzyme is associated with a complex of enzymes that are involved with folate reactions [A2844].

Hydantoin hydrolysis (c.f. E.C. 3.5.2.2)

Flavobacterium reversibly hydrolyzes a range of 5-aralkylhydantoins to N-carbamoylamino acids

(the corresponding L-amino acids are released by a further enzymatic hydrolysis). Both D- and L-N-carbamoylamino acids are formed with most substrates (DL mixtures), but the L-isomer is preferred. The optimum pH is about 8.6 [F938, F940].

Pseudomonas is also effective in catalyzing the reaction with 5-(*p*-hydroxyphenyl)hydantoin, both isomers of which yield D-*p*-hydroxyphenylglycine, but Achromobacter delicatulus is much less effective than Pseudomonas. The optimum pH for the Pseudomonas enzyme is 8.0 for a range of aryl-substituted hydantoins. A racemization step accompanied by asymmetric hydrolysis has been suggested [E391, E450, F943].

Methyl tetrahydroprotoberberine 1,4-monooxygenase (E.C. 1.14.13.37)

Corydalis vaginans enzyme fissions the heterocyclic ring system of (*S*)-N-methylcanadine and N-methylstylopine to form an oxo-azadecane ring system with both aromatic moieties unchanged [E577].

Morpholine and piperazine ring fission

Many studies have shown that these ring systems are subject to fission reactions. For instance, in rat the morpholino ring of doxapram is oxidized to bis(2-hydroxyethyl)amino and 2-hydroxyethylamino groups [A1389]. In rat trifluoperazine, fluphenazine, prochlorperazine, perazine and chlorcyclizine are oxidized to phenylenediamines [A576].

Lactone hydrolysis

Human serum Type Q and Type R hydrolases act on the lactones 2-coumaranone, dihydrocoumarin and homogentisic lactone as well as on many aliphatic lactones to release the free acids. The hydrolysis rate is not as great as for phenyl acetate, but it is much greater than for paraoxon [K327].

Human serum arylesterase (see paraoxonase) hydrolyzes the lactone analogue 4-((5-methyl-2-oxo-1,3-dioxol-4-yl)methylthio)benzenesulphonate [G892].

Acinetobacter calcoaceticus lactonohydrolase, molecular weight 30 000 and optimum pH 7, is specific for 3,4-dihydrocoumarin; its amino acid sequence has been determined. It also shows bromoperoxidase activity towards monochlorodimedon with peroxide in the presence of an organic acid; this is due to the formation of a low-molecular weight brominating species [K429].

Dioxin fission

Phanerochaete sordida acts on 2,3,7,8-tetrachlorodibenzo-*p*-dioxin and octachlorodibenzo-*p*-dioxin to form 4,5-dichlorocatechol and tetrachlorocatechol respectively [H911].

Methylenedioxy ring fission

Rat liver microsomes oxidize 3,4-methylenedioxymethamphetamine to 3,4-dihydroxymethamphetamine; the (+)-isomer is the preferred substrate. 3,4-Methylenedioxyamphetamine is also a substrate. It appears to be mediated by a NADH-dependent P450 enzyme [A1570, F805]. A range of other methylenedioxybenzenes are substrates, with the methylenedioxy carbonyl being oxidized to carbon monoxide, which then inhibits the reaction; the enzyme is a phenobarbital-induced P450. The optimum pH is 7.4 [A3947].

Rabbit liver P450IIB4 and probably other P450 isozymes oxidize methylenedioxybenzene, methylenedioxyamphetamine and methylenedioxymethamphetamine. It requires NADPH, and is inhibited by carbon monoxide [F761].

Pseudomonas converts piperonylate into vanillate and protocatechuate. The authors suggested (probably erroneously) that vanillate is the initial product [A2449].

Dibenzothiophene sulphone monooxygenase

Rhodococcus erythropolis enzyme, which has been crystallized, is a homodimer, molecular weight 97 000, monomeric molecular weight 50 000 and optimum pH about 7.5. It converts the above compound into 2′-hydroxybiphenyl-2-sulphonate; dibenz[*c*,*e*][1,2]oxathiin-6,6-dioxide is a second substrate. The terminal amino acid sequence has been determined. 8-Hydroxyquinoline, α,α-bipyridyl, Mn^{2+} and Ni^{2+} are inhibitory. This enzyme is the second in a sequence that desulphurises thiophenes; further steps desulphinate the reaction product [K315].

1.7 *Dearomatization*

Benzene 1,2-dioxygenase; (E.C. 1.14.12.3)

Benzene → *cis*-1, 2-dihydroxycyclohexa-3, 5-diene (*cis*-1, 2-dihydro-1, 2-dihydroxybenzene)

Mammalia and other vertebrates differ from microorganisms in that the latter form *cis*-dihydrodiols instead of *trans*- analogues (which arise from aryl epoxides) from benzene and polynuclear hydrocarbons.

Pseudomonas putida enzyme has a broad specificity for monosubstituted benzenes, with oxidation adjacent to the substituent group [J656]. It is composed of a dioxygenase, molecular weight 215 300, and an electron transport protein, molecular weight 12 300. Both are iron-sulphur proteins, the first with two 2Fe-2S clusters and the second with one such cluster [B45]. A further publication claims that the molecular weights are 186 000 and 21 000 respectively, with a third component, a flavoprotein, molecular weight 60 000. The system requires Fe^{2+} and NADH [A1611].

The reaction has also been observed in Moraxella [A638] and Rhodococcus [H873].

Toluene 2,3-dioxygenase (E.C. 1.14.12.11)

Pseudomonas putida enzyme, molecular weight 151 000, is composed of subunits, molecular weights 52 500 and 20 800. It requires NADH, Fe^{2+}, NADH cytochrome c reductase (E.C. 1.6.99.3) and a Fe-S enzyme (ferredoxin $_{TOL}$). The product is toluene-2,3-dihydrodiol [B291]. This enzyme (initially the product was misidentified as toluene-1,2-dihydrodiol) can utilise Fe^{3+}, Mg^{2+}, Ca^{2+} and Cu^{2+} (in decreasing order of effectiveness) in place of Fe^{2+} [A3184].

Naphthalene 1,2-dioxygenase (E.C. 1.14.12.12)

Naphthalene → *cis*-1, 2-dihydro-1, 2-dihydroxynaphthalene

Pseudomonas enzyme, which yields the (+)-dihydrodiol, is a three-protein system, and utilizes NAD(P)H and oxygen stoichiometrically [C144]. P. putida has been identified as one species exhibiting this activity [A1591].

Corynebacterium renale enzyme, a heterodimer, molecular weight 99 000, monomeric molecular weight 43 000 and 56 000, is not a P450. The reaction is stoichiometric, with an optimum at pH 6.5. The enzyme contains one FAD and one Fe^{2+}/mol, and requires NADH, which can be replaced by peroxide. Catalase, superoxide dismutase and hydroxyl radical scavengers are inhibitory. Hydroxyl radical is considered to be the oxidizing species, forming a dihydrohydroxynaphthalene radical. A hydroxyl ion then adds, to form a *cis*-1,2-dihydrodiol [B949, C714].

Biphenyl dioxygenase

Burkholderia enzyme forms *cis*-biphenyl-2,3-dihydrodiol from biphenyl. A number of polychlorinated biphenols are also substrates [K547].

Benzoate 1,2-dioxygenase (E.C. 1.14.12.10)

Pseudomonas arvilla enzyme is composed of NADH-cytochrome c reductase and the oxygenase. The latter, molecular weight 270 000–280 000 (depending on method), pI 4.5 and Stokes radius 5.6 nm, contains 10 mol of Fe, and about eight of labile sulphur/mol, but no haem or flavin. The product is benzoate-1,2-dihydrodiol. A range of benzoates monosubstituted with halide, methyl, methoxy, amino or hydroxyl groups in *o*-, *m*- and *p*-positions are substrates, although some of these are essentially inactive [B465].

Phthalate oxygenase

Rhodococcus erythropolis enzyme, optimum pH 6.5, is a tetramer, monomeric molecular weight 56 000. The reaction product is phthalate-3,4-dihydrodiol. Oxygen and NADH are required [H89].

Phthalate 4,5-dioxygenase (E.C. 1.14.12.7)

Pseudomonas cepacia enzyme is a two-component system, composed of a Fe-S-protein, molecular weight 34 000, with NADH-dependent oxidoreductase activity; its function is to keep the oxygenase (the second component) in a reduced form. The oxygenase is a nonhaem iron protein, molecular weight 217 000, monomeric molecular weight 48 000. The reaction is stoichiometric, requiring oxygen and NADH. 4-Chlorophthalate is also a substrate [K922].

Terephthalate 1,2-dioxygenase (E.C. 1.14.2.15)

Comamonas testosteroni enzyme, molecular weight 126 000, appears to be a tetramer with monomers, molecular weight 49 000 and 18 000; the N-terminals have been identified. The product is (1*R*,2*S*)-dihydroxy-3,5-cyclohexadiene-1,4-dicarboxylic acid. The enzyme requires a second protein fraction, oxygen and NADH, and its activity is enhanced by Fe^{2+}; it contains 2Fe-2S units. The specificity is narrow, but 1,4-dicarboxynaphthalene is a second substrate [H396].

Kynurenate 7,8-hydroxylase (E.C. 1.14.99.2)

This Pseudomonas fluorescens enzyme (incorrectly named kynurenine 7,8-hydroxylase in the E.C. list) forms kynurenate-7,8-dihydrodiol [K874].

Benzoyl CoA reductase (E.C. 1.3.99.15)

Thauera aromatica enzyme, molecular weight 160 000–170 000; is a heterotetramer, which contains FAD and ferredoxin. The product is 3,4-dihydrobenzoyl CoA [J527]. The subunit molecular weights are 48 000, 45 000, 38 000 and 32 000, and it contains 11 mol of Fe and acid-labile sulphur. It is greenish-brown with an absorption band typical of Fe-S. The reaction requires Mg^{2+} and ATP; Mn^{2+}, Fe^{2+} and (less effective) Co^{2+} can replace Mg^{2+}. It requires a strong reducing agent such as Ti(III) for activity, and oxygen inactivates. Several analogues of the substrate, with a single substituent on the nucleus are also reduced [J175].

Anthraniloyl CoA monooxygenase (E.C. 1.14.13.40)

Pseudomonas enzyme, a homodimer, molecular weight 170 000 and pI 5.3, requires NADH and oxygen. Three products are formed, 5-hydroxyanthraniloyl CoA, 2-amino-5-hydroxycyclohex-1-enecarboxyl CoA and 2-amino-5-oxocyclohex-1-enecarboxyl CoA, the latter being the main product. The aromatic and reduced ring systems are considered to be formed by separate routes [F463, F465, K949].

Azoarcus evansii 2-aminobenzoyl CoA monooxygenase/reductase is a flavoprotein that requires oxygen. It is postulated that 5-hydroxylation with migration of the hydrogen to position 6 is followed by a NADH-dependent

reduction at the same catalytic locus to form 2-amino-5-oxocyclohex-1-enecarboxyl CoA [K215].

Hydroxyquinol reductase

Desulphovibrio inopinatus enzyme forms, probably, 1,2,4-trihydroxycyclohexa-1,3-diene from hydroxyquinol [K483].

Phloroglucinol reductase

Eubacterium oxidoreducens enzyme, molecular weight 78 000, monomeric molecular weight 33 000, and optimum pH 7.8, requires NADPH; NADH is ineffective. It is not a metalloenzyme or a flavoprotein. The reaction, which is reversible, forms dihydrophloroglucinol [F75].

Penicillium simplissimum forms dihydrophloroglucinol; the enzyme requires NADPH, but NADH is inactive [F639].

Coprococcus enzyme, molecular weight 130 000 and optimum pH 7.4, requires NADPH. The reaction is reversible, but only slowly. It is inactivated at 53° [C99].

Tetrahydroxynaphthalene reductase (E.C. 1.1.1.252)

Pyricularia oryzae enzyme reduces 1,3,6,8-tetrahydroxynaphthalene to scytalone (3,6,8-trihydroxy-1-tetralone) and 1,3,8-trihydroxynaphthalene to vermelone [K703].

Magnaporthe grisea enzyme (vermelone formation) requires NADPH as co-substrate, and is inhibited by tricyclazole. It is an essential step in the formation of a melanin that is required for the initiation of blast disease in rice [K704].

Anhydrotetracycline oxygenase (E.C. 1.14.13.38)

Streptomyces aureofaciens enzyme, monomeric molecular weight 57 500 is a dimer, which hydroxylates one of the aromatic rings of anhydrotetracycline at the 6 position (already substituted with a methyl group); in effect a hydration of a double bond. It requires NADPH and oxygen to form 12-dehydrotetracycline [K900, K938].

Other reactions that involve dearomatization are found in sections 1.8, 2.2 and 2.9.2

1.8 *Ring expansion*

Alicyclobacillus converts phenylacetate into cycloheptanecarboxylate. There is a similar reaction with L-phenylalanine [H832].

2. Oxidations and reductions involving the aromatic nucleus and non-organic substituents

2.1 *Hydroxylation of the aromatic nucleus*

2.1.1 Hydroxylations associated with physiologically important amino acids and hormones

Phenylalanine hydroxylase (phenylalanine 4-monooxygenase; E.C. 1.14.16.1)

L-Phenylalanine →L-tyrosine

This vertebrate enzyme degrades dietary phenylalanine in excess of requirements for protein and hormone formation. In a group of closely associated inherited diseases in man (e.g. phenylketonuria, hyperphenylalaninaemia) that result in moderate to severe mental retardation, this enzyme is either inactive or has a very low activity, or, rarely, the enzyme for the formation of the tetrahydropteridine cofactor is inactive. The mental retardation is caused by grossly elevated concentrations of phenylalanine in body fluids, especially during brain development in the first few years of life.

One study on human liver enzyme demonstrated a molecular weight of 54 000 and pI 5.0–5.2 [F826]. Another study indicated a molecular weight of 165 000, apparently a trimer. It is not a phosphorylated enzyme, nor is it activated by phosphorylation; attempted phosphorylation does not incorporate phosphate into the enzyme molecule [D14]. Its activity increases twofold from foetus to adult [A3020].

Rat liver enzyme, which is activated by lysolecithin, acts on 4-methylphenylalanine to yield 3-methyltyrosine and 4-hydroxymethylphenylalanine. Isotope studies demonstrate that the hydroxyl groups originate from molecular oxygen and not from water. Kinetic studies with substrate labelled with different hydrogen isotopes suggest that the two products are formed by different mechanisms. In consequence, the authors question the generally accepted hypothesis that the formation of epoxide intermediates is obligatory in all aromatic hydroxylations [G150]. Purified enzyme is found as 2 forms, molecular weights 240 000 and 51 000; the former, pI 5.6, may be a tetramer. Analyses found 0.6 mol of Fe and 0.3 mol of phosphate per subunit. The amino acid composition has been determined [B19]. Another study indicated the presence of three isozymes in liver, pI 5.2, 5.3 and 5.6, one kidney isozyme, pI 5.35 and a hepatoma enzyme, pI 5.2 [A1736].

Chromobacterium violaceum enzyme is a monomer, molecular weight 32 000 and pI 4.5. The amino acid composition has been determined. It does not contain Fe, but (in line with other enzymes of this type) requires a tetrahydropteridine cofactor [A3884].

Studies with Pseudomonas enzyme and phenylalanine labelled with D or T at the *p*- position showed a 10-fold isotope effect between H and D labelled substrate and 2.8-fold between D and T labelled substrate, with migration of the substituent to the *meta* position. This 'NIH Shift' has been interpreted as indicative of an epoxide intermediate (but see above) [A757]. Enzyme found in a Pseudomonas species has a molecular weight less than 30 000 [A55].

Phenylalanine hydroxylation by xanthine oxidase (E.C. 1.1.3.22)

The product of this reaction, using enzyme from cow's milk with hypoxanthine as co-substrate, is a roughly equimolar mixture of *o*-, *m*- and *p*-tyrosines. The reaction is prevented by superoxide dismutase (E.C. 1.15.1.1) and catalase (E.C. 1.11.1.6); hydroxyl radical scavengers also prevent the reaction. Hence, hydroxyl radicals are considered to be the oxidizing species [D524].

Tyrosine 3-monooxygenase (tyrosine hydroxylase, E.C. 1.14.16.2)

L-Tyrosine+O_2→
3, 4-dihydroxy-L-phenylalanine

This enzyme catalyzes a key reaction in the formation of the neurotransmitters dopamine, noradrenaline and adrenaline.

Human medulla enzyme contains four isozymes [G190]. Brain enzyme is found mainly in the caudate and the substantia nigra, with smaller but significant amounts in the pons, mid-brain, mammillary body, amygdala, hypothalamus and nucleus accumbens [A3609] as well as in gastric mucosa and duodenum [J464].

As anticipated from the known disease process, post-mortem parkinsonian brain activity is decreased about five fold in caudate nucleus, putamen and substantia nigra, but not in other brain areas [A381].

Phosphorylation of human neuroblastoma enzyme activates by reducing the K_m for cofactor [A3687]. Human phaeochromocytoma enzyme has an optimum at pH 7.8 [A3442].

Rat striatal enzyme has a molecular weight of 61 300. Enzymatic phosphorylation using ATP and cAMP-dependent protein kinase incorporates one mol of phosphate/mol of hydroxylase. This form has a lower K_m for biopterin cofactor than the non-phosphorylated form. It is unstable, but inactivation does not involve phosphate removal [D733]. The molecular weight of caudate nucleus enzyme is 65 000, 130 000 in sympathetic ganglia and more than 200 000 in locus coeruleus, hypothalamus and adrenal, and both the small and large forms are found in substantia nigra. These forms, which may be polymeric with nucleotides being involved in the polymerisation, respond differently to tyrosine hydroxylase antibodies [A45]. Another study on rat enzyme claims that phosphorylation increases V_{max} without affecting K_m [A3687]. Striatal enzyme has an optimum at pH 6.0 [A3442]. Administration of the phenylalanine hydroxylase inhibitor *p*-chlorophenylalanine to rats increases the formation of the subsidiary products *o*- and *m*-tyrosine, whereas α-methyltyrosine, an inhibitor of tyrosine hydroxylase decreases the formation of these isomers, suggesting that they are formed by tyrosine hydroxylase [E69]. Brain synaptosomal enzyme is activated by lysolecithin and phosphatidylserine [A1698]. Apomorphine administration to rats leads to a 100 per cent increase in the activity of the enzyme in adrenal over a period of three days. This appears to be due to an increase in the absolute amount of enzyme [A1614]. It is not present in rat stomach tissues [H620].

Cultured rat phaeochromocytoma enzyme requires tetrahydrobiopterin as co-substrate. Peroxide, rather than being a substrate is inhibitory. The enzyme appears to be identical with that from other tissues, and contains one Fe^{2+}/ subunit. The cofactor is converted into a carbinolamine during hydroxylation; the authors in a different study suggest that a peroxytetrahydropterin is the hydroxylating species, which can be replaced by peroxide [G290, G290a].

As well as L-tyrosine, beef and adrenal chromaffin enzymes hydroxylate L-phenylalanine, forming a little *m*-tyrosine as well as L-tyrosine, both of which are converted into 3,4-dihydroxy-L-phenylalanine [F623]. Cytosolic adrenal medulla enzyme, molecular weight 280 000, appears to be a homotetramer, pI 6.0 and optimum pH 6.8. Its amino acid composition and terminal amino acids have been determined [A3442, C799]. Particulate adrenal enzyme can be solubilised with α-chymotrypsin to yield an enzyme, molecular weight 34 000 that contains Fe. Only the unsolubilized enzyme can be activated by phosphorylation or by phospholipids in

a manner similar to beef brain enzyme (see below) [A3017].

Beef corpus striatum enzyme (molecular weight about 60 000) is activated by incubation with ATP and cyclic AMP-dependent protein kinase, which yields a phosphorylated hydroxylase containing one mol of phosphate [B413]. Caudate nucleus enzyme is activated by phosphatidylserine and other polyanions, which reduce K_m for the pterin cofactor. Phosphatidylserine raises the optimum pH (from about 6) by 1 unit, whereas the effect of heparin is marginal. The enzyme is strongly inhibited by tyrosine at concentrations higher than 0.05 mM. Phenylalanine as a substrate has the same V_{max} as tyrosine, but high reaction rates only occur at high concentrations relative to physiological levels [A383].

In rabbit the enzyme is uniformly distributed between the white and grey matter in spinal cord [A2462].

Enzyme in neonatal mouse superior ganglia cultured cells is induced 30–40 per cent by actinomycin D or 80 per cent by K^+; their effects are additive. It is postulated that the effect of actinomycin D is to inhibit the formation of a substance that represses transcription of mRNA [A3].

Sulphate or heparin increase V_{max} for dog hypothalamus enzyme; heparin also decreases K_m for cofactor [A2064].

Guinea pig atrial enzyme is inhibited by 3,4-dihydroxyphenylglycol and by noradrenaline at 10^{-5}–10^{-6} M. Both compounds compete with cofactor, but 4-hydroxy-3-methoxymandelate, 3,4-dihydroxymandelate and 4-hydroxy-3-methoxyphenylglycol are poor inhibitors [A2060]. Vas deferens enzyme is activated by 10^{-6}M Ca^{2+}; it decreases K_m for both substrate and cofactor [A44].

Other studies on mammalian enzymes (including some in which the species is not stated) confirm activation by phosphorylation [A3442, A3686].

Chicken embryo brain enzyme is not detected at 10 days incubation, but is found in all regions at 14 days, and increases rapidly over the next 4 days [A1413].

Kinetic studies indicate a sequential reaction, and not a ping-pong mechanism for the reaction [A1904].

Helix pomatia enzyme is mainly soluble. Its optimum pH is 6.5, requires a tetrahydropteridine cofactor and is stimulated by Fe^{2+} and catalase. Inhibitors include dopamine, 6-hydroxydopamine, serotonin, noradrenaline and dodecyl sulphate [A1349]. Planorbis (water snail) enzyme shows very similar properties [A2055].

Hydroxylation by monophenol monooxygenase (tyrosinase; E.C. 1.10.3.1)

This type of reaction usually forms catechols from phenols. Its physiological importance in vertebrates is the formation of L-dopa from L-tyrosine by tyrosinase, usually in skin; L-dopa is the precursor of melanin. The presence of unusually high urinary concentrations of intermediate metabolites associated with melanin formation is observed (in man) both after exposure to sunlight, and in patients with melanoma without exposure to the sun. These metabolites can be used as a marker in the diagnosis of melanoma. In mouse pups devoid of tyrosine hydroxylase tyrosinase appears to be responsible for the appearance of significant amounts of neural catecholamines [K89].

Sea anemone tentacle enzyme is particulate, and oxidizes tyrosine and dopa; the latter reacts further to form 5-hydroxydopa. It is inhibited by diethyldithiocarbamate [D245].

Avocado enzyme hydroxylates D- and L-tyrosine and tyramine as well as *p*-cresol, but much more slowly than the oxidation of D- and L-dopa and other catechols to quinones. The initial time-lag in the reaction is eliminated by ascorbate or L-dopa [A3975]. (The time-lag reported in early studies on tyrosinase was caused by the time required for the build-up in dopa concentrations; dopa, as well as other catechols, acts as co-substrate which is oxidized to a quinone).

Banana pulp enzyme is found in both soluble and particulate fractions. It oxidizes both D- and

L-tyrosine, and also L-dopa. Ascorbate activates, and diethyldithiocarbamate is inhibitory [A541].

Berberis stolonifera phenoloxidase, molecular weight 60 000 and optimum pH 6.0, oxidizes both L-tyrosine and tyramine, as well as some phenolic tetrahydroisoquinoline natural products. Both ascorbate and oxygen are required for activity [F855].

Horseradish peroxidase and peroxide act on mixtures of dopa and phenols; the phenols accelerate the oxidation of dopa, although when the phenol used is tyrosine there is no indication of tyrosine hydroxylation. Peroxidase forms dopa from tyrosine in the presence of oxygen and dihydrofumarate, however [A2458].

Enzyme from Mucuna pruriens, in which one of the highest naturally-occurring concentrations of L-dopa is found (rendering its fruit toxic) acts on a range of phenols including L-tyrosine, generating catechols [E769]. This is the basis of a synthetic process for making L-dopa.

Papaver somniferum tyrosinase acts on tyrosine [A171].

Of the 17 phenoloxidase isozymes detected in potato, five act on tyrosine as well as L-dopa [A3190].

Portulaca grandiflora tyrosinase, molecular weight 53 000 and optimum pH 5.7, acts on L-tyrosine, but D-tyrosine is a poor although significant substrate. The dopa formed is further oxidized via dopaquinone to *cyclo*-dopa, an intermediate in the formation of betanidin [K93].

In wheat the enzyme that hydroxylates tyrosine can be separated electrophoretically from the enzyme that forms dopaquinone from L-dopa [A176], suggesting that it is a different class of enzyme from most tyrosinases, which catalyse these reactions sequentially with a single enzyme.

Agoricus (presumably a misprint for Agaricus) bisporus tyrosinase oxidizes N-acetyltyramine with a lag period (typical for phenols), but the lag for hordenine is indefinitely long. The lag is eliminated by the addition of a trace of a catechol. The normal lag period is terminated by the autocatalytic oxidation of phenol to catechol. N,N-Dipropyldopamine oxidation yields as final product N,N-dipropylindoliumolate [J460]. Mushroom (presumably A. bisporus) tyrosinase, molecular weight 122 500, has a Stokes radius stated to be 42.75×10^{-8} cm^2 sec^{-1} (units meant to be cm?) [B489]. It is not affected by superoxide dismutase or by superoxide scavengers [D2].

Aspergillus oryzae enzyme is activated at pH 2–5, and the resultant tyrosinase activity has an optimum at pH 6.0 [A1131].

Vibrio tyrosinaticus is composed of two tyrosinases, molecular weights 41 000 and 38 500; it does not cross-react with antiserum to hamster melanoma tyrosinase. It acts on L-tyrosine and slightly on the D- isomer and *m*-tyrosine, but catechol and L-phenylalanine are not substrates. It is inactivated by diethyldithiocarbamate, and this is reversed by Cu^{2+}, Mn^{2+}, Cd^{2+} or Fe^{2+} [A141].

Tyramine 3-hydroxylase

This reaction has been detected in nematode, locust, Thalictrum, avocado, Mucuna and mushroom [A2572, A2804, A3975, B765, E769, F112, F855, H242, H907]. At least in some instances, the reaction is probably catalysed by the same enzyme that forms L-dopa from L-tyrosine.

***p*-Hydroxyphenylpyruvate oxidase**; (4-hydroxyphenylpyruvate dioxygenase, E.C. 1.13.11.27)

$$p\text{-Hydroxyphenylpyruvate} + O_2 \rightarrow CO_2 + \text{homogentisate}$$

This is a key vertebrate enzyme, and is involved the catabolism of tyrosine. Tyrosine is a major dietary amino acid, and it is also formed from dietary phenylalanine, quantitatively greatly in excess of amounts required for the formation of protein and hormones, and a mechanism is required for its disposal. A deficiency of activity is found in premature infants and in the inherited diseases classified as Tyrosinosis. In man mutations in the gene controlling this enzyme lead to tyrosinaemia type III and hawkinsinuria [K665].

Mechanistic studies using beef liver enzyme and substrate specifically labelled with deuterium in the methylene group indicate that side-chain migration occurs with retention of configuration at the methylene group [B904]. Studies using an enzyme with unspecified origin, but presumably mammalian, have shown that the phenolic hydroxyl group is not exchanged during the reaction. This indicates that, although still possible, an intermediate with a peroxide 1,4-bridge is most unlikely [A844]. 1-Carboxymethyl-1-hydroxy-4-oxocyclohexa-2,5-diene is not an intermediate [A346].

Human enzyme is a dimer, molecular weight 87 000. It acts on the *keto* isomer with optima at pH 4.5 and 7.8. It is activated by reducing agents such as ascorbate and is very sensitive to inactivation by peroxide. Iron- and copper-chelating reagents are inhibitory, and reactivation by dialysis indicates that the chelators do not remove the metal from the enzyme molecule. It exists in three forms with different pI between 6.5 and 7.5. These appear to be dimers of two monomeric forms [A3128, A3129].

A genetic defect in mice leads to a deficiency of this enzyme [G216].

Pig enzyme is inhibited by pentafluorophenylpyruvate and thiophenyl oxalate. It is inactivated by tetrafluoro-4-hydroxyphenylpyruvate and by 2- and 3-thienylpyruvate [H382]. The enzyme is stable only after purification. During storage it polymerizes, and this is reversed by thiols. The molecular weight is 89 000 by ultracentrifugation, and 52 000 and 44 000, respectively, by gel filtration and electrophoresis. It contains Cu and Fe (not stoichiometric). The temperature coefficient was found to be unusually high, about five (even higher than that reported by Goodwin, B.L. (1972) Tyrosine Catabolism, Clarendon Press, Oxford). The activity is stimulated by some hydrophilic solvents, including alcohols and ethers [C208].

Rat liver enzyme, molecular weight 63 000 and pI 5.85, is inactivated by dialysis and other processes that remove small molecules, and is reactivated by Fe^{2+} and dichlorophenolindophenol [A2702]. At birth, about 25 per cent of the enzyme is in an active form, and this increases to 90 per cent in the adult [A771]. The molecular weight is 45 085 by mass spectrometry (theoretical value 45 082). It also shows α-oxoisocaproate dioxygenase activity. At the C-terminal a 14 amino acid sequence is essential for activity; a mutant with a deletion of these amino acids produces an inactive protein [J235].

Bamboo enzyme is highly specific, molecular weight about 10 000. It is stoichiometric, and no intermediate has been detected [B238]. Zea mays enzyme, molecular weight 43 000 and optimum pH 7.3, requires a reducing system or ascorbate and catalase [J247]. Its presence has also been reported in Drosophyllum lusitanicum [A1149].

Enzyme from Pseudomonas strain PJ874 is blue and contains both iron and zinc. It catalyzes a stoichiometric reaction involving the *keto* isomer of the substrate, with an optimum and maximal stability at pH 7.9. It appears to act by a mono-iso-ordered bi-bi mechanism, in which Fe^{3+} is reduced [C365, C728]. Another publication claims that enzyme from strain PJ874 is a tetramer, monomeric molecular weight 36 000, optimum pH 7 and pI 4.8, and contains both Fe and Cu. The Fe content parallels activity during purification and the ratio of activity towards *p*-hydroxyphenylpyruvate and phenylpyruvate remains constant [A3106].

Tryptophan 5-hydroxylase; (tryptophan 5-monooxygenase, E.C. 1.14.16.4)

L-Tryptophan
$+ O_2 \rightarrow$ 5-hydroxy-L-tryptophan

This reaction is a key step in the formation of the neurotransmitter serotonin, as well as the hormone melatonin, which responds to light and dark periods and is associated with the biological clock in vertebrates.

Activity in brain (presumably human) median and dorsal raphe nuclei is 50–100 times greater than in caudate nucleus and hippocampus [A1690].

Mouse gut mucosal enzyme is probably of enterochromaffin origin [E503]. Brain enzyme is activated by phosphorylation and inactivated by

phosphatase [A3813]. Mouse mastocytoma enzyme, pI 6.0, has a molecular weight of 270 000, and despite a monomeric molecular weight of 53 000 it is claimed to be a tetramer. L-Phenylalanine and (marginally) L-tyrosine are also substrates [C216].

Rat brain stem enzyme, which is stimulated by Fe^{2+}, is composed of two isozymes, one of which has a molecular weight of 300 000. Despite a monomeric molecular weight of 59 000 it is also claimed to be a tetramer. L-Phenylalanine is a substrate, but not L-tyrosine [C113]. Influences *in vivo* that reduce brain tryptophan concentration cause the enzyme activity to increase, apparently by an increase in V_{max} [A1920], an effect that should sustain brain serotonin levels in face of alterations in tryptophan availability. Liver enzyme (that also acts on phenylalanine) is stimulated by 5-fluorotryptophan and 7-azatryptophan by up to 20-fold, and at higher cofactor concentrations by phenylalanine and thienylalanine [A791]. Pineal enzyme shows a diurnal rhythm with raised activities at night, and this is eliminated in constant light. Cycloheximide but not actinomycin D causes a rapid loss in activity, which suggests that enzyme activity is controlled at the translation step. Sulphydryl compounds protect the enzyme from inactivation at 0° but not at higher temperatures, and dithiothreitol reactivates the inactivated enzyme. Rapid *in vivo* inactivation is caused by *p*-chlorophenylalanine, and this is reversed within 24h [A3237]. Presumably this diurnal rhythm is associated with the diurnal rhythm of melatonin concentrations.

Pig brain stem enzyme, molecular weight 55 000–60 000, is not stimulated by Fe^{2+} or by chelating agents and is unstable during storage [A1306].

The activity of chick brain enzyme, optimum pH 7.8–8.0 [A3236], increases about 10-fold just before and after hatching [A3130].

Enzyme from yellowfin tuna resembles mammalian enzyme. It is a trimer, molecular weight 280 000 [H910]. Skipjack liver enzyme is a homotrimer, molecular weight 288 000 and optimum pH 8.0 [H394].

Sedum morgaianum enzyme has an optimum at pH 7.5 [D41].

Chromobacterium violaceum enzyme, optimum pH 7, is inducible by tryptophan and (better) phenylalanine. D-Tryptophan is also a substrate, but phenylalanine is not. It requires oxygen, reduced pteridine cofactor and a thiol. Both phenylalanine and *p*-chlorophenylalanine are inhibitory [A1597].

Tryptamine 5-hydroxylation

Peganum harmala enzyme acts on tryptamine, α-methyl-, N-methyl- and 6-fluorotryptamine [A1330, F9, G906].

Kynurenine 3-hydroxylase; (kynurenine 3-monooxygenase; E.C. 1.14.13.9)

L-Kynurenine → 3-hydroxy-L-kynurenine

Studies on rabbit, rat, gerbil and mouse demonstrate that activity is found in liver, lung and brain, in decreasing order [J830].

Rat liver enzyme is associated with the mitochondrial outer membrane. When solubilized it can be separated into two fractions by chromatography; the major one has a molecular weight of 200 000, optimum pH 8 and pI 5.4. It contains dissociable FAD (one mol/mol) that cannot be replaced by FMN or riboflavin. It is activated by FAD, dithiothreitol and phosphatidylcholine, and maximal activity occurs in 10 mM KCl. Inhibition is brought about by *p*-chloromercuribenzoate and bathocuproinsulphonate [A2270, A2293, A2482].

Honeybee eye enzyme, which requires NADPH, has an optimum at pH 7.25 [A1064]. Drosophila melanogaster eye enzyme appears to be mitochondrial [A1194].

Anthranilate 3-hydroxylase; (anthranilate 3-monooxygenase; E.C. 1.14.16.3)

Anthranilate → 3-hydroxyanthranilate

Aspergillus niger enzyme, molecular weight 43 000–45 000, optimum pH 8.2 and pI 5.36,

requires FAD. Purified enzyme also catalyzes the formation of pyrocatechuate, which suggests that it also shows anthranilate 2,3-hydroxylase (deaminating) activity (E.C. 1.14.13.35); it is claimed that both activities reside on the same molecule. Cu^{2+} and *p*-chloromercuribenzoate are inhibitory [D231].

This reaction is also observed in rat liver and brain [A3653, F676].

Anthranilate 5-hydroxylase

This reaction is observed in rat liver [A3653, D296].

Indole hydroxylases

Indole 4-hydroxylase is found in pumpkin [A3530]. A similar reaction occurs in the mycological formation of psilocine, but the reaction does not appear to have been studied at an enzyme level.

Indole 5-hydroxylase is also present in pumpkin [A3530]. Both 5- and 6-hydroxylases are present in Tradescantia, Zebrina and Seterasia [A3538], and in rat [D158].

Oestradiol hydroxylases (and analogues)

a. 2- And 4-hydroxylase

Rat anterior pituitary enzyme catalyzes these reactions, in particular 4-hydroxylation. The latter is considered to be NADPH-dependent, whereas 2-hydroxylation may be peroxidase-dependent [F42]. Rat liver microsomes catalyze these reactions by 3 P450s, $P450_{VT\text{-}A}$, $P450_{PCN\text{-}E}$ and $P450_{ISF\text{-}G}$. The first two are constitutive, male-specific and are induced by testosterone [E40]. A report on 2-hydroxylation suggested that P450 is not involved, at least in the brain of male rats. This activity is greater in male rats than in female, and is found (in decreasing order of activity) in liver, brain, kidney, testis, adrenal and lung, with activity in the lung about 1 per cent of that in liver. Other organs show negligible activity. Activity is reduced by castration, and in hyperthyroid and euthyroid rats the activity is lower than in control animals [A3944]. A further study on brain enzyme suggested that it is probably P450, and that the enzyme also acts on 17α-ethynyloestradiol, stilboestrol and oestrone to yield catechols [A3295]. 17β-Oestradiol-17-sulphate is a substrate, undergoing both reactions, with lower activity for 4-hydroxylation. Again, highest activity is observed in liver, and much lower in kidney, brain, heart, lung, testis, ovary and uterus. At least in liver, there is no constant ratio between the two activities suggesting enzyme heterogeneity [E465]. Kidney enzyme is microsomal and lung enzyme is mitochondtial [B681].

Pig ovary enzyme catalyses 2-hydroxylation in particular, optimum pH 7.8; the enzyme requires NAD(P)H [E78].

Rabbit hypothalamus enzyme appears to be a soluble peroxidase with an optimum at pH 6 and pI about 7.7. It is stimulated by cumene hydroperoxide and yields similar amounts of 2- and 4-hydroxy-17β-oestradiol [E144].

Horse oestrogen 2-hydroxylase, a P450, is associated with testosterone aromatase [H891].

b. 3-Hydroxylase

Oestradiol is formed from 2-hydroxy-3-deoxyoestradiol by a P450 enzyme found in liver microsomes. This is possibly the same enzyme that 2-hydroxylates 17β-oestradiol [B1].

c. 6α-Hydroxylase

A human enzyme hydroxylates 17β-oestradiol at the 6α-position [A2465, K621]. The same reaction is observed in rat [A1487, A2192, E525]. Oestrone is a substrate in rat and hamster [A2408, C896, G625].

d. 6β-Hydroxylase (E.C. 1.14.99.11)

Rat liver and brain micromes hydroxylate 17β-oestradiol at the 6β-position [A1487, A2192, H342, E525]. The same reaction is observed in

man [A2465]. Oestrone is a substrate in rat and hamster [A2408, C896, G625].

e. 7α-Hydroxylase

A human enzyme hydroxylates 17β-oestradiol at the 7α-position [A2465]. The same reaction is observed in rat [A1487, A2192]. Oestrone is a substrate in rat and hamster [A2408, C896, G625].

f. 7β-Hydroxylase

A human enzyme hydroxylates 17β-oestradiol at the 7β-position [A2465].

g. 11β-Hydroxylase

This activity is found in Neurospora, with 17β-oestradiol as substrate [A944].

h. 14α-Hydroxylase

Rat liver micromes hydroxylate 17β-oestradiol and oestriol at the 14α-position [H342].

i. 15α-Hydroxylase

A human enzyme hydroxylates 17β-oestradiol at the 15α-position [K621]. The same reaction is observed in baboon, rat and pig [A545, E525, F511]. Oestrone is a substrate in man [A1588].

j. 15β-Hydroxylase

This activity has been detected in kidney and liver microsomes from hamster and rat, with oestrone as substrate [G625].

k. 16α-Hydroxylase

Human foetal liver enzyme hydroxylates 17β-oestradiol (to oestriol) and oestrone at the 16α-position, but these are poor substrates, whereas their 3-sulphate esters are readily hydroxylated. The optimum pH is 7 [E132]. The same reaction is observed in rat liver microsomes [H342] as well as in a number of other mammalian species.

l. 16β-Hydroxylase

In man 17β-oestradiol is converted into 16-epioestriol by hydroxylation at the 16β-position [A2309]. The same reaction is observed in guinea pig [A2868], monkey [A491, A3294] and rat [A2583].

2.1.2 Hydroxylations of natural products and miscellaneous compounds associated with normal animal physiology

Phenol 2-monooxygenase (E.C. 1.14.13.7)

Phenol → catechol

Trichosporon cutaneum enzyme acts on resorcinol and *m*-cresol to yield hydroxyquinol and 4-methylcatechol respectively, as well as on phenol [G196]. Its molecular weight is 148 000, it contains one mol/mol of FAD and requires NADPH. The optimum pH is 7.2–7.6. Bleaching by dithionite, which inactivates the enzyme is readily reversible. It is also inactivated by heavy metals and *p*-chloromercuribenzoate, the latter being reversed by dithiothreitol. The specificity is broad, with substrates not being limited to monophenols; catechol, for instance, yields pyrogallol. Activity towards hydroxylated benzyl alcohols, aldehydes and benzoic acids is negligible [A902].

Bacillus stearothermophilus enzyme requires NADH for activity [F47].

Comamonas testosteroni contains a phenol hydroxylase [K362].

Hydroquinone hydroxylase

Candida parapsilosus enzyme is a homodimer, monomeric molecular weight 76 000 containing dissociable FAD. It catalyses *ortho* hydroxylation of a range of phenols [K653].

Rhodococcus enzyme has an optimum at pH 7.9 and requires NADPH. Its specificity for

monophenols is broad, but catechol, nitrophenols and protocatechuate are not substrates [E565].

Phloroglucinol 2-monooxygenase

Rhodococcus enzyme, molecular weight 155 000 and optimum pH forms 1,2,3,5-tetrahydroxybenzene from phloroglucinol [H121].

Orcinol 2-monooxygenase; (E.C. 1.14.13.6)

$$\text{Orcinol} + O_2 \rightarrow 2,3,5\text{-trihydroxytoluene}$$

Pseudomonas putida enzyme, molecular weight 63 000–68 000 or 70 000, contains 1 mol of dissociable FAD. It utilizes one mol of oxygen and NAD(P)H; the latter can be replaced partially by FMN. Without orcinol, O_2 reacts with NADH and water to yield hydrogen peroxide, and at 60° the reaction with orcinol uncouples by about 50 per cent with resultant peroxide formation. Other substrates include resorcinol, 4-bromo- and 4-methylresorcinol, whereas non-phenolic substrate analogues accelerate peroxide formation. Resorcinol hydroxylase is very similar to this enzyme, but is distinguished by, for instance, absorption spectra, amino acid composition, stability to oxygen, specificity and reaction with antisera. For instance, *m*-hydroxybenzyl alcohol and a range of phenols are substrates for orcinol hydroxylase but not for resorcinol hydroxylase, whereas resorcinol hydroxylase acts on *m*-ethylphenol, but orcinol hydroxylase does not [A2172, A2391, A2696].

Resorcinol hydroxylase

$$\text{Resorcinol} + O_2 \rightarrow \text{hydroxyquinol}$$

This Pseudomonas putida activity is very similar to that of orcinol hydroxylase (see above), with some distinctive differences. Its molecular weight is 68 000–70 000; it could not be distinguished from orcinol hydroxylase on the basis of many parameters, however [A2391, A2696]. Rhodococcus enzyme has an optimum at pH 7.0 [G893].

Benzoate 2-hydroxylase

$$\text{Benzoate} \rightarrow \text{salicylate}$$

Benzoate is hydroxylated in all three positions by human blood granulocytes. It is postulated that the reaction is mediated by hydroxyl radical [E65].

Nicotiana tabacum enzyme is a soluble P450, molecular weight 160 000. It is specific for the formation of salicylate [H681].

This reaction has been observed in potato leaf [J691], rice [H593], Bacillus [A2217], Aspergillus niger and Cuninghamella bainieri [A1218].

Benzoate 3-hydroxylase

This reaction has been observed in man [E65], Flavobacterium [E355] and Pseudomonas [D771].

Benzoate 4-hydroxylase (E.C. 1.14.13.12)

$$\text{Benzoate} + O_2 \rightarrow p\text{-hydroxybenzoate}$$

Rhodotorula graminis enzyme is membrane-bound with optimum pH of 7.6. It requires NADPH and is stimulated by FAD. It differs from enzyme found in filamentous fungi, which requires a pteridine cofactor [D620].

Pseudomonas enzyme, molecular weight 120 000 and optimum pH 7.2, requires a tetrahydropteridine and oxygen, and is activated by Fe^{2+}. The reaction is not stoichiometric; a slight excess of oxygen is utilized [A2799].

Aspergillus niger enzyme, optimum pH 6.2, is specific for benzoate, requires a tetrahydropteridine and Fe^{2+}, and uses equimolar amounts of oxygen and NADPH. Thiol groups in the enzyme are required for activity [A1606].

Benzoyl CoA 3-monooxygenase (E.C. 1.14.13.58)

Pseudomonas enzyme, a monomeric flavoprotein, molecular weight 65 000, requires FAD or FMN, and NADPH [H397].

_m_-Hydroxybenzyl alcohol 6-hydroxylase

Penicilliun patulum microsomal enzyme, optimum pH 7.5, requires NADPH in the formation of gentisyl alcohol. It is suggested that the enzyme is *m*-cresol 2-hydroxylase [A2314].

Salicylate 3-hydroxylase

Salicylate →
2, 3-dihydroxybenzoate (pyrocatechuate)

Rat liver enzyme is considered to act via a free radical that non-specifically causes hydroxylation of salicylate rather than by the action of a hydroxylase [J754].

Salicylate 5-hydroxylase

Salicylate → gentisate

Rat liver enzyme is considered to act via a free radical that non-specifically causes hydroxylation of salicylate rather than by the action of a hydroxylase [J754].

Rhodococcus erythropolis enzyme, a homotetramer containing FAD, molecular weight 205 000, optimum pH 7.9 and pI 6.3, requires NADH, but NADPH is ineffective. Other substrates are 2,3- and 2,4-dihydroxybenzoates [H438].

Lignobacter enzyme requires NAD(P)H. Other (poor) substrates include *p*-hydroxybenzoate, 2,3-, 2,4-, 2,6- and 3,4-dihydroxybenzoates [B503].

3-Hydroxybenzoate 2-monooxygenase
(E.C. 1.14.99.23)

An enzyme in a Pseudomonas testosteroni mutant is induced by benzoate [K748].

***m*-Hydroxybenzoate 4-hydroxylase**;
(3-hydroxybenzoate 4-monooxygenase, E.C. 1.14.13.23, formerly E.C. 1.14.99.13)

m-Hydroxybenzoate + O_2 → protocatechuate

Aspergillus niger enzyme is a flavoprotein, optimum pH 7.2, requires NADPH and is inhibited by superoxide dismutase. Other substrates include 3-hydroxyanthranilate, pyrocatechuate, 3,5-dihydroxybenzoate and 3-hydroxy-5-methoxybenzoate. It is also inhibited by heavy metals, *o*-phenanthroline, salicylaldoxime, *m*-aminobenzoate, diethyldithiocarbamate and sulphydryl-binding reagents [A1130, A3526].

Comamonas (Pseudomonas) testosteroni enzyme, molecular weight 71 000, optimum pH in the range 6–7.5 (buffer-dependent), contains FAD and is activated by FAD and NADPH; the latter cannot be replaced by NADH. Other substrates include gentisate, pyrocatechuate and several other acids with a *m*-hydroxyl group, but not other analogues, which may be inhibitory [A1229, J519]. There is up to 70 per cent uncoupling of the oxygenation, when peroxide is formed, depending on substrate [A327].

3-Hydroxybenzoate 6-hydroxylase
(E.C. 1.14.13.24)

m-Hydroxybenzoate → gentisate

Klebsiella pneumoniae enzyme is monomeric, molecular weight 42 000. It contains FAD and requires NAD(P)H. Inactivation is rapid at 45° [G199, H399].

Pseudomonas aeruginosa enzyme requires oxygen and NAD(P)H, with a range of 3-hydroxybenzoates as substrates; there is 0–30 per cent decoupling of hydroxylation, depending on substrate [A236].

Pseudomonas cepacia enzyme, molecular weight 44 000 and optimum pH 8, contains one mol/mol of FAD with a requirement for NAD(P)H, and is inducible [E287]. The reaction mechanism has been suggested to involve random binding of substrate and NADH to the oxidized enzyme followed by reduction of the enzyme and release of NAD^+. Oxygen then binds, followed by release of water and gentisate from the now oxidised holoenzyme [E289].

Rhodococcus erythropolis enzyme is a homotetramer, molecular weight 196 000, optimum pH 8.6 and pI 6.7. It contains FAD and requires NADH, but NADPH is ineffective. A

second substrate is 2,3-dihydroxybenzoate [H438].

p-Hydroxybenzoate 1-hydroxylase

p-Hydroxybenzoate → gentisate

Klebsiella pneumoniae enzyme requires NAD(P)H; the activity is rapidly destroyed at 45° [G199]. It is also found in Bacillus and Bacterium [A489, B161].

p-Hydroxybenzoate 3-hydroxylases
(4-hydroxybenzoate 3-monooxygenase, E.C. 1.14.13.2 and 1.14.13.33)

p-Hydroxybenzoate + O_2 → protocatechuate

Corynebacterium cyclohexanicum enzyme is a monomer, molecular weight 47 000, and contains FAD. It requires Mg^{2+} and NADH or NADPH, and is specific for *p*-hydroxybenzoate [D554].

Moraxella enzyme is a dimer, molecular weight 85 000 and pI 6.55. It is specific for *p*-hydroxybenzoate [G793].

Pseudomonas fluorescens enzyme is mainly a dimer, molecular weight 70 000–75 000 and pI 5.8; it also exists as higher polymers. An amino acid analysis has been performed [B249]; Ser 212 is an important binding site [K109]. The reaction mechanism is complex, where the initial step appears to be oxidation of the FAD moiety to peroxyflavin. Other substrates include *p*-aminobenzoate and 2,4-dihydroxybenzoate; the latter yields 2,3,4- and 2,4,5-trihydroxybenzoates [A2554, K109]. Anions, such as Cl^-, Br^-, I^-, F^- and CNS^- compete with NADPH cofactor, quenching the fluorescence [A1082]. P. cephacia enzyme is inducible [E287].

Rhizobium leguminosarum enzyme is induced by 4-hydroxybenzoate [F224]

Rhodococcus erythropolis enzyme is a homotetramer, molecular weight 196 000, optimum pH 8.4 and pI 6.7, and contains FAD. It requires NADH, but NADPH is ineffective. A second substrate is 2,4-dihydroxybenzoate [H438].

4-Hydroxy-3-methylbenzoate hydroxylase

4-Hydroxy-3-methylbenzoate → 4-hydroxy-3-hydroxymethylbenzoate

Pseudomonas putida enzyme, which is composed of two proteins, requires oxygen and NAD(P)H. The proteins involved appear to be a hydroxylase and an electron-transferring protein acting on NADH; this makes it an unusual type of mixed-function oxidase [F223, F624].

3-Hydroxybenzoyl CoA 6-hydroxylase

Pseudomonas enzyme requires NAD(P)H to form gentisoyl CoA [H397].

Anthraniloyl CoA monooxygenase
(E.C. 1.14.13.40)

This activity is described in Section 1.7.

Phenylacetate 2-hydroxylase

Phenylacetate → *o*-hydroxyphenylacetate

Aspergillus niger microsomal enzyme, optimum pH 7.8, requires NADPH and oxygen. It is stimulated by thiols, and inhibited by thiol-binding reagents and by CO; it therefore appears to be a P450. It is highly specific [B133].

This activity has been demonstrated in bacteria [B950], Aspergillus fumigatus [C484], A. sojae [A2345], Trichosporon cutaneum [E332], Brevibacterium linens [D623], Pseudomonas fluorescens [C532] and Nocardia salmonicolor [A1329].

Phenylacetate 3-hydroxylase

Phenylacetate → *m*-hydroxyphenylacetate

Rhizoctonia solani enzyme, optimum pH 5–6, requires NAD(P)H and tetrahydrofolate. Benzoate, cinnamate, phenylpropionate and aryloxyacetates are not substrates.

Diethyldithiocarbamate and α,α-dipyridyl are inhibitors [A203].

This activity has been demonstrated in bacteria [B950], Aspergillus niger [A3787], A. fumigatus [C484], Brevibacterium linens [D623] and Trichosporon cutaneum [E332].

Phenylacetate 4-hydroxylase

Phenylacetate → *p*-hydroxyphenylacetate

This activity has been demonstrated in bacteria [B950], Brevibacterium linens [D623], Trichosporon cutaneum [E332] and Aspergillus niger [A329].

Mandelate 4-monooxygenase (E.C. 1.14.16.6)

L-Mandelate → *p*-hydroxymandelate

Pseudomonas convexa enzyme, molecular weight 91 000 and optimum pH 5.4, is inducible. It requires a tetrahydropteridine, NADPH, Fe^{2+} and oxygen, and is highly specific for mandelate. The activity is inhibited by thiol-binding reagents [A2662].

***o*-Hydroxyphenylacetate 5-hydroxylase**

o-Hydroxyphenylacetate → homogentisate

Rhodococcus erythropolis enzyme, molecular weight 45 000, contains FAD and requires NADH for activity [J23].

***m*-Hydroxyphenylacetate 4-hydroxylase** (E.C. 1.14.13.23)

m-Hydroxyphenylacetate → 3,4-dihydroxyphenylacetate

Klebsiella pneumoniae requires NADH or NADPH [G214]. The reaction has also been observed in Escherichia [B517], Trichosporon [E332], and possibly other microorganisms.

3-Hydroxyphenylacetate 6-hydroxylase (E.C. 1.14.13.63)

m-Hydroxyphenylacetate → homogentisate

Flavobacterium enzyme, which is mainly dimeric with one FAD/subunit and optimum pH 8.3, requires NAD(P)H as co-substrate; the amino acid composition and N-terminal sequence have been determined. It is stable between pH 5 and 9. Inactivation by thiol-binding reagents is reversed by dithiothreitol. Other substrates (less good) are 3,4-dihydroxyphenylacetate and *p*-hydroxyphenylacetate, with hydroxylation exclusively at position 6 [K779].

Rhodococcus erythropolis enzyme, molecular weight 45 000, contains FAD and requires NADH for activity [J23]. Flavobacterium enzyme, optimum pH 8.3, requires NAD(P)H. Poorer substrates include 3,4-dihydroxyphenylacetate and *p*-hydroxyphenylacetate, whereas homogentisate is not a substrate [G404].

***p*-Hydroxyphenylacetate 1-hydroxylase** (E.C. 1.14.13.18)

p-Hydroxyphenylacetate → homogentisate

In this reaction the side chain migrates during the hydroxylation ('NIH shift').

Bacterium enzyme, optimum pH about 7.5, is stoichiometric for oxygen and NAD(P)H, and is slightly stimulated by Mg^{2+}; its stability range is pH 6–9. Other substrates include *p*-hydroxyphenylpyruvate, 3,4-dihydroxyphenylacetate, *p*-hydroxyphenylpropionate and (poor) *p*-hydroxybenzoate. It is inhibited by iodoacetate, iodoacetanilide, *p*-chloromercuribenzoate, iodosobenzoate, N-ethylmaleimide, Hg^{2+} and EDTA [A489].

Pseudomonas acidovorans enzyme requires FAD, Mg^{2+} and NAD(P)H, and is inhibited by KCl. It is unstable when purified. Substrate substituted with deuterium in the *ortho* position shows 50 per cent label retention, consistent with no NIH shift. Other substrates include dopac, homovanillate, *p*-hydroxyphenoxyacetate,

p-hydroxyphenylacetate, *p*-hydroxyphenylpropionate, 4-hydroxy-2-methylphenylacetate and *p*-hydroxyhydratropate [A1480].

Rhodococcus erythropolis enzyme, molecular weight 45 000, contains FAD and requires NADH for activity. This enzyme is not identical with *o*-hydroxyphenylacetate 5-hydroxylase or *m*-hydroxyphenylacetate 6-hydroxylase; these enzymes are all different [J23].

p-Hydroxyphenylacetate 2-hydroxylase

This activity is associated with Flavobacterium 3-hydroxyphenylacetate 6-hydroxylase [K779].

p-Hydroxyphenylacetate 3-hydroxylase

(E.C. 1.14.13.2 and 1.14.13.3)

p-Hydroxyphenylacetate → 3, 4-dihydroxyphenylacetate

Studies on the reaction mechanism of Pseudomonas putida enzyme demonstrate the formation of three flavin-oxygen intermediates [H206]. Klebsiella pneumoniae enzyme requires NADH but not NADPH, which indicates that the enzyme is different from *m*-hydroxyphenylacetate 4-hydroxylase [G214].

trans-Cinnamate 2-monooxygenase

(E.C. 1.14.13.14)

Melilotus alba enzyme, optimum pH 7.0, is found in chloroplasts, attached largely to lamellar membranes. It is activated by glucose-6-phosphate or by light [A145].

trans-Cinnamate 3-monooxygenase

$$\text{Cinnamate} + O_2 \rightarrow m\text{-coumarate}$$

This reaction may be involved in orchinol formation from L-phenylalanine in Orchis species [C734].

trans-Cinnamate 4-monooxygenase

(E.C. 1.14.13.11)

$$\text{Cinnamate} + O_2 \rightarrow p\text{-coumarate}$$

Capsicum annuum enzyme, optimum pH 8, requires oxygen and NADPH. It is microsomal, possibly a P450 [F689].

Gherkin enzyme, optimum pH 7.5, is found in endoplasmic reticulum and requires NADPH; NADH is inactive. Inhibition by 2-mercaptoethanol and carbon monoxide is consistent with it being a P450 [A3146].

Petroselinum crispum enzyme is specific for *trans*-cinnamate; *cis*- is inhibitory. Reduction of the double bond prevents hydroxylation [A2820].

Enzyme from roots of Quercus pedunculata is microsomal [A622].

Sorghum etiolated seedling enzyme, a microsomal P450, requires oxygen and NADPH [K916].

Swede enzyme is also microsomal, requiring NADPH. It is inhibited by FMN, FAD, KCl and slightly by caffeate. Carbon monoxide inhibition is partially reversed by light [A198].

Melilotate hydroxylase

(melilotate 3-monooxygenase, E.C. 1.14.13.4)

Melilotate → 2, 3-dihydroxyphenylpropionate

Enzyme from a Bacterium (probably a Pseudomonad) is a tetramer, molecular weight 250 000 and contains four mol/mol of FAD. Its amino acid composition has been determined [A861]. A reaction mechanism has been proposed which includes binding of NADH [A863].

o-Coumarate hydroxylase

o-Coumarate + O_2 → 2, 3-dihydroxycinnamate

This activity has been found in Pseudomonas [A934].

m-Coumarate hydroxylase

m-Coumarate + O_2 → caffeate

Mouse liver enzyme requires oxygen and NADPH [A2871].

p-Coumarate 3-monooxygenase (E.C. 1.14.18.1)

p-Coumarate + O_2 → caffeate

Mytilus edulis hydroxyindole oxidase (which forms pigments from indoles) contains copper and haem iron (1:1 ratio) and catalyzes the above reaction. It appears to require peroxide, but not a reduced pyridine nucleotide [B314].

In Helianthus annuus, label is incorporated from $^{18}O_2$ into the reaction product [A178].

Ipomoea batatas root enzyme is monomeric, molecular weight 33 000, optimum pH 7.0 and pI 8.3. It hydroxylates *p*-coumarate, *p*-coumaroyl-β-D-glucose and *p*-cresol, but not a range of other phenols. Dopa and caffeate are also oxidized, presumably to quinones [F842].

Mung bean enzyme, optimum pH 5.0, (not a polyphenol oxidase) is specific for *p*-coumarate. It requires oxygen and NAD(P)H, ascorbate or 5,6,7,8-tetrahydro-6,7-dimethylpterin [F45].

Potato tuber enzyme requires FAD (or FMN) and NAD(P)H [D964].

Sorghum bicolor leaf enzyme, optimum pH about 6, requires ascorbate or a reduced pyridine nucleotide as electron donor. Activity is far higher for catechols than for *p*-coumarate, but shows no activity towards tyrosine. It exists as many interconvertible polymers, molecular weights 60 000–1 500 000 [A2433].

The reaction is also carried out by mushroom tyrosinase [H907], Mucuna pruriens phenoloxidase [E769] and Alnus rubra [A3343].

Ferulate 5-hydroxylase

Poplar stem enzyme is a P450 enzyme that requires NADPH; NADH is ineffective. It is different from cinnamate 4-hydroxylase (E.C. 1.14.13.11) [D179].

5-O-(4-Coumaroyl)-D-quinate 3′-monooxygenase (E.C. 1.14.13.36)

Daucus carota enzyme, which requires oxygen, ascorbate and NADPH but not NADH, is highly specific. The product is chlorogenate [E536].

p-Coumaroyl CoA 4-hydroxylase

Parsley enzyme is cytosolic, with a sharp optimum at pH 6.5. It requires ascorbate (a specific requirement) and Zn^{2+} or Ca^{2+}. The product is caffeoyl CoA [F66].

Coumarin 3-hydroxylase

This activity has been found in mammalia, including beef, gerbil, hamster, man, mouse rabbit and rat [A5, G73, G604, H154, J913].

Coumarin 7-hydroxylase

Coumarin → umbelliferone

Cumene hydroperoxide can act as the oxidant for rat and rabbit microsomal enzyme (considered to be P450) [A335]. Another study indicated that the enzyme is present in liver from man (very active), mouse, rabbit and guinea pig (less active), but absent from rat liver [D559]. In mouse liver it is found in microsomes and mitochondria [F8], the microsomal enzyme being $IIP450_{15\alpha}$ [F100].

Isoflavone 2′-hydroxylase

Cicer arietinum microsomal enzyme acts on biochanin A and formononetin with oxygen and NADPH as co-substrates; NADH is poorly active [K751].

Flavanone 3′-hydroxylase (flavonoid 3′-monooxygenase, E.C. 1.14.13.21)

Horseradish peroxidase oxidizes naringenin to many products including eriodictyol [A3777].

Matthiola incana enzyme is microsomal and requires NADPH. It oxidizes naringenin and dihydrokaempferol [B679].

Petunia hybrida enzyme (flavonoid 3′,5′-hydroxylase) is found in flower microsomes, and requires oxygen and NADPH, but not NADH. It oxidizes naringenin to eriodictyol, and eriodictyol to 3′,4′,5,5′,7-pentahydroxyflavanone [H310].

Zea mays enzyme, optimum pH 8.5, is found in seedling microsomes. It requires oxygen and NADPH, and oxidizes kaempferol, naringenin and apigenin [D947].

This reaction has also been observed in Sinningia cardinalis [E570], Verbena hybrida [D471], parsley [C772], Dianthus caryophyllus [C392] and in rat liver microsomes [J300].

Isoflavone 3′-hydroxylase (E.C. 1.14.13.52)

Cicer arietinum microsomal enzyme acts on biochanin A and formononetin to form calycosin and pratensein respectively, with oxygen and NADPH as co-substrates; NADH is poorly active. Genistein and daidzein are extremely poor substrates [K751].

Flavanone 4′-hydroxylase

This activity has been observed in rat, Absidia, Gibberella and Streptomyces [A1512, B222, F673, G14].

Flavonol 6-hydroxylase

Chrysosplenium americanum enzyme, molecular weight 42 000–45 000, requires Fe^{2+} and α-oxoglutarate. Substrates are 3,4′,7-tri-O-methylquercetin and 3,4′,7-tri-O-methylquercetagetin [K658].

Isoflavone 6- and 8-hydroxylases

Aspergillus saitoi converts genistein into 8-hydroxygenistein and daidzein into 8-hydroxydaidzein, probably with hydroxylation of the aglycones [K155].

A partly characterized bacterium converts genistein into 4′,5,6,7- and 4′5,7,8-tetrahydroxyisoflavones, and biochanin A into 5,6,7-trihydroxy-4′-methoxyisoflavone [J627].

Taxifolin 8-monooxygenase (E.C. 1.14.13.19)

Pseudomonas enzyme, which forms dihydrogossypetin is a flavoprotein requiring oxygen and NAD(P)H [K917].

Juglone 3-monooxygenase (E.C. 1.14.99.27)

Pseudomonas putida enzyme is composed of two dimeric isozymes, which require oxygen, molecular weights 56 000 and 59 000, one of which is induced by juglone. Further substrates include naphthazarin, 1,4-naphthoquinone and 2-chloro-1,4-naphthoquinone [K897].

Cyclopenine 3′-hydroxylase

Penicillium cyclopium enzyme requires oxygen and a hydrogen donor, e.g. NAD(P)H, ascorbate or tetrahydropteridine to form cyclopenol. It is inhibited by cyanide or thiocyanate, but not by carbon monoxide. It also hydroxylates a number of analogues [A1633].

Dihydrosanguinarine 10-monooxygenase (E.C. 1.14.13.56)

Eschscholtzia californica enzyme is a microsomal P450, specific for position 10. It requires oxygen, not replaceable by peroxide or superoxide [K777].

Dihydrochelirubine 12-monooxygenase
(E.C. 1.14.13.57)

Thalictrum bulgaricum enzyme, optimum pH 8.5, is a microsomal P450, specific for position 12. It requires oxygen and NAD(P)H [K776].

2.1.3 Hydroxylations of xenobiotics

Benzene hydroxylation

Rat liver mitochondrial enzyme, which requires NADPH, has a molecular weight of 52 000 [F686].

Methylococcus capsulatus methane monooxygenase (E.C. 1.14.13.25) hydroxylates benzene and halobenzenes by a NIH shift mechanism (products not stated) [F278].

Many other studies have also detected this reaction.

m-Cresol hydroxylase

Penicillium patulum enzyme acts on *m*-cresol to form methylquinol, as well as to form *m*-hydroxybenzyl alcohol. The enzyme, optimum pH 7.5, is a P450, which requires oxygen and NADPH, and is inhibited by carbon monoxide and cytochrome c. *m*-Cresol is a precursor of the antibiotic patulin, the formation of which requires both ring hydoxylation and side chain oxidation as well as ring fission and lactonisation [A1468].

Aniline hydroxylations

Aniline → *o*-aminophenol

This reaction has been detected in beef, mouse, pig, rat, sheep, rainbow trout, Boophilus and Nephila [A1795, A2788, A3460, D532, E60, J582].

Aniline → *m*-aminophenol

This reaction has been detected in Apocynum, Catharanthus and Conium [A2619].

Aniline → *p*-aminophenol

Species in which activity has been found in liver microsomes include bandicoot, beef, bettong, kangaroo, man, monkey, mouse, pig, possum, quokka, rat, shrew, tree shrew, rainbow trout, Boophilus, Cunninghamella and Nephila [A1218, A1795, A1997, A2420, A3460, B145, D532, E60, J639]. In mammalia the reaction requires three factors for maximal activity: cytochrome P450 or P448, a reductase and a lipid component [A627, A735]. Cumene hydroperoxide can act as the oxidant [A335]. The activity of aniline-4-hydroxylase is not detectable in rat before birth. After birth, activity increases 30-fold to a maximum at weaning, and then declines until at six months it has decreased by 90 per cent [A71]. At birth, the activity is five times greater in female than in male rats, with higher activity at 10 than at five weeks age. The development pattern only follows the activity of P450 in broad outline [A736].

Besides P450, catalase, haemoglobin and myoglobin can catalyse this reaction [B940, D43, H614]. Human and sheep erythrocytes oxidize aniline to *p*-aminophenol, with NADPH as co-substrate; the enzyme appears to be oxyhaemoglobin [B64]. Human foetal haemoglobin is more active than adult haemoglobin [B145]. Other substrates hydroxylated are *o*- and *m*-toluidine and N-methylaniline, and associated reactions involve N- and O-demethylation [D135]. Ferrihaemoglobin α-chains are less active than β-chains [D283]. Methaemoglobin is also active [D43]. In haemoglobin and methaemoglobin hydroxylation of aniline, ascorbate and dihydrofumarate can replace NADH as electron donor [D557].

Chlorobenzene hydroxylation

Rat liver forms all three chlorophenols from chlorobenzene. Pre-treatment with 3-methylcholanthrene induces *o*-hydroxylation,

whereas phenobarbital induces the formation of all three phenols [A2320].

Methylococcus capsulatus soluble methane monooxygenase (E.C. 1.14.13.25) hydroxylates chlorobenzene and a number of analogues by a NIH shift mechanism [F278].

Chlorophenol 4-monoxygenase

Burkholderia cepacia chlorophenol 4-monooxygenase not only catalyzes the formation of benzoates from benzaldehydes, but also the formation of *o*-hydroxybenzaldehydes, for instance with syringaldehyde as substrate. The reaction involves a NIH shift of the formyl group [K107].

2,4-Dichlorophenol hydroxylase (E.C. 1.14.13.20)

Acinetobacter enzyme is a homotetramer, molecular weight 240 000 and optimum pH 7.6; it requires FAD and NADPH, but NADH is not so effective; FMN and riboflavin are inactive. It also acts on *p*-chlorophenol and 4-chloro-2-methylphenol, but some non-substrate chlorophenols induce the reduction of oxygen to peroxide [C232].

Proteobacteria enzyme, molecular weight 256 000, subunit molecular weight 65 000, pI 5.2 and optimum pH 8.0, requires NAD(P)H; the product is 3,5-dichlorocatechol. It has a broad specificity, but not for compounds in which both *ortho* positions are blocked [J466].

Pseudomonas cepacia enzyme is a homotetrameric flavoprotein, monomeric molecular weight 69 000 that requires FAD and NADPH; NADH is not so effective [G221].

4-Nitrophenol 2-monooxygenase (E.C. 1.14.13.29)

Nocardia enzyme, optimum pH 7.3, is soluble, requires oxygen, NAD(P)H and FAD. It is inducible, inactivated on dialysis and is somewhat unstable, even when frozen [D182].

5-Hydroxyisophthalate 4-hydroxylase

Bacterium enzyme, which is highly specific, is a flavoprotein containing FAD that cannot be replaced by FMN; it requires NAD(P)H [A2985].

Hydroxylation of phenoxyacetate

Aspergillus niger hydroxylates phenoxyacetate in *o*- and *p*-positions; oat and pea hydroxylate in the *p*-position. Arene oxides are postulated intermediates [A2849].

Biphenyl hydroxylations

Biphenyl → 2-, 3- and 4-hydroxybiphenyl, and dihydroxybiphenyls

Hamster liver enzyme is a mixture of P450 and P448; 2-hydroxylation is induced preferentially by phenobarbital, and 3-methylcholanthrene induces 2- and 4- monohydroxylations [A323]. Carbon monoxide, SKF 525A and NADH inhibit 4-hydroxylation [A11].

Rat liver 2-hydroxylation (but not 3- and 4-hydroxylation) is induced by corticosteroids, especially by betamethasone. 4-Hydroxylation is, quantitatively, most important, and 3-hydroxylation the least [A3680]. All three monohydroxylations are induced by 3-methylcholanthrene [B195, A3680], and 3- and 4-hydroxylation by phenobarbital [A2371, A3680]. The reaction system involves P450, NADPH and NADPH-cytochrome c reductase; NADPH and reductase can be replaced by cumene hydroperoxide [A2371].

Rabbit intestinal and liver microsomal enzyme activity increases two- to four-fold from nine days after birth to the adult level [A1980].

Avocado mesocarp 2-hydroxylase is found in both microsomal and cytosolic fractions; microsomal activity is increased by pre-incubation with safrole or 3,4-benzpyrene. Activity in both fractions is only slightly inhibited by classical P450 inhibitors such as carbon monoxide or SKF 525A [A11].

Benzpyrene hydroxylases

The intense interest in this and related enzyme activities is consequential to the central role that 3,4-benzpyrene plays in the aetiology of human lung cancer.

Several publications have briefly reported on benzpyrene hydroxylase without specifying the site of hydroxylation. Many publications (see 3,4-Benzpyrene) report on 3-hydroxylation, but a significant number additionally report hydroxylation at positions 1 (rat, man and sole, e.g [A458, C473, J94]), 4 (rat [C204]), 7 (rat, man, mouse and scup, e.g. [A458, B122, D965, G445]), 8 (rainbow trout [A1424]) and 9 (rat, monkey, hamster, rabbit, mouse, man and Saccharomyces, e.g. [A458, A2327, A2379, A2814, A3326, A3412, A3681]). 3-Hydroxylation (E.C. 1.14.14.2) occurs in a large range of species, including man, rat [A13], monkey [A1869], tree shrew, pig [A1997], rabbit [A2729], camel [H103], quokka, kangaroo, bandicoot, [A2420], mouse [A3681], guinea pig [B82], pigeon, crow, kite, egret [C307], trout [A2145], goldfish, bullhead [D465], bluegill [E480], scup [D965], sole [G374], killifish [B259], mullet [C141], barnacle [B744], Saccharomyces [A3326] and Candida [B775].

Studies on monohydroxylation of benzpyrene and other polynuclear hydrocarbons is complicated by the ready dehydration of dihydrodiols under acid conditions to monophenols; the former are metabolic products formed by hydration of epoxides generated in metabolism of polynuclear hydrocarbons. In rat, it has been suggested that at least some 3-hydroxybenzpyrene is formed by a spontaneous rearrangement of benzpyrene-2,3-oxide [A3277].

In man, 3-hydroxylation has been described in bronchus [A13], placenta, [A114], lung [A1644], liver [A2379], blood [B122], hair follicle [B350], bladder [C138], hepatoma [E480], melanocyte [G360] and P450 isozymes [H10]. Placental enzyme is largely microsomal [A985].

In man and rat, liver enzyme is primarily microsomal, and is activated by low molecular weight cofactors. In man, the activity is twice as high in smokers compared with non-smokers. In rat, activity is three times higher in males than in females, but there are only small sex differences in man, rabbit and guinea pig [A313]. Rat liver microsomal enzyme activity is reduced by extraction with organic solvents [A331].

In rabbit, the liver enzyme activity remains low up to 16 days after birth, and then increases to or above the adult level at about 30 days [A1980].

2-Hydroxybiphenyl 3-monooxygenase (E.C. 1.14.13.44)

Pseudomonas azelaica enzyme, pI 6.3, is a homotetramer, molecular weight 256 000 and monomeric molecular weight 60 000, each monomer containing one mol of unbound FAD. It requires NADH and oxygen; the latter is incorporated into the substrate. Other 2-hydroxybiphenyls and substituted phenols are also substrates. Uncoupling of the reaction results in the formation of peroxide [E960, J392].

D-Amphetamine hydroxylation

Rat liver activity is mainly microsomal, but some is mitochondrial. Microsomal activity requires NADPH, with a fairly sharp optimum at pH 7.0 [A77].

Indole-3-butyrate 4-hydroxylation

Bupleurum and Phytolacca enzymes, molecular weights 10 000–12 000 (both native and denatured) and optimum pH 5–6, hydroxylate the indole nucleus [J838].

Carbostyril formation from quinolines

Rat and guinea pig liver aldehyde oxidase (E.C. 1.2.3.1) oxidize several N-alkylquinoliniums and analogues. N-Methyl- and N-phenylquinolinium both form the corresponding carbostyrils and 4-quinolones, and a similar reaction has been observed with N-methylphenanthridinium and N-methyl-5,6-benzoquinolinium [D147].

Comamonas testosteroni quinoline 2-oxidoreductase, molecular weight 360 000, is composed of subunits, molecular weights 87 000, 32 000 and 22 000, and contains molybdenum, iron, acid labile sulphur, FAD and molybdopterin cytosine dinucleotide [K769].

Pseudomonas putida quinoline oxidoreductase, molecular weight 300 000 is composed of subunits, molecular weights 85 000, 30 000 and 20 000. It contains eight Fe and two FAD/mol as well as molybdopterin cytosine dinucleotide. Other substrates are 5-, 6-, 7- and 8-hydroxyquinoline, and 8-chloroquinoline; the product from quinoline is carbostyril [F856, G151, K766].

Rhodococcus quinoline 2-oxidoreductase (E.C. 1.3.99.17), optimum pH 9.5, molecular weight 300 000, monomeric molecular weights 82 000, 32 000 and 18 000, contains molybdenum, iron, acid labile sulphur, FAD and molybdopterin cytosine dinucleotide. Further substrates include quinolines substituted with hydroxyl, methyl and chloro groups [K767].

This reaction has also been detected in Nocardia [E694] and Desulfobacterium [H917].

Quinaldine 4-oxidoreductase

Rat and guinea pig liver aldehyde oxidase forms 4-quinolones (see Carbostyril formation, above) [D147].

Arthrobacter enzyme, molecular weight 340 000 and monomeric molecular weights 82 000, 35 000 and 22 000, contains molybdenum, iron and FAD. Molybdenum is present as molybdopterin cytosine dinucleotide. It forms 4(1*H*)-quinolones from several quinolines, and isoquinolines and analogues form the corresponding 1(2*H*)-oxo compounds. Aldehydes are also substrates [G803, J33].

Quinoline-4-carboxylate 2-oxidoreductase (E.C. 1.3.99.19)

An enzyme in Agrobacterium species, molecular weight 320 000, is composed of subunits, molecular weights 85 000, 35 000 and 21 000. It contains eight mol of Fe, two Mo, and two FAD; molybdopterin cytosine dinucleotide is required for activity. Carbostyrils are formed from quinoline, 4-carboxyquinoline, 4-chloroquinoline and 4-methylquinoline [G778].

4-Hydroxyquinoline 3-monooxygenase (E.C. 1.14.13.62)

Pseudomonas putida enzyme is a trimer, molecular weight 126 000. It requires oxygen and NADH, and it is specific for 1*H*-4-oxoquinoline [G812].

2-Hydroxyquinoline 8-monooxygenase (E.C. 1.14.13.61)

Pseudomonas putida enzyme is a highly specific two-component system. One is a yellow reductase, molecular weight 38 000 which contains FAD and [2 Fe-2 S] units. It transfers electrons to an oxygenase, a homohexamer, monomeric molecular weight 55 000, and contains about six [2 Fe-2 S] units and additional Fe. The oxygenase requires the reductase, oxygen and NADH for activity, and activity is enhanced by polyethylene glycol and Fe^{2+} [K778].

Isoquinoline 1-oxidoreductase (E.C. 1.3.99.16)

Pseudomonas diminuta enzyme is dimeric, monomeric molecular weight 16 000 and 80 000, and pI in the range 6.2–6.8. It contains molybdenum, iron, acid labile sulphur, phosphate and cytosine monophosphate (probably as molybdopterin cytosine dinucleotide), but no FAD. It requires an electron acceptor, but not oxygen or NAD, and acts on isoquinoline and quinazoline (to form 1- and 4-oxo compounds, respectively) as well as analogues; quinolines are not substrates [K765]. DNA sequencing indicates monomeric molecular weights of 16 399 and 84 249 for the monomers [K764].

Debrisoquine 4-hydroxylase

Human enzyme is microsomal, requiring NADPH. It is not found in all human subjects [C324].

Rat liver microsomal enzyme has been purified as a specific P450. It also N- and O-dealkylates other compounds [D98].

Hydroxylation with internal hydroxyl transfer

Horse liver alcohol dehydrogenase (E.C. 1.1.1.1) acts on 2-hydroxylaminofluorene to form 2-amino-1- and 3-hydroxyfluorene [H291].

Comamonas enzyme reduces 1-chloro-4-nitrobenzene anaerobically to 2-amino-5-chlorophenol, suggesting that there is an initial reduction to the hydroxylamine, followed by a Bamberger rearrangement, with hydroxyl migration to form the final product [K80].

2.1.4 Hydroxylation with elimination of substituent

4-Hydroxybenzoate 1-hydroxylase (decarboxylating) (E.C. 1.14.13.64)

Candida parapsilosis enzyme is a monomer, molecular weight 50 000 and optimum pH 8 containing FAD, which requires oxygen and NAD(P)H. Quinol is formed, with molecular oxygen incorporated into the new hydroxyl group. It also acts on a range of ring-substituted 4-hydroxybenzoates [J461].

This reaction has also been found in Pycnoporus cinnabarinus [D569].

Gentisate 1-hydroxylase (decarboxylating)

Trichosporon cutaneum acts on gentisate to form hydroxyquinol [B368].

3,4-Dihydroxybenzoate 1-hydroxylase (decarboxylating)

Trichosporon cutaneum enzyme is highly specific. It requires oxygen and NADH, and forms hydroxyquinol with the release of carbon dioxide [E288]

Salicylate 1-monooxygenase (E.C. 1.14.13.1)

e.g. Salicylate $\rightarrow$ catechol + CO_2

Pseudomonas putida enzyme is a monomer, molecular weight 54 000. The amino acid composition and the terminal amino acids have been determined [A1216]. Another study using a different strain found a molecular weight of 45 000, with a different amino acid composition [F658]. The reaction requires oxygen and NADH, with carbon dioxide as the second product. Salicylaldehyde is also a substrate, and this releases formate [B751]. By using specifically ring-labelled salicylate it has been found that decarboxylation and hydroxylation with P. cepacia enzyme occur at the same carbon atom [B883]. It is an inducible enzyme [E287]. A Pseudomonas enzyme also acts on 3- and 5-chlorosalicylate and 3,5-dichlorosalicylate [H506].

Trichosporon cutaneum enzyme, molecular weight 45 300 and optimum pH 7.5, contains FAD. It also acts on salicylates substituted with a hydroxyl group at positions 3, 4, 5 and 6, an amino or chloro group at 4 or 5, a methyl at 4, or a methoxy or fluoro at 5 [D232].

This reaction has been found to occur non-enzymatically in rat, catalysed by free radicals formed by the parkinsonism-inducing ion MPP^+ [J681]. In rat liver the formation of catechol and other products from salicylate is catalysed by the action of hydroxyl free radicals rather than by the direct action of a decarboxylating hydroxylase [J754].

Vanillate 1-hydroxylase (decarboxylating)

Sporotrichum pulverulentum enzyme acts on vanillate, protocatechuate, gallate, 2,4-dihydroxybenzoate and *p*-hydroxybenzoate. Homovanillate and 2,3,4-trihydroxybenzoate are less effective as substrates, whereas gentisate, syringate, ferulate, veratrate and *p*-methoxy-

benzoate are poor substrates, and benzoate and *m*-methoxybenzoate are not substrates. The product from vanillate is methoxyquinol [B73]. The enzyme has a molecular weight of 65 000 and requires NADPH and FAD for maximal activity. Tiron, Cu^{2+}, Ag^{+}, Hg^{2+} and *p*-chloromercuribenzoate are inhibitory, whereas EDTA, diethyldithiocarbamate and Fe^{3+} are not. Further substrates are 3,4-dihydroxy-5-methoxybenzoate and 2,4,6-trihydroxybenzoate [C57].

Phanerochaete chrysosporium enzyme, optimum pH 7.5–8.5, requires NAD(P)H and oxygen, and is cytosolic [B312].

4-Hydroxyisophthalate hydroxylase

Pseudomonas enzyme, which is different from *p*-hydroxybenzoate hydroxylase, is a homodimer, molecular weight 103 000, containing one mol of FAD, with protocatechuate as the reaction product. It also acts on 5-sulphosalicylate at a much lower rate; other compounds are not substrates. It is inhibited by substrate analogues and thiol-binding compounds, and is stabilized by thiols [A3066].

Aniline oxidation to catechol

Nocardia carries out this reaction, with the incorporation of molecular oxygen; a cyclic peroxide intermediate has been suggested [A1520].

Anthranilate 3-monooxygenase (deaminating) (E.C. 1.14.13.35; formerly E.C. 1.14.12.2)

Anthranilate → pyrocatechuate

Trichosporon cutaneum enzyme, molecular weight 95 000 and monomeric molecular weight 50 000, contains two mol of FAD and exhibits a sharp optimum pH at 7.7. The oxygen in position 2 comes from water, and in position 3 from molecular oxygen. Other substrates are N-methyl- and N,N-dimethylanthranilate. Under some conditions 3-hydroxyanthranilate is also formed; this requires a reducing agent that acts on imines [C393, E270].

Aspergillus niger, molecular weight 44 000, pI 5.36 and optimum pH 8.2, requires FAD and Fe^{2+}. It is inhibited by Cu^{2+}, *o*-phenanthroline and *p*-chloromercuribenzoate. Another activity associated with this enzyme is anthranilate 3-hydroxylation [A778, B327, D231].

This reaction has also been observed in Aspergillus soyae [A1299].

Anthranilate hydroxylase (with deamination and decarboxylation; E.C. 1.14.12.1)

Pseudomonas cepacia 2-halobenzoate 1,2-dioxygenase acts on anthranilate and other benzoates with a considerable range of substituents [G434].

Trichosporon cutaneum enzyme, molecular weight 94 000 and optimum pH 7.7, appears to be a dimer. Substrates are anthranilate and N-methylanthranilate; some benzoates are non-substrate effectors, with the formation of peroxide from oxygen [C393].

This reaction has been observed in Micrococcus, Aspergillus soyae and Pseudomonas pyrrocinia [A1299, C120, D56].

4-Aminobenzoate hydroxylase (E.C. 1.14.13.27)

4-Aminobenzoate → *p*-aminophenol + CO_2

Agaricus bisporus enzyme, molecular weight 49 000, pI 6.0 and optimum pH 6–8 (partly dependent on cofactor), contains about one mol of FAD. It requires oxygen and NAD(P)H. Other substrates include aminobenzoates and *p*-hydroxybenzoate. Unlike 4-aminobenzoate, these substrates also form peroxide non-stoichiometrically, whereas peroxide is formed stoichiometrically relative to cofactor oxidation in the presence of other benzoates that are not substrates. Neither FMN nor riboflavin can replace FAD [D770, E162].

2-Aminobenzenesulphonate 2,3-dioxygenase (E.C. 1.14.12.14)

Alcaligenes enzyme is monomeric, molecular weight 42 000, and requires two oxygen molecules to form 2,3-dihydroxybenzenesulphonate. Maximal activity is found near the end of the exponential growth phase [H239, K775].

Alcaligenes enzyme, molecular weight 134 000 according to another study, is composed of two pairs of monomers, monomeric molecular weights 45 000 and 16 000, with one [2Fe-2S] centre associated with each of the larger chains. Inhibition by *o*-phenanthroline indicates the presence of another Fe-binding site. The N-terminal sequences have been determined. The product formed from 2-aminobenzenesulphonate is 2,3-dihydroxybenzenesulphonamide. Other substrates are benzenesulphonate, and benzenesulphonates substituted with nitro, amino, chloro and hydroxyl groups; the reaction products from these compounds were not identified [K293].

4-Sulphobenzoate 3,4-dioxygenase (E.C. 1.14.12.8)

Comamonas testosteroni contains two isozymes. One is a red dimer, monomeric molecular weight 50 000, and the other a yellow monomer, molecular weight 36 000, with NADH and Fe^{2+} as cofactors. The enzyme is highly specific, forming sulphite and protocatechuate. The reaction does not appear to involve two steps or to involve an intermediate dihydrodiol [G244].

Pseudomonas putida oxidizes benzenesulphonate to catechol and *p*-toluenesulphonate to 4-methylcatechol [J657]. The same reaction is observed in Alcaligenes [H297].

Salicylaldehyde hydroxylation

Pig liver microsomal flavin-containing monooxygenase-1 forms catechol and formate in equimolecular amounts from salicylaldehyde [H482].

Dechlorination with concomitant hydroxylation by microorganisms

a. 4-Chlorobenzoate dehalogenase (E.C. 3.8.1.6)

p-Halobenzoate → *p*-hydroxybenzoate

Studies have found that this reaction occurs in three stages: conjugation with CoA (E.C. 6.2.1.33) followed by dehalogenation (E.C. 3.8.1.7) and hydrolysis (E.C. 6.2.1.33) [K191]; detailed information is found under these headings.

An Arthrobacter enzyme, optimum pH 6.8, is activated by Mn^{2+} and inhibited by peroxide. Other substrates are *p*-fluoro- and *p*-bromobenzoates [D544]. Another study claims that although *p*-iodobenzoate is a substrate *p*-fluorobenzoate is not, nor are *p*-chlorophenylacetate or *p*-chlorocinnamate. The molecular weight is about 45 000 and the optimum pH 7–7.5. Unlike all other similar dehydrogenases reported at the time it is not inhibited by EDTA or activated by Mn^{2+} [E752].

A Pseudomonas dehalogenase requires ATP, CoA and Mg^{2+} [G205]. The incorporated oxygen comes entirely from water, indicating that molecular oxygen is not involved [D473] (but see *b*. below). This enzyme, optimum pH 7–7.5, is activated by Mn^{2+} or Co^{2+}, and is inhibited by EDTA. It acts on chloro-, bromo- and iodobenzoates, but not on *p*-fluorobenzoate [E359].

b. p-Chlorobenzoyl CoA dehalogenase (E.C. 3.8.1.7)

p-Chlorobenzoyl CoA →
p-hydroxybenzoyl CoA

This is the second step in the reaction sequence leading to the oxidative dehalogenation of *p*-chlorobenzoate.

Pseudomonas 4-chlorobenzoyl CoA dehalogenase also acts on the bromo- and iodo- analogues, but not on the fluoro- analogue [G920, H645]. About 75 per cent of the incorporated oxygen comes from molecular oxygen, and the remainder from water [H216]. It is a homotetramer with high temperature

stability, molecular weight 120 000, pI 6.7 and optimum pH 10 [H645, K191].

Acinetobacter enzyme also acts on bromo-analogues [G896].

Arthrobacter enzyme is a tetramer, monomeric molecular weight 33 000, pI 6.1 and optimum pH 8, with a stability range pH 6.5–10. It also acts on the fluoro-, bromo- and iodo- analogues, but not on *o*- and *m*- chloro analogues [H279].

c. Chlorophenol 4-monooxygenase

Burkholderia enzyme is a two-component system. One is a reductase, molecular weight 22 000 that contains FAD, and the other has a molecular weight of 58 000. The reaction requires oxygen and NADH. 2,4,5-Trichlorophenol is oxidized to 2,5-dichloroquinol and then to 5-chloro-2-hydroxyquinol. Other substrates are 2,3,5,6-tetrachlorophenol, 2,4,6-trichlorophenol and 2,5-dichlorophenol [J177].

Dechlorination with catechol formation

a. 2-Chlorobenzoate 1,2-dioxygenase
(E.C. 1.14.12.13)

Pseudomonas cepacia forms pyrocatechuate from 2-chlorobenzoate [F401].

b. 2-Halobenzoate 1,2-dioxygenase

o-Halobenzoate → catechol

Pseudomonas cepacia enzyme is composed of two protein fractions, and acts on a range of *o*-halobenzoates as well as other *o*-substituted benzoates. In many instances the products have not been identified, but benzoate, *o*-toluate, *m*-hydroxybenzoate and *p*-hydroxybenzoate form benzoate-1,2-dihydrodiol, *o*-cresol, gentisate and quinol respectively; in none of these compounds is there a readily displaceable *ortho* substituent, which drives the reaction in a different direction [G434].

c. 4-Chlorophenylacetate 3,4-dioxygenase
(E.C. 1.14.12.9)

p-Chlorophenylacetate →
3, 4-dihydroxyphenylacetate

This Pseudomonas activity involves a two-component, intensely red-brown enzyme system. One of the enzymes is a homotrimer, molecular weight 140 000 and pI 5.0. In the reaction two oxygen atoms are incorporated from molecular oxygen [E163].

d. 2,4,6-Trichlorophenol 4-monooxygenase

Azotobacter enzyme is a homotetramer, molecular weight 240 000, which forms 2,6-dichloroquinol from 2,4,6-trichlorophenol. It requires FAD, and utilizes one mol of oxygen and two mol of NADH. Other substrates include a range of *para*-chlorinated or brominated phenols; *o*-chlorophenol is a poor substrate [H884].

Pentachlorophenol monooxygenase
(E.C. 1.14.13.50)

Arthrobacter enzyme, optimum pH 7.5, is stimulated by EDTA and requires NADPH and oxygen, with formation of tetrachloroquinol. Other substrates include 2,3,4- 2,4,5-, and 2,4,6-trichlorophenol, and 2,3,4,5-tetrachlorophenol, but other analogues are not substrates [K750].

A Flavobacterium enzyme, molecular weight 63 000, pI 4.3 and optimum pH 7.5–8.5, can exist as polymeric forms. The monomer is a flavoprotein containing one mol of FAD, and the reaction requires two mol of NADPH. It hydroxylates pentachlorophenol to tetrachloroquinol [G272].

Sphingomonas pentachlorophenol 4-monooxygenase, which requires NADPH, is a flavoprotein, molecular weight predicted to be 59 993 with 538 amino acid residues by DNA studies. Other substrates include 4-nitrocatechol and *p*-nitrophenol [K73].

Quinol formation from *para* substituted phenols

Rat liver microsomes form quinol from phenols substituted in the *para* position with nitro, cyano, hydroxymethyl, acetyl, benzoyl or halide groups. Results from experiments using $^{18}O_2$ suggest that

the initial reaction is the formation of a 4-hydroxy-1-oxo-2,5-diene, involving oxygen transport by the Fe in the enzyme. This intermediate may then either form quinol directly, by elimination of the substituent (as a positively charged ion) from the 4-position, or the formation of *p*-quinone, with the substituent forming a negatively charged ion. Trapping experiments suggest that both mechanisms may occur, depending on the identity of the substituent. In the case of *p*-cresol the side chain is not eliminated; instead there is a NIH shift to form toluquinol [J81].

Defluorination with catechol formation

Pseudomonas converts 3-fluorinated compounds into the corresponding 2,3-dihydroxy analogues. Although fluorobenzene is not a substrate, toluene, anisole, fluorobenzene, chlorobenzene, bromobenzene, iodobenzene, benzonitrile and benzyl alcohol fluorinated at position 3 are substrates [F76].

2-Nitrotoluene 2,3-dioxygenase

$$\text{2-Nitrotoluene} + O_2 \rightarrow \text{3-methylcatechol} + \text{nitrite}$$

Pseudomonas enzyme is a three-component system which forms 3-methylcatechol as well as *o*-nitrobenzyl alcohol from 2-nitrotoluene (the best substrate). A series of other nitrotoluenes and nitrobenzene are also catechol-forming substrates. Both oxygen atoms are incorporated from molecular oxygen [H344, J524].

2-Nitrophenol 2-monooxygenase (E.C. 1.14.13.31)

$$o\text{-Nitrophenol} + O_2 \rightarrow \text{catechol} + \text{nitrite}$$

Pseudomonas forms catechol and nitrite from *o*-nitrophenol [E726]. P. putida enzyme, molecular weight 58 000–65 000, optimal activity and optimum stability at pH 7.5–8.0, requires NADPH and oxygen. It is activated by Mg^{2+} or Mn^{2+}, but not by flavins. It is very sensitive to heat inactivation, but is stabilized by substrate. It also acts on a range of other *o*-nitrophenols, but not all *o*-nitrophenols are substrates [E607, H65, K898].

2,4-Dinitrotoluene 3,4-dioxygenase

$$\text{2,4-Dinitrotoluene} + O_2 \rightarrow \text{4-methyl-5-nitrocatechol} + \text{nitrite}$$

A Pseudomonas enzyme catalyzes this reaction [G407, J524].

***p*-Nitrophenol hydroxylation**

$$p\text{-Nitrophenol} + O_2 \rightarrow \text{quinol} + \text{nitrite}$$

Penicillium chrysogenum enzyme is found in a membrane fraction. It requires oxygen and NAD(P)H, and is stimulated by FAD; the oxygen atom is incorporated from molecular oxygen [E94].

Moraxella forms quinol and nitrite from *p*-nitrophenol [G153].

4-Nitrocatechol hydroxylation

Sphingomonas pentachlorophenol 4-monooxygenase (see above) oxidizes 4-nitrocatechol to hydroxyquinol, and *p*-nitrophenol (poorly) to quinol, with the release of nitrite [K73].

Bacillus sphaericus and Arthrobacter enzymes form hydroxyquinol with the release of nitrite [H270, J679].

6-Nitrobenzo[*a*]pyrene hydroxylation

Rat lung and liver catalyse the conversion of 6-nitrobenzo[*a*]pyrene into 6-hydroxybenzo[*a*]pyrene, also with the formation of a trace of benzpyrene [E467]. The same reaction has been observed in mouse [E971].

2.2 *Formation of quinones and analogues from catechols, quinols and other precursors*

Monophenol monooxygenase (E.C. 1.14.18.1)

Tyrosinase (classically from mushroom or skin melanocytes), polyphenol oxidase (from potato) and laccase (E.C. 1.10.3.2; originally from the lacquer tree) are old classifications for enzymes that are now grouped together under the heading of Monophenol Monooxygenase, although these classifications are still commonly found in the literature. In the current section, this classification (except polyphenol oxidase) has been used because it is still in such common use. They are all copper-containing enzymes, but they differ in specificity; laccases preferentially oxidize *p*-phenylenediamine relative to oxidation of catechols to quinones, but they differ from tyrosinase in that they do not oxidize tyrosine to dopa. However, the distinctions between these classes of enzyme are not clear-cut.

One study with *o*- and *p*-diphenol oxidases (considered to be catecholases and laccases respectively) from apple, banana, Agaricus, Glomerella, Sclerotina (*o*-oxidases), peach, spruce, Botrytis, Coriolus, Trametes, Glomerella and Rhus (*p*-oxidases) distinguishes between the activites on the basis of the following parameters:

Some distinguishing features between catechol oxidase and laccase

Test	*Catechol oxidase*	*Laccase*
Catechols	Oxidized	Oxidized
Quinols	Zero or poor oxidation	Oxidized
p-Phenylenediamine	Zero or poor oxidation	Oxidized
p-Cresol	Orange-red pigment*	–
1-Naphthol	–	Purple colour*
Cinnamates	Inhibitory	No inhibition
PVP	Inhibitory	No inhibition
Cationic detergents	No inhibition	Inhibitory
Dodecyl sulphate	Activates	No action

* with whole microorganisms [A3974].

2.2.1. Tyrosinase and unspecified types.

a. Plant and fungal enzymes

Apple enzyme is composed of isozymes, molecular weights 46 000, 120 000, 460 000 and 800 000. They are considered to be polymers of a common monomer [A1133].

Amasya apple enzyme contains three isozymes, with optima at pH 6.6–9.0, dependent on the substrate; substrates are catechol, 4-methylcatechol, pyrogallol and L-dopa [H567].

Four Arachis peroxidase isozymes, which additionally exhibit polyphenol oxidase activity towards L-dopa, have optima at pH 7.6, 8.0, 8.0 and 8.0 [A2519].

Artichoke enzyme, molecular weight 116 000, pI 4.5, and broad optimum pH 5–8 is activated by Cu^{2+} and Fe^{3+}. Substrates include catechol, caffeate and 5-O-caffeoylquinate [F664].

Avocado cultivars show different isozyme patterns. Two cultivars each contain six major isozymes and probably some trace components, and a third cultivar contains a smaller number of isozymes. It would appear that some isozymes are cultivar-specific. They oxidize L-dopa and other catechols [A1636].

Banana fruit pulp contains a soluble enzyme that acts on catechol, but with rapid inactivation. Denaturation above 70° has an activation energy of 85 000 cal/mol; at lower temperatures a slower inactivation occurs, activation energy 18 000 cal/mol [A212]. More detailed studies have demonstrated nine isozymes separable by electrophoresis in the inner pulp, eight in the outer pulp and 10 in the skin. They all act on catechol, but each has its own pattern of specificity towards 4-methylcatechol, dopamine, pyrogallol, *d*-catechin, caffeate and DL-dopa. Two in the inner pulp, and one in the outer pulp act on L-tyrosine. Inhibitors include diethyldithiocarbamate, cyanide, metabisulphite, mercaptoethanol, propane-1,2-dithiol and mercaptoethanol [A218].

Cabbage phloroglucinol oxidase, molecular weight 39 000–40 000, which oxidizes phloroglucinol and phloroglucinolcarboxylate (the reaction products are unclear) additionally

shows peroxidase properties towards guaiacol, with optimum pH 7.6 and 6.4 for these reactions respectively. Catechols are not substrates for the oxidase activity. It is moderately stable at 100° [H412].

Helianthus (sunflower) enzyme exhibits optima at pH 5.3, 5.8, 6.0 and 6.5, with best stability between pH 5.5 and 7 [A2152, A2153].

Ipomoea batatas (sweet potato) enzyme is composed of 12 isozymes, optimum pH 6–6.5 [F208].

Longan (Dimocarpus longan) fruit peel enzyme, optimum pH 6.5, acts on pyrogallol, catechol and 4-methylcatechol, but not on chlorogenate, *p*-cresol, resorcinol or tyrosine. It is inhibited by glutathione, cysteine, thiourea, Fe^{2+}, Sn^{2+}, and is activated by Mn^{2+} and Cu^{2+} [K96].

Green olive enzyme, molecular weight 42 000, has been separated into seven to nine bands of activity by isoelectric focussing, with pI 5, 5.6 and 7 for the main bands, and pI 4.8–5.6 for the remainder. They act on catechols including DL-dopa, dopamine and catechol, but monophenols are not substrates. Inhibition (in decreasing order, at 10^{-3}–10^{-5} M) is brought about by diethyldithiocarbamate, 2-mercaptoethanol, bisulphite, thiourea and 8-hydroxyquinoline. Halides inhibit at higher concentration, and chloride inhibition is strongly pH-dependent [A2360].

Pear enzyme (Bartlett) contains two isozymes that act on chlorogenate with an optimum at pH 4 [A1007].

Enzymes from two species of Phoenix exhibit a molecular weight of 17 000–17 500, optimum pH about 6 and maximal stability about 7. Substrates include catechol and other diphenols, but not monophenols or *meta*-diphenols [F151].

Potato enzyme is a complex mixture, with 17 isozymes separable by electrophoresis with L-dopa as substrate. Only five of these act on L-tyrosine, a pattern of specificities that is repeated by other catechols and monophenols. Isoelectric focussing shows multiple peaks in the range of pH 4.0–4.7 and 5.1–5.4. The monomeric molecular weight is 36 000, and monomer, dimer, tetramer, octamer and polymeric forms are found. Only high molecular weight forms exhibit monophenol oxidase activity [A2997, A3190].

A spinach phenoloxidase is a monomer, molecular weight 36 000. It dimerizes in the presence of 5 mM pyrocatechualdehyde without loss of activity; other aldehydes are ineffective. On freezing, it polymerizes [A1735]. Root enzyme develops after germination and differs from two chloroplast oxidases [A1730].

Sugar cane enzyme is composed of two fractions, molecular weight 32 000 and 130 000, both with broad optima between pH 4.5 and 7.5. It acts on chlorogenate, a better substrate than caffeate or L-dopa. Thiols, especially thioglycollate, inhibit non-competitively [A180].

Tea catechol oxidase, optimum pH 5.7 and pI 4.1, acts on catechol, pyrogallol and a series of catecholic flavonoids. Flavonoid gallate esters undergo oxidative degallation. A flavanol gallate oxidase exhibits pI 9.6 [A972] and contains Fe^{2+} [A1004]. In another study six isozymes were detected, optimum pH 6.2–6.6 [A1128].

Vitis vinifera (grape) enzyme is devoid of laccase activity. Substrates include 4-methylcatechol, (+)-catechin, caffeate, chlorogenate, and caffeoyltartrate. *p*-Coumarate and *p*-coumaroyltartrate, but not quinol are substrates [E458]. It exists as multiple forms, eight having been detected [A1038], and pI 4.7, 4.9 and 5.2 [A208]. Kinetic studies indicate random binding of 4-methylcatechol and oxygen followed by release of quinone, then a second catechol molecule binds and is oxidized to quinone [A1631].

Wheat contains an enzyme that acts on L-dopa [A176].

A study on *o*-diphenol oxidases has detected activity in apple, banana, Agaricus, Sclerotina and Glomerella. 4-Methylcatechol is substrate in all these species, and chlorogenate in some. Inhibition is caused by cinnamate, *p*-coumarate, ferulate, usually competitively, and by polyvinylpyrrolidine. They are activated by dodecyl sulphate [A3974].

Agaricus bisporus enzyme is composed of three dimeric isozymes, pI 5.12, 5.41 and 6.25, formed from combinations of two different subunits. L-Dopa and catechol are substrates; only one

hydroxylates tyrosine effectively [A3135]. It is inhibited competitively by thiambutosine [A2185]. 4-*tert*-Butylcatechol is oxidized to 4-*tert*-butyl-*o*-quinone, with ethyl hydroperoxide as 2-electron acceptor [A1495].

Mushroom (Xerocomus) enzyme is inhibited by lamprene [A2185].

Portabella mushroom tyrosinase has a molecular weight of 48 000–50 000 and pI 5.1–5.3 [K101].

Mushroom tyrosinase acts on 3,4-dihydroxybenzyl cyanide to form the corresponding *o*-quinone. The time sequence indicates the initial formation of a semiquinone radical from a single electron oxidation, followed by dismutation. The quinone rapidly forms the corresponding quinone methide [K834]. It also oxidizes poly(*p*-hydroxystyrene) to the corresponding quinone, but only a small proportion of the phenolic groups are oxidized [K285].

Streptomyces glaucescens tyrosinase, molecular weight 29 100, optimum pH 6.8, pI 6.95 and maximal stability at pH 8.0, acts on both L-tyrosine methyl ester and L-dopa; it contains one mol of Cu^+. K_m increases as pH decreases below 8, due to a change of ionisation at the active centre; K_m is also strongly dependent on oxygen concentration for the oxidation of catechols but not monophenols [A749].

b. Animal enzymes

Beef uterus enzyme has been separated into two components, one with molecular weight 80 000. Substrates are catecholamines and analogues; for instance, oxidation of adrenaline is the first step in the formation of adrenochrome. No activity was observed with monophenols or *m*-diphenols [A624].

Calliphora erythrocepha (blowfly) enzyme is found as a pro-enzyme, molecular weight 115 000 [A900].

Corcyra cephalonica enzyme, which is found in larval and pupal haemolymph, oxidizes a series of catechols related to L-dopa and catecholamines, including N-acetyldopamine [A2556].

Fleshfly enzyme, obtained from the anterior end of the third instar, molecular weight 400 000, appears to be a lipoprotein. It acts on dopa, methylcatechol and *p*-cresol, but tyrosine is not a substrate [A7]. Probably at least five isozymes oxidize L-dopa [A27].

Studies on the oxidation of L-dopa by frog epidermis enzyme suggests a uni-uni-bi-bi ping-pong mechanism [D15]. It is present as a pro-enzyme whose amino acid composition has been determined, and is activated by peptidases. It appears to exist as monomeric (molecular weight 50 000) and tetrameric forms, each monomer containing one copper atom. Both tyrosine and dopa are substrates [A1208].

Gerbil eye enzyme, which is involved in melanogenesis utilizes both L-tyrosine and L-dopa; the latter is the cofactor in the oxidation of the former [H687].

The sea squirt Halocynthia roretzi polyphenol oxidase is a heterotetramer, molecular weight 170 000, monomeric molecular weights 55 000 and 30 000. It acts on L-tyrosine, DL-dopa and catechol with an optimum at pH 6.4 [J313].

Mytilus edulis byssus enzyme is polymeric, monomeric molecular weight 120 000 and optimum pH 8–8.5. 4-Methylcatechol is substrate, and it requires sodium chloride concentrations of 0.5–0.6 M [D726].

Squid tyrosinase, which oxidizes L-dopa, exhibits three precipitin lines [A883].

Caeruloplasmin oxidizes D- and L-dopa, dopamine and *p*-phenylenediamine; the catechol substrates inhibit each other, but not the diamine oxidation. This suggests two separate oxidation sites on the molecule [A677].

2.2.2. Enzymes classified as laccase and quinol oxidases

Sarcophaga bullata laccase, optimum pH 4.5, acts on quinol and a range of catechols including L-dopa and N-acetyldopamine. It is inhibited by azide [E407].

Silkworm laccase, optimum pH 5.5, acts on quinol and L-dopa [A702].

Arum maculatum quinol oxidase, a mitochondrial enzyme that oxidizes menadiol, is very unstable after solubilization [E87].

Lentinus edodes laccase, molecular weight 74 000, pI 3.42, and optimum 4–4.2, has a carbohydrate content of 7.5 per cent. Its absorption spectrum is indicative of a copper-containing protein. [H834].

Mangifera (mango) laccase oxidizes quinol as well as 4-methylcatechol, but *p*-cresol is not a substrate. A similar enzyme is found in Schinus, Pistacia and Pleiogynium [A3138].

Peach laccase, molecular weight 73 500, contains two Cu/mol; its amino acid composition has been determined. It is inhibited by diethyldithiocarbamate [A186].

Shinus molle enzyme, molecular weight 105 000 and optimum pH 6.2, acts on quinol. It contains three to four mol/mol copper and is about 50 per cent polysaccharide composed of a variety of saccharide residues. Its amino acid composition has been determined [B491].

Botrytis cinerea laccase, a blue enzyme, acts on quinol, a range of catechols, monophenols and phenylenediamines at a similar rate, whereas tyrosine is oxidized at a considerably slower rate [A1930, E458]. Optimum pH is substrate-dependent, between pH 3.5 and 5; it is stable down to pH 2.5, its pI, but is inactivated above pH 7. It is rapidly inactivated above 40°. Slight inhibition is caused by cyanide and EDTA [A1930].

Coriolus hirsutus laccase is a glycoprotein molecular weight 73 000, optimum pH 2.5–4.0 (substrate dependent) and pI 7.4, with three copper-containing centres. The N-terminal sequence shows low homology with other Basidiomycetes laccases. Oxidation of 2,2′-azino-bis(3-ethylbenzothiazoline-6-sulphonic acid) forms a cation radical. Many phenols and *p*-phenylenediamine are substrates [K677].

Trametes polyphenol oxidase is composed of two isozymes considered to be laccases, molecular weights 61 000 and 90 000, and pI 3.4 and 2.7 respectively, with optimum pH 4.5–5.0. The larger molecule is stable up to 50°, whereas the smaller is stable up to 60°, at neutral to acidic pH. They act on (+)-catechin, but not on tyrosine, and are inhibited by copper chelators, reducing agents and N-bromosuccinimide, but not by carbon monoxide [K106].

A study has detected *p*-diphenol oxidase in peach, spruce, Rhus, Botrytis, Coriolus, Trametes and Glomerella. Substrates include quinol, *p*-phenylenediamine and 4-methylcatechol in all species, whereas catechol and chlorogenate are substrates in some species. Inhibition is not brought about by cinnamate, dodecyl sulphate or polyvinylpyrrolidine [A3974].

4-Methyl-5-nitrocatechol oxygenase

Burkholderia enzyme, molecular weight 60 000–65 000, contains one mol of FAD, and requires oxygen and NAD(P)H. The product is 2-hydroxy-5-methyl-*p*-quinone. 4-Nitrocatechol is also a substrate, but other catechols are not [J249].

Chlorogenate oxidase

Ipomoea batatas enzyme is composed of two isozymes, molecular weights 39 000 and 40 000 [J822].

Tyrosylprotein oxidation

Arthrobacter globiformis oxidizes a tyrosyl residue in the active centre of phenylethylamine oxidase to a topaquinone residue. The reaction requires two molecules of oxygen, and one mol of peroxide is formed. The stoichiometry suggests that a trihydroxyphenylalanyl residue is an intermediate [J905].

Phloroglucinol oxidation

Brassica oleracea contains three isozymes, two of which have molecular weights 43 000 and 32 000, and optimum pH 8.0 and 7.4 respectively, which oxidize phloroglucinol and phloroglucinolcarboxylate but not other phenols; they are polyphenol oxidases which are activated

by Mn^{2+}. The products are possibly quinones. At lower pH these enzymes show peroxidase activity, inhibited by Mn^{2+} [H878].

Naphthohydroquinone dehydrogenase

Human enzyme is found in an inactive form in saliva, and is activated by gastric juice. It is a metalloenzyme that requires oxygen, but no cofactors, oxidizing rifampicin to its quinone; quinol is not a substrate. It is inhibited by sulphide, cysteine, cyanide and citrate [A3399].

trans-Dihydrodiols as quinone precursors

Rat liver cytosol 3-hydroxysteroid dihydiol dehydrogenase converts *trans*-dihydrodiols into *o*-quinones. Substrates are benzene dihydrodiol and 3,4-dihydrodiols of benzanthracene, 7-methylbenzanthracene, 12-methylbenzanthracene and 7,12-dimethylbenzanthracene [E740]. Enzyme from rat lens, optimum pH 9.0, oxidizes naphthalene-1,2-dihydrodiol to the corresponding 1,2-dione. It has been identified as aldol reductase [J552].

It is claimed that benzpyrene 3,6-quinone formation and reduction in rat liver microsomes are catalyzed by different enzymes [A3637].

Polynuclear hydrocarbon quinone formation

Because of their key role in carcinogenesis by xenobiotics, polynuclear hydrocarbons have been the subject of a large number of metabolic studies, which have demonstrated that they can be oxidized to quinones. Most of the studies have been carried out solely by examining the identity of metabolic end-products. Benzpyrene (benzo[*a*]pyrene) illustrates these findings; *trans*-dihydrodiols are probable intermediates (see above).

Studies with benzpyrene have shown that 1,6-, 3,6- and 6,12-quinones are formed, the oxo groups of which are conjugated through the aromatic nucleus. Most studies have been carried out in rats, but these reactions have also been observed in man, mouse, monkey, rabbit, trout, catfish, goldfish, bullhead, sea anemone, starfish, Petroselinum, Glycine max, Pycnoporus, Phanerochaete and Cunninghamella.

In man, the reaction is catalyzed by P450 [H10] and in melanocyte [G360].

In rat the reaction occurs in liver nucleus [A3164, A3782], liver microsomes [G445], and is also catalyzed by cytosolic lipoxygenase (E.C. 1.13.11.12) [G101]. With liver microsomes benzpyrene metabolism is slower with peroxide as oxidant than with oxygen, which has suggested a peroxide-dependent oxidation as a second pathway [B656]; it is possible that peroxide may have released oxygen spontaneously or by the action of traces of catalase, however. A liver microsomal P450 designated $P450_{MC}$ catalyzes these reactions [E226].

In mouse the reaction occurs in liver microsomes [G445].

In rabbit the reaction occurs in lung [A2394].

In trout and catfish the reaction occurs in hepatocytes [J311].

The activity in goldfish and bullhead liver is an order of magnitude lower than in rat [D465].

In sea anemone, the reaction is catalyzed by microsomes [J503].

Pycnoporus cinnabarinus enzyme is a laccase [J907].

Crinipellis, Marasmius and Marasmiellus (fungi) act on pyrene-1,6- and 1,8-diols to form the corresponding quinines [H879].

Phaseollin oxidation

Fusarium solani oxidizes phaseollin to 1α-hydroxyphaseollone, with the oxidation of one of the aryl rings to a 4-oxo-2,5-diene ring [A209].

Lipoxygenase as peroxidase

Glycine max lipoxygenase and peroxide oxidize 5-(S-cysteinyl)-L-dopa and 5-S-cysteinyldopamine. Both substrates form two types of phaeomelanin [J252].

Guaiacol peroxidase

Spruce needle chloroplast enzyme, a tetramer, monomeric molecular weight 41 000, pI 4.4 and optimum pH 5–6.8, may be a glycoprotein. The reaction it catalyzes is not stated in Chemical Abstracts, but it may yield *o*-quinone [J318].

Arachis peroxidase isozymes have optima at pH 4.4, 5.2, 5.6 and 6.4 [A2519].

Chloroperoxidase (E.C. 1.11.1.10) in Caldariomyces fumago is composed of two isozymes, molecular weights 46 000 and 40 000. They produce a brown pigment from guaiacol [A3764].

2-Amino-4-nitrotoluene oxidation

Phanerochaete chrysosporium manganese peroxidase (E.C. 1.11.1.13) oxidizes this compound to 4-nitro-*o*-quinone, with the release of methanol [G436].

Catechol formation with desulphonation

Both Alcaligenes and Pseudomonas putida desulphonate benzenesulphonate and toluene-*p*-sulphonate, forming catechol and 4-methylcatechol respectively [H297, J657].

Quinone methide formation

Sarcophaga bullata forms quinone methides from 4-alkylcatechols, (including 4-methylcatechol), 3,4-dihydroxyphenylethanol, 3,4-dihydroxyphenylacetic acid and N-acetyldopamine, with quinones as intermediates [C692, G184]. The quinone methides are unstable and further products are formed by attack at the α-carbon, to form α-hydroxy-3,4-catechols; in aqueous methanol some of the methoxy analogue is formed, suggesting that water, rather than a hydroxyl ion may be the other reactant [C692, F793]. In Sarcophaga bullata, Manduca sexta and Periplaneta americana N-acetylnoradrenaline is formed from N-acetyldopamine by this pathway [F68].

Sarcophaga bullata 4-alkyl-*o*-quinone: 2-hydroxy-*p*-quinonemethide isomerase, molecular weight 98 000 and optimum pH 6.0, is found in larval haemolymph. It acts on quinones of 3,4-dihydroxyphenylethanol, N-(β-alanyl)dopamine and N-acetyldopamine. A further attack on the quinones formed from these products form in turn the corresponding α-oxo products [F792, F793].

Mushroom tyrosinase converts 3,4-dihydroxymandelic acid into 3,4-dihydroxybenzaldehyde, possibly with a quinone methide intermediate [E963].

2.3 *Free radicals from phenols*

Hydroxybenzpyrenes

Rat liver oxidizes 1-, 2-, 4-, 5-, 6-, 7-, 8-, 9-, 10- and 11-hydroxybenzpyrene to free radicals. The formation of radicals from 1-, 4-, 9- and 11-hydroxybenzpyrene requires NADPH [B476].

2.4 *Oxidation of nuclear amino groups and analogues*

Formation of substituted hydroxylamines

$$R_1R_2NH + O_2 \rightarrow R_1R_2NOH$$

Dibenzylamine is substrate for liver microsomal enzyme in guinea pig, rabbit, hamster, mouse and chick, but it is virtually absent from cat liver. In rabbit the optimum pH is 6.9 with NADPH as cofactor, and 7.7 with NADH as cofactor. Inhibitors for one or both systems include cyanide, *p*-chloromercuribenzoate, FMN and to a lesser extent cysteine, N-ethylmaleimide, l,10-phenanthroline, azide, imidazole and SKF 525-A [A1737].

Mouse and pig liver enzymes contain FAD, require NAD(P)H, with an optimum at about pH 9 [D446]. Substrates include N-methyl- and

N-ethylaniline and various secondary aliphatic amines, with oxygen as oxidizing agent. It is solubilized from microsomes with Triton X-45 and Triton X-102 [Kl60].

Aniline is substrate for a rabbit liver microsomal enzyme. Inhibition by acylation using diethyl pyrocarbonate is partially reversed by hydroxylamine, and is prevented by pyridine. Photo-inactivation occurs in the pH range 6–8 with rose bengal as photon acceptor [A1746].

Maize microsomes N-hydroxylate 2-hydroxy-1,4-benzoxazin-3-one, with optimum pH 7.5. The enzyme appears to be a NADPH-requiring P450 [G245].

There are many publications dealing with N-hydroxylation of primary amines of polynuclear hydrocarbons and their amides, in particular carcinogens, such as 1- and 2-aminonaphthalene, 4-biphenylamine and 2-aminofluorene. Few studies have been carried out at an enzyme level beyond determining that hydroxylation of 2-aminonaphthalene by pig liver microsomes requires oxygen and NADPH [A1791]. In addition, this reaction type has been observed in beef, dog, monkey, guinea pig, man, mouse and hamster; and bladder is a further organ in which it occurs [A880, B172, B179, C397, C727, D738].

N-Oxide formation (dimethylaniline monooxygenase (N-oxide-forming); E.C. 1.14.13.8)

$$R_1R_2R_3N \rightarrow R_1R_2R_3NO$$

Human foetal liver N,N-dimethylaniline-oxidizing activity requires NADPH. It is not inhibited by CO, which indicates that it is not a P450 enzyme [A1143].

N,N-Dimethylaniline is substrate for a rabbit liver microsomal enzyme. Inhibition using diethyl pyrocarbonate is partially reversed by hydroxylamine and is prevented by pyridine. Photo-inactivation occurs in the pH range 6–8 with rose bengal as photon acceptor [A 1746]. The enzyme system is composed of P448, NADPH-cytochrome c reductase and a lipid cofactor. The authors of this work postulate the existence of two N-oxide forming microsomal systems, one a haemoprotein and the other a flavoprotein oxidase. The flavoprotein is more stable at 37° and pH 7.4 than the P450, which, after solubilization is separable into two fractions, one of which is far less stable than the other. Both the P450 and the flavoprotein systems have similar activity [A3161, B230]. Lung activity, optimum pH 8.9, is three times greater than in liver. Lung enzyme is stimulated by Mg^{2+} and, surprisingly, by low concentrations of Hg^{2+}, whereas both these ions inhibit liver enzyme. Both are activated by 1 mM Ni^{2+} and inhibited by 10 mM Ni^{2+} [A1144].

Mouse liver dimethylaniline-oxidizing activity increases threefold just after birth, and then only slightly until 15 days post-partum. In males it is then near the adult level. In females it increases by a further 50% to the adult level by 25 days post-partum [A2498].

Mouse and pig liver microsomal enzymes, optimum pH about 9, contain FAD and require NAD(P)H. Substrates include N,N-dimethyl- and N,N-diethylaniline, and imipramine [D446]. Pig liver enzymes appears to be the same as alkylhydrazine N-oxidase [A1041].

Oxidation of *p*-phenylenediamines

This type of reaction has been extensively studied, but few have studied the reaction products. A free radical is likely to be the initial product, but in lieu of further information the product is recorded as a quinone in the compounds section for the sake of completeness, although this may be incorrect.

Beef lactoperoxidase acts on N,N-dimethyl-*p*-anisidine with ethyl hydroperoxide as oxidant in the presence of bromide. The product is *p*-quinone. It is considered that the peroxidase releases bromine, which is the oxidizing species [F500].

Nitrosomonas europaea enzyme, molecular weight 127 500, subunit molecular weight 40 100, and pI 4.63 contains copper. It utilizes oxygen in the oxidation of *p*-phenylenediamine, presumably to a free radical [D564]. Caeruloplasmin shows similar activity [A677]. Peach, spruce, Botrytis,

Trametes, and Coriolus versicolor laccases oxidize *p*-phenylenediamine [A1930, A3974, E369].

Oxidation of *o*-dianisidine

Peroxidases from Arachis oxidize *o*-dianisidine; the identity of the product is uncertain. Four isozymes are found with pH optima at 4, 4.4, 6, and 6.4 [A2519].

p-Benzoquinone imine formation

Human P450 oxidizes paracetamol to an active intermediate. Trapping with glutathione indicates that it is N-acetyl-*p*-benzoquinone imine [K330].

Oxidation of amino to nitroso groups

Human haemoglobin oxidizes *p*-chloroaniline and 3,4-dichloroaniline to nitrosobenzenes and nitrobenzene [C879].

Rat liver microsomes oxidize *p*-toluidine to 4-methylnitrosobenzene [G580].

Pea seed microsomes oxidize *p*-chloroaniline to *p*-chlorophenylhydroxylamine and *p*-chloronitrosobenzene, as well as to *p*-chloronitrobenzene; it was demonstrated that this represented a stepwise oxidation sequence. Nitrosobenzenes were also formed from aniline, *p*-toluidine, *p*-bromobenzene and 3,4-dichloroaniline [C797].

Chloroperoxidase, with peroxide, oxidizes *p*-chloroaniline to *p*-chloronitrosobenzene with optimum pH 4.4 [A3838]. A similar reaction is observed with a series of *para*-substituted anilines [A3579].

Oxidation of amino to nitro groups

$$R.NH_2 \rightarrow R.NO_2$$

Human oxyhaemoglobin oxidizes *p*-chloroaniline to *p*-chloronitrobenzene, apparently with *p*-chloronitrosobenzene as intermediate; the same reaction was observed with 3,4-dichloroaniline. The reaction is claimed to be a peroxidase type [C879].

Rat liver microsomes oxidize dapsone to 4-amino-4′-nitrodiphenylsulphone, and rat and chicken liver microsomes oxidize 4-amino-4′-ureidodiphenylsulphone to 4-nitro-4′-ureidodiphenylsulphone [A970].

Nitrosomonas oxidizes aniline to nitrobenzene [H219].

Serratia marcescens chloroperoxidase oxidizes 2- and 4-aminophenol, 2-, 3- and 4-chlorophenol, *p*-toluidine and *p*-aminobenzoate to the corresponding nitro compounds in high yield [K143].

Pseudomonas putida bromoperoxidase acts on aniline and peroxide to form azobenzene, azoxybenzene and nitrobenzene; it is suggested that this is the reaction sequence [H12].

Oxidation of hydroxylamines to nitro groups

Rat and rabbit liver oxidize N-hydroxyphentermine to 2-nitro-1-phenylpropane. It appears that superoxide is the oxidizing species; superoxide dismutase is inhibitory, and peroxide is not involved. It is thought that the reaction may be non-enzymatic [B654]. Rat liver microsomal enzyme is inhibited by haemoglobin, catalase or carbon monoxide [A3671].

Rabbit liver acts on N-hydroxyamphetamine [A3621].

Oxidation of hydroxylamino to nitroso groups

Rat haemoglobin oxidizes 4-hydroxylaminobiphenyl to 4-nitrosobiphenyl [G5].

Chloroperoxidase, with peroxide, oxidizes *p*-chlorophenylhydroxylamine to *p*-chloronitrosobenzene; the reaction is more rapid than with *p*-chloroaniline as substrate [A3838].

Oxidation of hydroxylamino to nitro groups

Ram seminal vesicle oxidizes 2-hydroxylaminofluorene to 2-nitrofluorene [C754].

Oxidation of nitroso to nitro groups

Ram seminal vesicle oxidizes 2-nitrosofluorene to 2-nitrofluorene [C754].

Mouse oxidizes 1-nitrosopyrene to 1-nitropyrene [E721].

Aniline conversion into azobenzenes

Horseradish peroxidase and Geotrichum candidum aniline oxidase both oxidize aniline and a range of substituted anilines, particularly those substituted with halogens. These are converted into azobenzenes [A661]. Geotrichum candidum aniline oxidase and peroxidase both oxidize aniline to azobenzene, optimum 5.0 (with oxygen) and pH 4.5 (with peroxide) respectively [A690].

Pseudomonas putida bromoperoxidase acts on aniline and peroxide to form azobenzene [H12].

Human placenta and Glycine max lipoxygenases act on 4-aminobiphenyl and linoleate to form 4,4′-azobis(biphenyl). A radical reaction appears to be involved [J95].

Ram seminal vesicle and horseradish peroxidase both oxidize 2-aminofluorene to 2,2′-azobisfluorene [C754].

Oxidation of azo to azoxy compounds

Azobenzene N-oxidase is found in (in reducing order) hamster, guinea pig, mouse, rabbit and rat. The reaction has been observed in liver, lung, heart and kidney and the activity in hamster liver is mainly microsomal. Substrates (in reducing order) are ω,ω′-azotoluene, ω-(phenylazo)toluene and azobenzene [G258, G259].

Nitrone formation

Hamster liver microsomes catalyze the formation of nitrones from some but not all benzanilides. These include benzanilide, 4-chlorobenzanilide, 4-methylbenzanilide, 2,4,6-trimethylbenzanilide, 2′,4′-dichlorobenzanilide and 2′,6′-dichlorobenzanilide [G951].

Nitroxide radical formation

$$R.NH_2 \rightarrow R.NH\text{–}O$$

Rabbit liver microsomes oxidize a range of carcinogenic amines including 2-aminofluorene, 2-aminonaphthalene, 2-aminoanthracene, 4-aminostilbene, 4-aminoazobenzene and benzidine as well as aniline, N-methylaniline and phenacetin to the corresponding nitroxide radicals. The reaction requires the participation of NADPH [B184].

2.5 *Oxidation of heterocyclic amines*

Hydroxyindole oxidase

An enzyme in Mytilus edulis oxidizes indoles such as serotonin, 5-hydroxytryptophan, psilocin and 5-hydroxyindole, presumably to pigments. Mono- and diphenols, such as adrenaline, L-dopa, tyrosine and *p*-coumarate are also substrates. The enzyme contains Cu and haem in a 1:1 ratio, and appears to require peroxide, but not a pyridine nucleotide. It is inhibited by copper-chelators [B314].

2.6 *Reduction of nitro groups and analogues*

Reduction of nitro compounds to anilines

$$R.NO_2 \rightarrow R.NH_2$$

This reaction often, if not always, involves the formation of intermediate nitroxides and hydroxylamines, although in many studies these intermediates were not detectable.

Human placenta reduces *p*-nitrobenzoate to *p*-aminobenzoate. Fractionation indicates that

the active enzymes are haemoglobin or methaemoglobin. Studies with pure proteins found that the reaction can be catalyzed by haem-containing proteins such as methaemoglobin, metmyoglobin and cytochrome c, with NADPH as reducing agent. Placental reduction and the haem-model system (haematin, NADPH, FMN and *p*-nitrobenzoate) are inhibited by carbon monoxide [A621].

Formation of *p*-aminobenzoate from *p*-nitrobenzoate is observed in conventional rats, but is, relatively, very low in germ-free animals. Studies with microorganisms have found reduction by the gut flora Lactobacillus plantarum, Bacteroides fragilis, Peptostreptococcus productus, Clostridium, Proteus mirabilis, S. faecalis and E. coli [A124]. The reduction rate in rat gut wall and contents is reduced by treatment with oral antibiotics, whereas liver activity is unaffected [A3480].

Rat liver microsomal reduction of *p*-nitrobenzoate is inhibited by carbon monoxide and oxygen; presumably the enzyme is a P450. The reaction is enhanced four-fold by haemoglobin (boiled or native) and haemin. In contrast, azoreductase acting on neoprontosil is not activated in this manner [A3049].

Rabbit liver microsomal P450 reduces 1-nitropyrene and 2-nitrofluorene; the reaction requires NADPH (NADH is a poor cofactor). A cytosolic reductase has been identified as aldehyde oxidase, with electron-donating co-substrates. N′-Methylnicotinamide is best, but methotrexate, 2-hydroxypyrimidine and a series of aldehydes can also be used, but not NAD(P)H [C702]. Liver aldehyde oxidase (E.C. 1.2.3.1) also reduces 1-nitropyrene and 3-nitrofluoranthrene. FMN and FAD are alternative cofactors; oxygen is inhibitory. The intermediate nitroso and hydroxylamino analogues have been detected [G361].

p-Nitrobenzoate is reduced in the nematode Ascaris lumbricoides. Activity is found in the intestinal brush border but not in other tissues. The enzyme is cytosolic, it has a stability range of pH 4–7 (it rapidly loses activity at 0° outside this range), and has a sharp optimum at pH 6.5. It requires NADH, a low molecular weight thiol such as glutathione and a divalent cation such as Mn^{2+} or Cu^{2+}; NADPH is not a cofactor [A349]. Its molecular weight is about 130 000. A large range of nitrobenzenes and analogues are reduced to the corresponding anilines, and no intermediates are detected. This activity could not be separated from azoreductase by ammonium sulphate fractionation [A304].

Mouse and sheep liver, Ascaris suum and Moniezia expansa enzymes require NADH and GSH for the reduction of disophenol, nitroxynil and nitrodan [A3694]. The same species (except A. lumbricoides) reduce a range of nitrobenzanilides, all at about 10 per cent of the rate for *p*-nitrobenzoate [A2037].

Moniezia expansa enzyme acts on nitrobenzene and a range of substituted nitrobenzenes, with optimum pH 6.4–6.7; the preparation was free from xanthine and aldehyde oxidase activities. It was stimulated by hypoxanthine, and inhibited by FAD, FMN, riboflavin, allopurinol, dicoumarol, 5-nitro-2-furaldehyde, azide and cyanide [A1785]. The enzyme, molecular weight 125 000, is cytosolic, requires NADH (NADPH is not so good), and glutathione or cysteine. It is not inhibited by oxygen, carbon monoxide, EDTA or by azide [A1741]; the properties are so similar to those of azoreductase that they may be the same enzyme. M. expansa (pI 4.50) and Ascaris lumbricoides (pI 4.75) azo and nitroreductases could not be separated by isoelectric focussing [A1792].

Bacteroides fragilis contains four isozymes that reduce 1-nitropyrene to 1-aminopyrene. Isozyme I, molecular weight 52 000 and optimum pH 7.5, requires NADH for activity. The corresponding parameters, respectively, for isozyme II are 320 000, 6.3 and NADPH, for isozyme III 180 000, 7–8 and NADPH, and for isozyme IV 680 000, 5–9 and NADPH [C791].

E. coli contains four isozymes that reduce 1-nitropyrene to 1-aminopyrene, with NAD(P)H as co-substrate. Additionally, they appear to reduce FAD, and three of the isozymes reduce nitrofurazone [D217].

Reduction of nitro compounds to hydroxylamines

Spinach leaf ferredoxin: NADP oxidoreductase (E.C. 1.18.1.2) reduces nitrobenzene stoichiometrically to phenylhydroxylamine [J501].

Rat nitroquinoline-N-oxide reductase (E.C. 1.6.6.10), optimum pH 6.4, is highly specific. Supernatant enzyme (found in many tissues) requires NAD(P)H, and the minor, microsomal enzyme requires NADH, and utilizes two mol of co-substrate [K903].

Dog and human liver microsomes reduce N-hydroxysulphamethoxazole to sulphamethoxazole with NADH as co-substrate; NADPH is not so good. The enzymes from both species appear to have both low and high affinity components. They are not inhibited by oxygen, carbon monoxide, azide, or by other P450 inhibitors [K338].

Phenylhydroxylamine is reduced to aniline in rat and quail [B174, B175].

Reduction of nitroso compounds to hydroxylamines and amines

Human erythrocytes condense nitrosobenzene with glutathione to form glutathione sulphinanilide, a reaction that is probably non-enzymatic. This compound is reduced by two mol of NADPH to form aniline, as well as glutathione and glutathione sulphinate [B177, B228].

Rat liver reduces nitrosobenzene to phenylhydroxylamine and aniline [B174] and 1-nitrosonaphthalene to 1-naphthylhydroxylamine [A2173].

Horse liver alcohol dehydrogenase reduces 2-nitrosofluorene to 2-hydroxylaminofluorene and 2-aminofluorene, and *p*-nitrosophenol to *p*-aminophenol [H291].

Mouse reduces 1-nitrosopyrene to 1-aminopyrene [E721].

Reduction of hydroxylamines to amines

Mouse liver enzyme reduces 4-hydroxylaminoquinoline-1-oxide to 4-aminoquinoline-1-oxide. The activity is increased by administering molybdenum salts, and reduced by tungsten salts. It is suggested that, as with the other molybdenum-containing enzymes, xanthine oxidase and sulphite oxidase, tungsten slowly reduces the body load of molybdenum, thereby reducing the availability of molybdenum for the enzyme [A3227].

Reduction of hydroxylamides to amides

Rat liver microsomal reductase, which acts on N-hydroxy-2-acetamidofluorene to form 2-acetamidofluorene, requires NADPH. It is inhibited by oxygen and carbon monoxide; inhibition and induction studies suggest that it belongs to the P450 group, probably a P448. Activity is also found in lung, kidney and small intestine, and in decreasing order in hamster, guinea pig, rabbit, rat and mouse [A3965].

Horseradish peroxidase and horse cytochrome c catalyze a complex series of reactions with N-hydroxy-2- and 3-acetamidofluorenes as substrates. It is postulated that a free radical (apparently a nitroxyl radical, with the acetyl moiety still *in situ*) formed by the action of peroxide undergoes dismutation to form the corresponding nitroso, acetamido and N-acetoxyacetamidofluorenes [D32]. A similar series of complex reactions is found in rat and rabbit with N-hydroxy-2-acetamidofluorene, N-hydroxy-4-acetamidobiphenyl, N-hydroxyphenacetin and N-hydroxy-4-chloroacetanilide as substrates [B178].

Rabbit blood reduces both N-hydroxy-2-acetamidofluorene and N-hydroxyphenacetin to the parent amines, using NAD(P)H and FAD, and the reaction is inhibited by oxygen and carbon monoxide. Haemoglobin and catalase (native or boiled) catalyse the reaction; it is postulated that the reduction is a direct action of the haem moiety [K111].

N-Oxide reduction

Rat liver cytosolic 4-(N,N-dimethylamino)azobenzene-N-oxide reductase is a tetramer, molecular weight 370 000 and requires NADPH for oxygen removal; other N-oxides tested were not substrates. Lower activities are found in other tissues [E187].

A rat liver mitochondrial enzyme, bound to the inner membrane, requires NAD(P)H and reduces dimethylaniline-N-oxide as well as aliphatic N-oxides. The activity is also found in microsomes, but the relative reaction rates for the substrates are different from those in mitochondria. It is inhibited by oxygen, and partially by carbon monoxide [A1913].

Rat liver microsomal enzyme, apparently a P450, reduces dimethylaniline-N-oxide. It requires NADH, and is inhibited by oxygen or carbon monoxide. It also reduces imipramine-N-oxide [A1847].

A cytochrome c reduces dimethylaniline-N-oxide [B185].

Reduction of N-nitroso compounds

Rabbit liver converts N-nitrosodibenzylamine into bibenzyl, which is thought to be a breakdown product of an unstable 1-hydroxy-2, 2-dibenzylhydrazine [A3868].

Azobenzene reductase (E.C. 1.6.6.7)

$$Ar–N=N–Ar' \rightarrow ArNH_2 + Ar'NH_2$$

Rat microsomal enzyme reduces a range of substituted azobenzenes, including methyl red, *p*-methyl red and methyl orange [G511]. A liver enzyme that acts on methyl red but not on analogues lacking an *o*-carboxyl group is probably dimeric, monomeric molecular weight 30 000, and contains two mol FAD/mol [B28]. A reductase has been detected with an optimum at pH 6.2 [A2351]. Liver DT diaphorase (E.C. 1.8.1.4), molecular weight 30 000, reduces methyl red but not butter yellow [A2730].

Rabbit liver cytosol aldehyde oxidase (E.C. 1.2.3.1) acts as an azoreductase towards methyl red, amaranth, methyl orange and *p*-dimethylaminoazobenzene, with an electron donor such as acetaldehyde as second substrate [C884].

In perfused rat liver neoprontosil is reduced to sulphanilamide. It requires a pO_2 less than 200 mm for maximal activity, and above 400 mm the enzyme is inactive. This may explain previously reported low activities in liver [A3048].

Methyl red azoreductase is present in liver cytosol from rat, guinea pig, rabbit and hamster, but the activity in mouse and sheep liver is much lower. Microsomal enzyme activity is similar to that in cytosol, but is less variable between species. Particularly in rat, but less so in mouse, 3-methylcholanthrene induces both cytosolic and microsomal enzymes [B187].

Moniezia expansa enzyme acts on azobenzene and a range of substituted azobenzenes, with optimum pH 6.4–6.7; the preparation was free from xanthine and aldehyde oxidase activities. It is stimulated by hypoxanthine, and inhibited by FAD, FMN, riboflavin, allopurinol, dicoumarol, 5-nitro-2-furaldehyde, azide and cyanide [A1785]. The enzyme, molecular weight 125 000, is cytosolic, requires NADH (NADPH is not so good), and glutathione or cysteine. It is not inhibited by oxygen, carbon monoxide, EDTA or azide [A1741]; the properties are so similar to those of nitroreductase that they may be the same enzyme. M. expansa (pI 4.50) and Ascaris lumbricoides (pI 4.75) azo and nitroreductases could not be separated by isoelectric focussing [A304, A1792].

A Pseudomonas enzyme, molecular weight in the range 20 000–22 000 and optimum pH 6.2–6.8 depending on the substrate, requires NAD(P)H. Studies with 1-naphthols substituted at the 4-position with the azo moiety found that absence of the 1-hydroxyl or the presence of a hydroxyl in another position may reduce the activity to zero. Phenolic analogues are also inactive [D180].

Cautobacter subvibrioides enzyme has a molecular weight of about 30 000 [K314].

Shigella dysenteriae contains two azoreductases. One is a dimer, molecular weight 28 000, and the other a monomer, molecular weight 11 000. Both require NAD(P)H and are flavoproteins containing one mol FMN/mol. Substrates are Ponceau SX, Tartrazine, Amaranth and Orange II [G767].

Azide reduction

In man, the azo group in azidomorphine is reduced to an amino group [A3050].

Mouse reduces *m*-azidopyrimethamine to the *m*-amino analogue [F319].

Substituted hydroxamates from nitroso compounds

In this reaction nitrosobenzenes are converted into N-substituted hydroxamates; the oxo group is reduced to a hydroxyl, with N-conjugation.

Rat liver enzyme is associated with an organelle larger than microsomes (mitochondria?), and requires glucose-6-phosphate as the energy source. 4-Chloronitrosobenzene forms N-(4-chlorophenyl)glycollhydroxamate [B130]. A similar reaction occurs with aryl-substituted nitrosobenzenes and several 2-oxoacids such as pyruvate, with elimination of the carboxyl group and the formation of N-aryl-N-hydroxyacylamides. For instance, 2-oxoisocaproate and nitrosobenzene form N-hydroxy-N-phenylisobutyramide [J429].

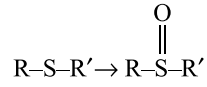
In Chlorella both nitrosobenzene and phenylhydroxylamine are substrates, but it appears that phenylhydroxylamine conversion to nitrosobenzene occurs first. Both N-phenylacetohydroxamate and N-phenylglycollhydroxamate are formed. It is postulated that 'active acetaldehyde' and 'active glycollaldehyde' (presumably bound to thiamine) are involved as co-substrates [A3531].

Yeast enzyme appears to be a pyruvate decarboxylase (E.C. 1.2.4.1), with α-hydroxyethylthiamine as coenzyme [A2344].

2.7 *Oxidation and reduction of sulphur atoms*

Few of the reactions in this section have been studied at an enzyme level. The examples quoted for each reaction are purely illustrative.

Oxidation of thioethers to sulphoxides



A soluble enzyme that oxidizes chlorpromazine is found in guinea pig liver and serum, but only in small amounts in kidney, spleen and pancreas; it is not a P450. The molecular weight is 85 000, with an optimum at pH 7.4. It is rapidly inactivated at 50° [A1353].

In mouse liver, Ascaris suum and Moniezia expansa fenbendazole, albendazole, bithionol and phenothiazine are oxidized to sulphoxides, optimum pH 7.0–7.2 [A3849].

Mouse and pig liver microsomal FAD-containing monooxygenases, optimum pH about 9, require NAD(P)H, and oxidize nitrogen and sulphur atoms. Substrates include thioanisole, benzyl methyl sulphide, diphenyl sulphide, benzyl disulphide, benzyl mercaptan, 2-mercaptobenzimidazole, phenylthiocarbamide and thiocarbanilide [D446].

Rabbit (the enzyme source may be liver) flavin-containing monooxygenase acts on *p*-tolyl and 2-naphthyl thioethers with methyl or ethyl thio substituents. The reaction rate rapidly falls as the length of the alkyl group increases [H484].

Rat liver microsomal albendazole monooxygenase (E.C. 1.14.13.32) contains FAD; it is not a P450 [K749]

An enzyme (source unclear) converts promazine and chlorpromazine into cation radicals which disproportionate, with sulphoxides as one product [K386].

Horseradish peroxidase forms sulphoxides from thioanisole and *para* substituted thioanisoles, with peroxide as co-substrate. The substituents were methyl, chloro, acetamido, acetoxy, nitrile and nitro groups [E403].

Oxidation of sulphoxides to sulphones

Many sulphur-containing drugs are oxidized to the corresponding sulphones, and the intermediate sulphoxides are sometimes detected.

In rat and dog liver butaperazine is oxidized to the sulphone, a sulphoxide is the presumed intermediate [A295].

In mouse liver, Ascaris suum and Moniezia expansa, albendazole sulphoxide is further oxidized to the sulphone [A3849].

Dimerization of thiophenol (thiol oxidase; E.C. 1.8.3.2)

$$ArSH \rightarrow ArSSAr$$

Horseradish peroxidase and mushroom tyrosinase oxidize thiophenol to diphenyl disulphide [J593].

Reduction of sulphoxides

Many sulphinyl analogues of drugs and xenobiotics, unlike sulphones, are reduced to the parent thio compound, for instance N-methylsulphinylbenzamide in rat [D705], and sulphinylpyrazole in mammalia and microorganisms [B711, E241, H560].

In mouse liver, Ascaris suum and Moniezia expansa the sulphoxides of fenbendazole, albendazole, bithionol and phenothiazine are reduced to the parent compounds, optimum pH 7.2–7.4 [A3849].

Reduction of disulphide bond

Rat liver mitochondria reduce 5,5′-dithiobis(2-nitrobenzoate) to 5-mercapto-2-nitrobenzoate [D611].

Methylthio incorporation

Rat liver converts N-hydroxy-2-acetamidofluorene into 2-amino-3-methylthiofluorene, with N-acetylmethionine as co-substrate. The first reaction appears to be:

$$R\text{–}\underset{\displaystyle OH}{\underset{|}{N}}\text{–}COCH_3 \rightarrow R\text{–}NH\text{–}O\text{–}COCH_3$$

The product then reacts with N-acetylmethionine to form a sulphonium condensate, with the sulphur atom bound to position 3 of the fluorene moiety, which then, by fission of the S–C bond in the methionine moiety forms 2-amino-3-methylthiofluorene. A similar reaction is observed with N-hydroxy-4-acetamidobiphenyl as substrate [A729].

2.8 *Reduction of quinones and analogues*

Quinone reductases (NAD(P)H: quinone oxidoreductase, E.C. 1.6.99.2, 1.6.99.5 and 1.6.99.6)

$$Quinone \leftrightarrow quinol$$

Human erythrocyte NAD(P)H dehydrogenases reduce *p*-quinone, but rather poorly [B260].

Rat liver mitochondrial reductase forms the quinol from 5-demethylubiquinone 9, with NADH as co-substrate [A3084].

Guinea pig lens $NADPH_2$: quinone reductase (E.C. 1.5.5.5) is ζ-crystallin, which requires oxygen and NADPH, with peroxide and superoxide as products. A range of quinones and 2,6-dichlorophenolindophenol are substrates [K773].

Ubiquinol cytochrome-c reductase (E.C. 1.10.2.2) has been reviewed [K816]. Beef heart enzyme is composed of many isozymes, seven of which have molecular weights in the range 4000–29 000 [K930].

Pig liver mitochondrial electron-transferring flavoprotein dehydrogenase (E.C. 1.5.5.1), optimum pH 5.2 and molecular weight 69 000–73 000 (dependent on method) acts on ubiquinone. Its amino acid composition has been determined [K814].

Sporotrichum pulverolentum enzyme reduces a series of quinones including *p*-quinone,

toluquinone, methoxyquinone, 1,4-naphthoquinone, menadione and 4,5-dimethoxy-*o*-quinone [B301].

Phanerochaete chrysosporium enzyme is soluble, possibly a homodimer, molecular weight 44 000, optimum pH 5.0–6.5 and pI 4.3, which contains flavin mononucleotide and requires NAD(P)H. Substrates are 2-methoxy- and 2,6-dimethoxy-*p*-quinone, and menadione [H611].

Hydrogen: quinone oxidoreductase (E.C. 1.12.99.3)

Wolinella succinogenes enzyme utilizes molecular hydrogen to reduce 2,3-dimethyl-1,4-naphthoquinone. This cytoplasmic membrane enzyme is composed of three proteins including cytochrome b [K772].

Benzpyrene-3,6-quinone reduction

Rat liver microsomes reduce this quinone to benzpyrene-3,6-diol, with NADPH as co-substrate [A3637].

Rabbit liver morphine 6-dehydrogenase reduces polynuclear quinones with NAD(P)H as coenzyme, but does not reduce *p*-quinones [H920].

Dichlorophenolindophenol (quinone imine) reduction (DT diaphorase; NAD(P)H dehydrogenase (quinone), E.C. 1.6.99.2)

2, 6-Dichloroindophenol →
N-(3, 5-dichloro-4-hydroxy)-4-hydroxyaniline

Two human erythrocyte NAD(P)H dehydrogenases, molecular weight about 18 000, reduce a range of substrate types including 2,6-dichlorophenolindophenol [B260]. The rat liver enzyme exhibits complex kinetics, which possibly involves two separate active sites and the interconversion of heat- and cold-stable forms [A2223].

Rat liver cytosolic quinone reductase, which requires NAD(P)H, reduces N-acetyl-*p*-benzoquinone imine, 2-amino-1,4-naphthoquinone imine, N,N-dimethylindoaniline and 2-acetamido-N,N-dimethylindoaniline [E214].

Bacillus stearothermophilus NADH: dichlorophenolindophenol oxidoreductase is a flavoprotein, molecular weight 43 000, activated by FMN or cyanide. It is inhibited by EDTA or *p*-chloromercuribenzoate, but it is stable up to 70° [B725].

Phanerochaete chrysosporium benzoquinone reductase also exhibits this activity [H611]. This reaction has been detected in Escherichia [A1228], beef [A1899], Diphyllobothrium [A679], Pseudomonas [A2952], Saccharomyces cerevisiae [K229], guinea pig [K773] and Eubacterium [B426].

Xanthommatin reductase (E.C. 1.3.1.41)

Drosophila melanogaster enzyme, which utilizes NADH, forms 5,12-dihydroxanthommatin by reduction of the quinoneimine moiety [E192].

2.9 *Halogens and the aromatic nucleus*

Halogenation

The thyroid hormone thyroxine is formed by the incorporation of iodide into tyrosyl residues of the protein thyroglobulin; this is explored in an extensive early literature.

Human neutrophil myeloperoxidase acts on ticlopidine both to dechlorinate and to introduce a further chlorine in the 2 position [K53].

Iodinating enzyme present in goat submaxillary gland appears to be iodide peroxidase (E.C. 1.11.1.8), optimum pH 4. It iodinates L-tyrosine and L-3-iodotyrosine, as well as exchanging labelled iodine in 3,5-diiodotyrosine with inorganic iodine [A997].

Glycine max seed coat peroxidase acts on veratryl alcohol, with bromide and peroxide, to form 2-bromo-4,5-dimethoxybenzyl alcohol quantitatively, with optimum pH below 2.5.

Pyrazole and indole are also brominated; iodide but not chloride can substitute for bromide [K439].

Bromoperoxidase (non-haem type) from the red alga Corallina pilulifera catalyses a variety of reactions. Anisole is brominated at all the nuclear positions, 1-methoxynaphthalene is 4-brominated, phenol and salicyl alcohol yield 2,4,6-tribromophenol. In addition styrene and analogues are brominated on the side-chain [E597].

Ulva lactuca (a green marine alga) bromoperoxidase forms 2,4,6-tribromophenol from phenol, and for a series of phenols with carbon side chains at the *ortho* and *para* positions (listed below) the side chains are replaced by bromine. Phenol forms *o*- and *p*-bromophenol, 2,4- and 2,6-dibromophenol as intermediates. In contrast, *o*-hydroxybenzyl alcohol forms *o*-, but little *p*-bromophenol. *p*-Hydroxybenzaldehyde forms *p*-bromophenol. *p*-Hydroxyphenylacetate forms a little *p*-bromophenol, a trace of 2,4-dibromophenol, but no 2,6-dibromophenol. *p*-Hydroxybenzoate and *p*-hydroxybenzyl alcohol form *p*-bromophenol and 2,4-dibromophenol, but no *o*-bromophenol or 2,6-dibromophenol [K153].

Pseudomonas putida bromoperoxidase acts on aniline with bromide and peroxide to form *o*- and *p*-bromophenol; other anilines are not substrates. In the absence of bromide azobenzene, azoxybenzene and nitrobenzene are formed [H12].

Streptomyces venezuelae bromoperoxidase-catalase (a homogeneous enzyme), molecular weight about 130 000, appears to be a dimer, pI 4.5 and optimum pH 6.9. It brominates 2-(3,5-dibromo-2-methoxyphenyl)-1-methylpyrrole to form one pentabromo and two tetrabromo analogues. The position of the bromo substituents is not known, but some appear to be on the aromatic nucleus [F276].

Chlorination by molecular chlorine

Myeloperoxidase in human neutrophils generates molecular chlorine with peroxide and chloride; the chlorine reacts with L-tyrosine to yield 3-chloro-L-tyrosine [J226]. The potential scope of this reaction for synthetic chemistry is enormous, in which free halogens can react with a large range of compounds under controlled conditions.

Deiodination of thyroxine and analogues (without hydroxylation; E.C. 1.11.1.8 and 3.8.1.4)

Rat liver type I enzyme deiodinates thyroxine and a series of partially deiodinated analogues and their O-sulphate and N-sulphonate conjugates [G337]. Deiodination of the outer ring of thyroxine and analogues is optimal at pH 6–6.5; inner ring deiodination is optimal at above pH 8.5, whereas inner ring deiodination of T_3 ocurs at pH 8 [A3752]; a second apparent optimum for rT_3 of 4.5 with no apparent formation of halogenated products at physiological pH is an experimental artifact arising from the rapid disappearance of rT_3 at physiological pH under the conditions used [A3117, A3549]. A monomeric 5′-deiodinase, molecular weight 56 000 appears to be a metalloenzyme, possibly containing iron [F821]. The observed similarities between 5′-deiodination of rT_3 and rT_2 in rat liver suggest that a single enzyme is involved [B833]. No cofactors were detected in one study, nor was oxygen involved. Inhibition has been observed with both particulate and cytosolic enzymes using Zn^{2+} or propylthiouracil, but not with α-methyltyrosine [A3312, A3549, A3889].

Solubilized liver microsomal 5′-deiodinase has a molecular weight of 55 000 and pI 5.7 [F802]. Another study claims that both 5- and 5′-deiodinase activities are entirely microsomal [B504]. Parenchymal cell microsomal enzymes convert thyroxine into T_3 and rT_3, both of which are further converted into 3,3′-T_2, the deiodination of rT_3 being by far the fastest [B126]. Another study reports that the molecular weight of solubilized microsomal enzyme is 65 000 or 200 000, depending on the method; the reason for the differencies between these results is obscure [B427]. A further study on microsomal enzyme found that it is a lipoprotein that requires Fe^{2+}, but it is not a P450 [A1095].

A rat enzyme that deiodinates T_2 to T_1 is found mainly in liver. Some is microsomal, but most of the activity is associated with the plasma membrane. It is stimulated by dithiothreitol and inhibited by oxygen. It is claimed that its properties closely resemble those of 5′-deiodinase [C108].

Liver, thyroid and kidney enzymes that 5′-deiodinate iodothyronines contain one mol of selenium/mol, presumably present as selenocysteine [F882]. Astrocyte type III iodothyronine deiodinase, which removes an iodine from the inner ring of triiodothyronine is also a selenoprotein [J197].

Glial cell Type I deiodinase is a dimer, with monomeric molecular weight of 27 000, and Type II a hexamer, monomeric molecular weight 29 000. Both are membrane-bound [G121].

5′-Deiodinase from rat cerebral cortex appears to involve two activities, one with low affinity and the other with high affinity [B914]. Its optimum pH is 8.0, and it requires dithiothreitol. Its distribution through the brain is different from that of thyroxine and T_3 5-deiodinases [C48].

Rat pineal 5′-deiodinase has an optimum pH of 6.5 [E104].

Rat 5′-deiodinase (type 3) activity is found in the pituitary; the enzyme acting on thyroxine may be different from the one that deiodinates rT_3 [D79]. In pregnant rat uterus, Type 3 deiodinase at day nine of pregnancy is found in mesometrial and antimesometrial decidual tissue. At days 12 and 13 it is localised to epithelial cells lining the uterine lumen [K69].

Human kidney microsomal thyroxine 5′-deiodinase has an optimum at pH 6.5. Another enzyme, a 5-deiodinase, forms rT_3 [E193].

In beef cattle the conversion of T_4 into T_3 is most active in liver, with lesser activity in kidney. Trace activity is found in muscle [D461].

In monkey hepatocarcinoma deiodination of the outer ring of thyroxine and analogues is optimal at pH 6.3; inner ring deiodination is optimal at pH 7.9; activity is enhanced by dithiothreitol and inhibited by Zn^{2+} [A3889].

Reductive dehalogenation

3-Chloro-4-hydroxybenzoate → *p*-hydroxybenzoate

Desulfitobacterium chlororespirans dehalogenase, optimum pH 6.5, fulfils the entire energy requirements for the growth of this organism. The best co-substrate reductant is reduced methylviologen. It dechlorinates a series of chlorinated benzoates, phenylacetates and phenols *ortho* to the hydroxyl group [J232].
D. dehalogenans enzyme, optimum pH 8.2, also requires reduced methyl viologen as electron donor. It acts on a range of chlorinated phenols, and converts 3-chloro-4-hydroxyphenyl acetate into 4-hydroxyphenyl acetate [K247].

Desulfomonile tiedje enzyme acts on *m*-chlorobenzoate to yield benzoate, and on analogues with various substituents in the 5- and 6-positions with reduced methylviologen as reductant. It is a heterodimer, subunit molecular weights 64 000 and 37 000 and optimum pH 7.2. It may be a haem protein [G152, H642].

Tetrachloroquinol reductive dehalogenase

In Phanerochaete chrysosporium dehalogenation takes place in two steps. The first is the replacement of a chlorine atom with glutathione, and the second, catalysed by glutathione conjugate reductase, removes the glutathione moiety, with glutathione or another thiol as co-substrate. The first step is catalyzed by a membrane-bound enzyme, optimum pH 6.3, and the second enzyme is cytosolic, optimum pH 8.3. Other substrates are trichloroquinol and 2,6-dichloroquinol, which gives a pathway for serial dechlorination [K138].

Dehalogenation of other xenobiotics

Human neutrophil myeloperoxidase dechlorinates ticlopidine [K53].

2.10 *Epoxide formation and reduction*

Epoxide formation

Epoxides are key intermediates in the metabolism of aromatic polynuclear hydrocarbons in animals, and in the formation of DNA adducts that lead to carcinogenesis. They are very reactive and usually cannot be detected, except as their degradation products, such as *trans*-dihydrodiols and glutathione conjugates. Most of the published information on the pathways can be found under dihydrodiol formation or the *See also* entries under the oxide formation from the parent hydrocarbons in Part 1.

Rat liver cytochrome P450c catalyses the formation of naphthalene and anthracene 1,2-oxides. Trapping experiments indicate that the (+)-(1*R*,2*S*) enantiomers are the predominent products [D261]. However, cytochrome P450b forms the (1*S*,2*R*) oxides predominently from these compounds [D792]. P450c forms 5,6- and 8,9-oxides from benz[a]anthracene. Liver microsomes form principally (+)-(3*S*,4*R*)- and (+)-(5*S*,6*R*)-oxides from benzo[*c*]phenanthrene [E748]. Pyrene forms pyrene-4,5-oxide [A739].

Rat lung and liver form the 4,5-oxide from benzo[*a*]pyrene and 5,6-oxide from benz[*a*]anthracene and 7-methylbenz[*a*]anthracene [A70].

Rabbit lung and guinea pig liver microsomes form 4,5-oxide from benzo[*a*]pyrene [B286, B812].

Benzene yields benzene oxide in rat; it is found in blood [J351].

Carbamazepine forms a 10,11-epoxide in man [A3122].

The role of epoxides as mandatory intermediates in the formation of phenols in xenobiotics, including polynuclear hydrocarbons, has not been unambiguously demonstrated. Epoxides have been suggested as intermediates in the hydroxylation of bromobenzene by rat liver microsomes, involving a non-enzymatic step. Dihydrodiols formed from epoxides are dehydrated to phenols under acidic conditions, often used in extraction of metabolites from urine [B825]. Acetanilide hydroxylation has been considered to involve an epoxide [A3626]. On the other hand, a range of hydroxylations in Nitrosomonas europaea by ammonia monooxygenase involve a NIH shift mechanism, but the reaction is considered not to involve epoxide formation [H631].

6β-Hydroxyhyoscyamine epoxidase (E.C. 1.14.11.14) is described in section 1.3.

Vitamin K epoxidase

Human liver enzyme shows high activity at 10–30 weeks gestation, and then declines to the adult level at birth [K414].

Epoxide reduction

Rat liver microsomes reduce benzpyrene-4,5- and 7,8-oxides to the parent hydrocarbon, with NADP as co-substrate. Activity is enhanced in 3-methylcholanthrene-treated rats, and further increased by riboflavin. Milk xanthine oxidase also catalyzes the reaction, with enhancement by riboflavin. Other oxides, including styrene oxide, show little or no reduction [B558]. Rat liver reductase system is composed of cytochrome P448, NADPH, a reductase and a lipid fraction. Methylcholanthrene-induced P448 can be replaced less effectively by P450, either from methylcholanthrene- or phenobarbital-treated animals. The purified reductase used was free from P450 [A3527]. Activity is stimulated by FMN or methylviologen and inhibited by oxygen, dimethylaniline-N-oxide, cumene hydroperoxide or carbon monoxide. It is absent at birth, but the activity develops by 28 days post partum to about 50 per cent of that found at 49 days [A2601]. Other substrates include the 5,6-oxides of benzanthracene, 7-methylbenzanthracene, 7-hydroxymethylbenzanthracene and 7,12-dimethylbenzanthracene, benzanthracene-8,9-oxide and 3-methylcholanthrene-11,12-oxide. A dihydromonohydroxy compound is not an intermediate [A350].

Vitamin K epoxide reductase
(E.C. 1.1.4.1 and 1.1.4.2)

Human liver enzyme activity is lower than adult at 10–30 weeks gestation, it is then very variable until birth, after which it settles to the adult level [K414].

2.11 *Deamination of arylamines without hydroxylation*

Desulphovibrio converts aniline into benzene; the amino group is released as ammonia.
2,4-Dinitrophenol forms phenol with the release of ammonia but not nitrite; reduction to 2,4-diaminophenol appears to be the initial step [G827].

2.12 *Dehydroxylation of phenols*

a. Dehydroxylation

Many studies have detected the removal of the *para* hydroxyl group in catechols, usually by gut flora. Little information is available about the enzymes involved. Dehydroxylation of dihydrocaffeate occurs, for instance, in conventional rats, but not in germ-free animals [A557]. Rats, fed with L-dopa and dopamine form small amounts of *m*-hydroxy analogues and metabolites [A2961]; the excretion of *m*-hydroxy metabolites formed from dietary plant catecholic compounds is dramatically reduced in germ-free rats compared with conventional rats, indicating that gut flora are involved [H73]. However, studies with rat brain striatum have shown that trace amounts of dopamine are converted into *m*- and *p*-tyramine [C465].

A denitrifying bacterium converts salicylate into benzoate. Enzymes have been detected that catalyze salicylate CoA ligation and reductive dehydroxylation of salicyloyl CoA as part of the reaction sequence [J213].

A mixture of E. coli and S. faecalis converts pyrogallol into resorcinol; pure cultures did not catalyze the reaction. The activity is inducible [E113].

Human faeces dehydroxylate phloretate to phenylpropionate [A2767].

b. Apparent intermolecular hydroxyl transfer

Pelobacter acidigallici forms phloroglucinol from pyrogallol in the presence of 1,2,3,5-tetrahydroxybenzene stoichiometrically. It is considered that the reaction sequence is:

$$\text{Pyrogallol} + 1,2,3,5\text{-tetrahydroxybenzene} \rightarrow$$
$$1,2,3,5\text{-tetrahydroxybenzene} + \text{phloroglucinol}.$$

A similar reaction occurs with other phenols; some of the listed products have not been fully characterized:

$$1,2,3,5\text{-Tetrahydroxybenzene} \rightarrow \text{phloroglucinol} + \text{pentahydroxybenzene}$$

$$1,2,3,5\text{-Tetrahydroxybenzene} + \text{hydroxyquinol} \rightarrow \text{phloroglucinol} + 1,2,4,5\text{-tetrahydroxybenzene}$$

$$1,2,3,5\text{-Tetrahydroxybenzene} + \text{resorcinol} \rightarrow \text{phloroglucinol} + \text{hydroxyquinol}$$

$$\text{Pyrogallol} + \text{hydroxyquinol} \rightarrow \text{resorcinol} + 1,2,4,5\text{-tetrahydroxybenzene}$$

$$\text{Hydroxyquinol} \rightarrow \text{resorcinol} + 1,2,4,5\text{-tetrahydroxybenzene}$$ [F434].

Dihydrophloroglucinol formation appears to be the first reaction step with phloroglucinol as substrate; the enzyme for this step, optimum pH 7.2, requires NADPH [E189].

Eubacterium oxidoreducens pyrogallol-phloroglucinol isomerase (E.C. 1.97.1.2) converts pyrogallol into phloroglucinol [E388]; the reaction requires 1,2,3,5-tetrahydroxybenzene [G772]. The reaction is apparently anaerobic, optimum pH 7.3, and requires dimethyl sulphoxide, which is converted into methyl sulphide. Hydroxyquinol forms resorcinol and 2,6-dihydroxy-*p*-quinone. The reaction sequence proposed is:

Pyrogallol → 1,3-dihydroxy-2-oxocyclohexa-3,5-diene → 3-hydroxy-*o*-quinone → 3,5-dihydroxy-1,2-dioxocyclohex-3-ene → 1,2,3,5-tetrahydroxybenzene → 2,3,5-trihydroxy-1-oxocyclohexa-3,5-diene → 1,2-dihydroxy-3,5-dioxocyclohexane → phloroglucinol

This mechanism may be different from that for Pelobacter [E507].

Penicillium simplissimum converts phloroglucinol into a mixture of hydroxyquinol and resorcinol. It is proposed that dihydrophloroglucinol is an intermediate [F639].

2.13 *Nitro group addition and removal*

Nitro substitution

Phanerochaete chrysosporium lipid peroxidase with peroxide and tetranitromethane acts on veratryl alcohol to form several products, which include 3,4-dimethoxynitrobenzene and 4,5-dimethoxy-2-nitrobenzaldehyde. The reaction appears to be the result of the formation of nitro radicals, which then nitrate with or without displacement of the side chain [J624].

Mouse brain forms nitrotyrosine from tyrosine; nitric oxide synthase (E.C. 1.14.13.39) appears to be responsible [K385].

Removal of nitro groups

In rat 2,3,5,6-tetrachloronitrobenzene forms 1,2,4,5-tetrachlorobenzene. The mechanism is unclear, but conjugation with glutathione may be involved [H512]. 6-Nitrobenzpyrene yields benzpyrene; this reaction occurs in liver [D207, E252] and is also observed in mouse [E971].

3. Oxidations and reductions of substituent side chains and non-aromatic ring systems (without altering chain length)

3.1 *Hydroxylation of the carbon side-chain*

Dopamine-β-hydroxylase (dopamine-β-monooxygenase; DBH; E.C. 1.14.17.1)

$$Ar.CH_2.CH_2NH_2 + \text{ascorbate} + O_2 \rightarrow Ar.CHOH.CH_2NH_2 + \text{dehydroascorbate}$$

Substrates for this enzyme are phenethylamines, including tyramine and dopamine. The physiologically important substrate dopamine yields the neurotransmitter noradrenaline.

Human serum enzyme requires ascorbate and is stimulated by fumarate, N-ethylmaleimide and by low concentrations of copper. Two isozymes are found, molecular weights 368 000 and 188 000, both with optima at pH 5.0. The K_m for the smaller isozyme is 10 times greater than for the larger isozyme [A3375].

Human umbilical cord plasma activity is about 2 per cent of the adult level [A3403]. Plasma DBH activity shows a familial correlation [A1336]. A diurnal rhythm has been observed for the serum enzyme, in which bed rest is partially responsible for a drop in activity. On a normal regime, a rise of 10 per cent after waking is followed by a steady maximal activity during the afternoon and a decline in the evening and night [A1245]. Measurements of plasma enzyme in different human subjects by immunoassay shows a three-fold range, whereas measurement by activity shows a 150-fold range, suggesting that much of the enzyme is present in an inactive form [A1158]. Dialysis increases activity, suggesting the presence of a low-molecular weight inhibitor. Pure beef enzyme is inhibited by boiled human plasma, suggesting that this inhibitor is heat stable [A1956].

Human adrenal enzyme does not act on dopamine 3-or 4-sulphate [K459].

Beef adrenal enzyme, molecular weight 290 000, exhibits an optimum at pH 5.0 [C387]. However, a further study claims a molecular weight of 290 000 in the pH range 4–11, and that urea can cause it to dissociate into three inactive subunits [A885]. According to another study the molecular weight is 130 000, and is probably a homotetramer composed of two pairs of monomers that are bound by disulphide bridges [A1093]. The dimer and tetramer are reversibly interconverted, polymerisation (from molecular weight 145 000 to 290 000, with an increase in Stokes radius from 5.8 to 6.9 nm) is enhanced by increasing the pH from 5.0 to 5.7. With tyramine as substrate, changes in activity correlate with polymerization of the enzyme [K157]. Since the pH of chromaffin granules is 5.6, this polymerisation is probably physiologically important. Dissociation of the tetramer into the dimer is caused by firm binding to ADP; this is independent of pH between pH 5 and 7. At pH 5.5 the K_m for both ascorbate and tyramine is lower than at neutrality without affecting V_{max} [K154]. The enzyme contains two Cu/subunit, but it is not stimulated by Ni^{2+}, Co^{2+}, Mn^{2+}, Fe^{3+} or Zn^{2+}; the amino acid composition has been measured [A885, K156]. Medullary enzyme has an optimum pH 4.8–5.5, and this is sharpened, moved and skewed to a lower pH as

the concentration of tyramine is raised from 0.2–10 mM [A1008].

All four subunit chains from chromaffin granule enzyme, solubilized with sodium dodecyl sulphate, contain about 4.8 per cent of carbohydrate, most of which is mannose. In consequence, it is able to complex with concanavalin A from which it can be displaced by α-methyl-D-mannoside; this property has led to a purification procedure [A332, K193].

The enzyme has been detected in cerebrospinal fluid [A2838] and in lymph [Al136].

Beef enzyme is released from adrenal by treatment with acetylcholine [A3532]; it is present in the cytoplasm of all medullary cells [A1409], where it is partially (1/3) membrane-bound, with the remainder soluble. These forms are immunologically identical. The soluble enzyme appears to be homogeneous, and the insoluble to be represented by two forms. Partial proteolysis of the insoluble form releases enzyme that has the same properties as the soluble form [A1907, A3580].

Beef adrenal enzyme is inhibited by the anti-thyroid agents methimazole and propylthiouracil, by thiouracil and 2-mercaptoimidazole [A1918]. Thioureas inhibit by several mechanisms; N-phenyl-N′-3-(4*H*-1,2,4-triazolyl)thiourea and N-(*n*-butyl)-N′-3-(4*H*-1,2,4-triazolyl)thiourea both inhibit noncompetitively relative to substrate, but the former is a mixed type inhibitor with respect to ascorbate, and Cu^{2+} does not reverse the inhibition. Inhibition by N-(*n*-butyl)-N′-3-(4*H*-1,2,4-triazolyl)thiourea is noncompetitive relative to ascorbate, and inhibition is reversed by Cu^{2+} [A797]. Catalase protects against denaturation, and diethylpyrocarbamate, a histidine-binding compound, inactivates it. It is inhibited by diethyldithiocarbamate [A1097]. Incubation with cysteine inactivates it irreversibly. Although the mechanism has not been identified [A800], reduction of disulphide bridges possibly followed by bonding with cysteine may occur. It is not stimulated by N-ethylmaleimide [A3375].

Beef adrenal enzyme acts on D-amphetamine, forming *l*-norephedrine, thus removing the *pro-R* hydrogen [Al101], which is replaced by a hydroxyl group while retaining the configuration, i.e., there is no Walden-type inversion [A1410]. Isotope effects indicate that β-C–H cleavage is the rate-limiting step, with a secondary, possibly steric effect from the α-CH [A3689]. The enzyme acts on 2-indanamine, which is a cyclic analogue of phenethylamine in which rotation at the hydroxylation site is prevented. The product is almost stereochemically pure *trans*-(1*S*, 2*S*)-2-amino-1-indanol [J666]. The reaction rate is reduced by 50 per cent in D_2O, possibly by D exchange in a histidyl residue involved in H transfer [A330]. Mechanistic studies suggest that a ping-pong mechanism is not involved; it is suggested that a ter bi sequential type is more likely, with electron donor, oxygen and substrate adding in that sequence [A1465]. Adrenal enzyme activity is enhanced by a superoxide-generating system, and is inhibited by superoxide dismutase [A1163]. Activation by fumarate or sodium chloride shifts the optimum pH from about 6.2 to 7, with increased activity at the optimum. This is thought to be due to anion binding at a basic group adjacent to an ionizable group at the active site [Al093]. A study in the absence of fumarate suggested that ascorbate and tyramine add sequentially; the apparent ping-pong mechanism only occurs at saturating concentrations of fumarate (acetate or chloride show a similar effect) [K189].

Pure beef enzyme, free from sulphatase activity, is claimed to act on dopamine-3-sulphate to generate unbound noradrenaline. The reaction is inhibited by fusaric acid, a DBH inhibitor [A3334].

Beef brain enzyme has a molecular weight of 400 000, optimum pH 5.0 [C387].

Rat brain enzyme exhibits maximal activity in the presence of N-ethylmaleimide (50 mM) and Cu^{2+}; it may activate by interaction with an endogenous inhibitor [A1723]. The enzyme exists as multiple forms, which may be interconverted, with molecular weights 73 000 and 77 000 [K460]. It is inhibited by some methimazole analogues including 1-cyclohexyl-2-mercaptoimidazole [A1697].

Rat serum enzyme activity remains fairly constant from birth until weaning, followed by a 50 per cent drop over five days, and then a slow

decline to the adult level. In heart the activity increases fourfold between birth and weaning, and then remains constant [A1700]. The enzyme has also been detected in rat stomach, heart, stellate ganglion, superior cervical ganglion and salivary gland as well as adrenal [A368, H620].

In dog, hypotension produced by haemorrhage raises plasma DBH activity by 40 per cent [A3576].

Hen adrenal enzyme appears to be a homotetramer, molecular weight 320 000 and optimum pH 5–6, with subunits linked by disulphide bridges. It requires ascorbate (ferrocyanide can act as substitute) and fumarate (acetate is a poor substitute). The product from substrate β-labelled with tritium retains an excess of label. Kinetic studies have suggested a ping-pong mechanism [C56].

Opuntia converts N-methyltyramine into normacromerine (N-methyl-3,4-dimethoxyphenylethanolamine) [A3977].

Tryptamine and tryptophan β-hydroxylation

An enzyme in beef adrenal medulla and in most rat tissues acts on tryptamine; it is unclear whether this has any physiological role [B469].

Pseudomonas indole-3-alkane α-hydroxylase (tryptophan 2′-dioxygenase, E.C. 1.13.99.3) acts on tryptamine to form (*R*)-β-hydroxytryptamine, removing the *pro-S* hydrogen from C-2 of the side chain. It also acts on tryptophan methyl ester and DL-homotryptophan. A mixture of (2*S*, 3*R*)- and (2*R*, 3*S*)-β-methyltryptophan is also hydroxylated, but a mixture of (2*R*, 3*R*)- and (2*S*, 3*S*)-β-methyltryptophan is inactive [B84]. The molecular weight of the enzyme is 250 000, pI 4.8 and optimum pH about 4. Its amino acid composition has been determined, and it contains 0.8 mol Fe/mol. Cyanide and hydroxylamine are inhibitory. A range of tryptophans and tryptamines as well as indoles with 3-alkyl moieties are also substrates. L-Tryptophan is hydroxylated and decarboxylated to β-hydroxytryptamine, with decarboxylation apparently as the second reaction step. Decarboxylation does not occur with, for instance, indole-3-propionate or peptide-linked tryptophan [A3007]. During the reaction an oxygen atom is introduced from water, but not from molecular oxygen; oxygen can be replaced by other electron acceptors. The reaction produces an olefinic intermediate that is then hydrated, possibly spontaneously [A3148].

NADPH-dependent L-phenylalanine monooxygenase

Carica papaya enzyme is found only in leaves. It is highly specific; other phenylalanines are not substrates. The reaction involves oxidative decarboxylation to form benzylaldoxime [H947].

Mandelic acid formation from phenylacetic acids

$$R.CH_2.COOH \rightarrow R.CHOH.COOH$$

Substrates include phenylacetate and *p*-hydroxyphenylacetate. Species in which the reaction has been detected include plants (barley, wheat, parsley and Glycine max) and microorganisms (Aspergillus and Pseudomonas) [A329, A2691, A3594, G929].

Hydroxyphenylacetonitrile 2-monooxygenase (E.C. 1.14.13.42)

Etiolated sorghum seedling enzyme requires oxygen and NADP to form the corresponding mandelonitrile [K711].

Hydroxylation of nuclear methyl groups

$$R.CH_3 \rightarrow R.CH_2OH$$

a. Polynuclear hydrocarbons

Rat liver enzyme oxidizes 7-methyl- and 7,12-dimethylbenzanthracene, incorporating

oxygen from molecular oxygen, but not from water [A339].

b. Phenols

A Pseudomonas putida enzyme, which acts on 4-hydroxy-3-methylbenzoate is a 2-protein system, molecular weight 115 000, that appears to be composed of a flavin-containing hydroxylase and an electron-transfer system that uses NADH. It is claimed to be an unusual type of mixed-function oxidase [F223]. The electron transfer system appears to be a flavocytochrome c [A3870].

p-Cresol is converted into *p*-hydroxybenzyl alcohol by Pseudomonas 4-cresol dehydrogenase (hydroxylating) (E.C. 1.17.99.1), a dimer, molecular weight 115 000. One component is a c-type cytochrome and the other a flavoprotein [A3276]; the oxygen is incorporated from water [A3829, K410]. Studies on *p*-cresol oxidation with 3 Pseudomonas strains including P. putida found that each has a different molecular weight and K_m. The enzyme is anaerobic, with 8α-(O-tyrosyl)FAD as cofactor [B853, K841]. It further oxidizes the substrate to the corresponding aldehyde [A3829].

Pseudomonas *p*-cresol methylhydroxylase is a cytochrome c flavoprotein that catalyzes the incorporation of oxygen from water, and oxidizes the product further to the aldehyde [K203]. The enzyme is a tetramer with two pairs of identical polypeptide chains, one with molecular weight 119 000, and the other a cytochrome, molecular weight 9300; each of the latter binds a flavin molecule. In the wild-type enzyme this is covalently bound, but in enzyme expressed in E. coli it is not covalently bound [K289]. Growth on *p*-cresol induces the *p*-cresol oxidizing enzyme, which is a dimer, molecular weight 100 000, composed of a flavoprotein and cytochrome c, with different molecular weights and K_m (not quoted) for the enzyme from three different strains [A3870, B853]. *p*-Cresol and *p*-ethylphenol are oxidized adjacent to the aromatic nucleus. A ping-pong mechanism has been suggested for the oxidation [E361].

3,5-Xylenol is oxidized in Pseudomonas putida by an enzyme that does not oxidize *p*-cresol. It requires NADH, and is inhibited by cyanide but not by carbon monoxide [A3870].

Penicillium simplicissimum vanillyl alcohol oxidase (E.C. 1.1.3.38) is a flavoprotein that acts on *p*-cresol [G662]; it also forms *p*-hydroxbenzaldehyde very slowly [J680].

P. patulum enzyme is microsomal, optimum pH 7.5, and requires molecular oxygen and NADPH for oxidation of *p*-cresol. Carbon monoxide and cytochrome c are inhibitory [A1468].

Achromobacter enzyme, molecular weight 130 000, is composed of subunits, molecular weights 54 000 and 12 500. The substrate is *p*-cresol [F868].

c. Toluenes and xylenes

Pseudomonas aeruginosa enzyme is composed of three proteins, and requires FAD and NADH [A1009].

E. coli xylene monooxygenase oxidizes toluene and pseudocumene to the corresponding alcohols and aldehydes [K491].

Ethylbenzene dehydrogenases

Ethylbenzene → 1-phenylethanol

Azoarcus enzyme, which is membrane-bound, requires quinone as an electron acceptor; the product is pure (*S*)-1-phenylethanol. Not all analogues are substrates, but propylbenzene and *p*-ethylfluorobenzene are hydroxylated [K241].

Byssochlamys fulva vanillyl alcohol oxidase is a homodimer, monomeric molecular weight 58 000, which oxidizes *p*-hydroxyphenylethane and *p*-hydroxyphenylpropane to the corresponding (*S*)-1-(*p*-hydroxyphenyl)alcohols [K164].

E.coli enzyme forms mainly the (*R*)-isomer [G740]

Mortierella isabellina enzyme forms both (*R*)- and (*S*)-phenylethanols, and the identity of the *para* substituent determines which predominates. In no case was one isomer found to be the exclusive product. With bromo and nitro

substitution the enantiomeric enrichment was only slight, whereas with methoxy and chloro (*S*) predominates (between 20 per cent and 40 per cent enantiomeric excess), but with cyano, methyl, ethyl and fluoro (*R*) predominates [D969].

A Penicillium simplicissimum vanillyl alcohol oxidase acts on 4-allyl- and 4-alkylphenols (1–3 C chain). Further oxidation forms the corresponding acetophenone and propiophenone. *p*-Propylphenol also forms a small amount of *p*-coumaryl alcohol, and ethylphenol and propylphenol form vinylphenol and propenylphenol respectively. A quinone methide intermediate is probable for the formation of (*R*)-benzylic alcohols, which are formed in about 94 per cent enantiomeric purity. The hydroxyl group comes from water [J16, J664, J680].

The (*S*)-isomer is formed by Pseudomonas from ethylbenzene [J219]. P. fluorescens eugenol dehydrogenase forms (*S*)-1-(*p*-hydroxyphenyl)ethanol and (*S*)-1-(*p*-hydroxyphenyl)propanol from the corresponding 4-alkylphenols [K177].

Pseudomonas putida 4-ethylphenol methylenehydroxylase is a flavocytochrome c composed of two pairs of subunits, molecular weight about 120 000. One subunit, molecular weight 50 000 is a flavoprotein and the other, molecular weight 10 000 is a cytochrome c. The mechanism involves dehydrogenation followed by hydration to form 1-(*p*-hydroxyphenyl)ethanol. It acts on a range of 4-alkylphenols with up to nine carbon atoms in the side chain and on 5-indanol (a cyclic analogue of 4-ethylphenol). *p*-Cresol and 2,4-xylenol are substrates; and 1-(*p*-hydroxyphenyl)ethanol is further oxidized to *p*-hydroxyacetophenone. It is considered that the reaction proceeds via a quinone methide [F381]. In another study the enzyme was called 4-ethylphenol methylenehydroxylase [E396].

This type of reaction has also been observed in man [D482], rat [D365], rabbit [A287], chinook salmon [E710], Desulfobacula toluolica [J847], Nocardia tartaricans [B144] and in Nitrosomonas [H219]; in N. europaea ammonia monooxygenase catalyzes the reaction [H631]; in many studies, particularly the early ones the chirality of the product was not established.

4-Allylphenol ω-hydroxylation

Penicillium simplicissimum vanillyl alcohol oxidase hydroxylates eugenol and chavicol to the corresponding cinnamyl alcohols [H389]. The enzyme also carries out a range of other activities, such as oxidizing secondary vanillyl alcohols, including phenylethanolamines, to the corresponding ketones [J16].

Byssochlamys fulva enzyme is a homodimer, monomeric molecular weight 58 000, which additionally oxidizes vanillyl alcohol to vanillin, and (*p*-hydroxyphenyl)alkanes to (*S*)-1-(*p*-hydroxyphenyl)alcohols [K164].

Pseudomonas fluorescens eugenol dehydrogenase, a dimer, monomeric molecular weights 10 000 and 58 000, is a flavoprotein that requires an oxidizing agent, such as ferricyanide. It forms coniferyl alcohol from eugenol, as well as oxidizing *p*-hydroxybenzyl alcohols [J890].

Acetophenone ω-hydroxylation

Solanum khasianum enzyme, which hydroxylates the terminal carbon of acetovanillone, requires oxygen and NADPH. Its inhibition properties are like those of P450 [H906]. A similar reaction probably occurs in Pseudomonas with acetophenone [J219].

In rat a similar reaction occurs with paeonol [E849].

Cannabinoid side chain hydroxylases

Extensive studies with cannabinoids have demonstrated that hydroxylations occur at various positions in the molecule; however, little appears to have been done at an enzyme level. The literature on this subject is extensive, and the references given (for Δ^1-tetrahydrocannabinol) are illustrative.

Cannabinoid 1″-hydroxylation

This reaction has been detected in guinea pig and Thamnidium [B458, B742].

Cannabinoid 2″-hydroxylation

This reaction has been detected in man, guinea pig, Fusarium, Gibberella and Thamnidium [B458, B742, C2, F819].

Cannabinoid 3″-hydroxylation

This reaction has been detected in mouse, rat, guinea pig, monkey, Chaetomium, Fusarium, Gibberella and Thamnidium [A3628, B458, B742, E598, F599, F819, H418].

Cannabinoid 4″-hydroxylation

This reaction has been detected in guinea pig, rat, rabbit, Fusarium, Gibberella, Syncephalastrum and Thamnidium [A2595, B458, B742, E7, F7]

Cannabinoid 5″-hydroxylation

This reaction has been detected in mouse, rabbit and guinea pig [A3449, F7].

Cannabinoid 7-hydroxylation

This reaction has been detected in rat, rabbit, monkey, man, mouse and Chaetomium [A108, A116, A438, A680, A879, A3628].

Agroclavine hydroxylation

Claviceps microsomal enzyme, a P450 that requires NADPH, hydroxylates agroclavine to elymoclavine [B809].

3.2 *Alkyl oxidation to ketone*

Phenylacetyl CoA: acceptor oxidoreductase

$$\text{Phenylacetyl CoA} + 2\ \text{quinone} + 2\ H_2O \rightarrow \text{phenylglyoxylate} + 2\ \text{quinol} + \text{CoASH}$$

Thauera aromatica enzyme is a membrane-bound trimer, subunit molecular weights 93 000, 27 000 and 26 000, with an assumed native molecular weight of 280 000. Analyses indicate that this contains 0.66 Mo, 30 Fe and 25 acid-labile S. The reaction is anaerobic, with duroquinone, menadione or (best) dichlorophenolindophenol as electron acceptors. Phenylglyoxylyl CoA is an intermediate, but mandelyl CoA is not [K173].

3.3 *Oxidations and reductions of alcohols, aldehydes and ketones*

Alcohol dehydrogenases (aryl-alcohol dehydrogenase; E.C. 1.1.1.90, aryl-alcohol dehydrogenase (NADPH); E.C. 1.1.1.91)

$$R.CH_2OH \rightarrow R.CHO$$

Human brain enzyme is composed of at least five isozymes, pI 5.3, 6.0, 6.3, 7.0 and 7.9. They all act on *p*-nitrobenzaldehyde and indole-3-acetaldehyde, but are distinguished by their relative activities towards menadione, daunorubicin, *p*-hydroxyphenylacetaldehyde and *p*-hydroxymandelaldehyde as potential substrates. All require NADPH; one that can also utilize NADH appears to be succinic semialdehyde reductase (E.C. 1.2.1.16/ E.C. 1.2.1.24). The pI 7.9 enzyme is strongly inhibited by quercetin and quercitrin [B569].

Human brain aflatoxin B_1 aldehyde reductase is identical with succinic semialdehyde reductase, which also reduces phenanthrene-9,10-quinone, phenylglyoxal and *p*-nitrobenzaldehyde [K273].

Horse liver enzyme oxidizes benzyl alcohol reversibly; the enzyme has two active sites [A2174].

A Glycine max (soyabean) cinnamyl alcohol dehydrogenase isozyme (E.C1.1.1.195), molecular weight 43 000 and optimum pH 9.2, oxidizes coniferyl alcohol. A second isozyme in addition reversibly oxidizes several substituted cinnamyl alcohols with optimum pH 8.8, and optimum pH 6.6 for reduction [A2325].

Rye aromatic alcohol dehydrogenase is composed of 3 NADP-dependent isozymes, one

NAD-dependent isozyme and one without nucleotide specifity [D45].

Acinetobacter calcoaceticus benzyl alcohol dehydrogenase is a monomer, molecular weight 38 923 with 370 amino acid residues, based on nucleotide sequencing. It requires NADH and zinc; it is a member of a family of zinc-dependent long-chain alcohol dehydrogenases (E.C. 1.1.1.192) [J621]. Other substrates include coniferyl alcohol, cinnamyl alcohol and other (unspecified) aromatic alcohols, but few aliphatic alcohols are substrates [E473]. Another study claims that the enzyme is a tetramer with a monomeric molecular weight consistent with the above value. The optimum pH for oxidation is 9.2, and for reduction 8.9 [E596].

Azoarcus 1-phenylethanol dehydrogenase, which is inducible, only acts on the (*S*)-isomer; it requires NAD^+ [K241].

Geotrichum candidum converts (*S*)-arylethanols into (*R*)-arylethanols via acetophenones; (*R*)-arylethanols are not substrates. A range of phenylethanols substituted on the aromatic nucleus with chloro, methyl and methoxy groups (but not in the *ortho* position) are also substrates [H749].

A methanol dehydrogenase (E.C. 1.1.1.244) in Methylomonas methanica, molecular weight 60 000, oxidizes 2-phenoxyethanol and a range of aliphatic alcohols at similar rates, but does not act on benzyl alcohol or secondary alcohols. It requires NH_4^+, with optimum pH 9.5 [A27l2].

Mycobacterium tuberculosis enzyme has an optimum of 6.5–8, depending on the nature of the buffer and other parameters. It oxidizes benzyl alcohols as well as reducing benzaldehyde. It is inhibited by *p*-chloromercuribenzoate, benzoate and *o*-phenanthroline [A150].

Penicillium urticae 3-hydroxybenzyl-alcohol dehydrogenase (E.C. 1.1.1.97), molecular weight 120 000 and optimum pH 7.6, requires NADP. It is a key enzyme in the formation of patulin from 6-methylsalicylate [K946].

Penicillium simplicissimum vanillyl alcohol oxidase (E.C. 1.1.3.38) is an octomer, monomeric molecular weight 65 000. It is a flavoprotein (1 mol/mol of monomer), with covalently bound 8a-(N^3-histidyl)FAD. It is highly specific for *p*-hydroxybenzyl alcohols [G662]. It forms the corresponding acetophenone and propiophenone from *p*-ethylphenol and *p*-propylphenol; there is good evidence that the corresponding alcohols are intermediates [J664, J680].

Phanerochaete chrysosporium enzyme, molecular weight 78 000, has a FAD prosthetic group. It is specific for benzyl alcohols [H613].

Pleurotus eryngii alcohol oxidase (E.C. 1.1.3.13), molecular weight 72 600 and pI 3.9, contains 15 per cent carbohydrate. It oxidizes a series of benzyl and cinnamyl alcohols [G668]. P. pulmonarius enzyme which contains 14 per cent carbohydrate, molecular weight 70 500 and pI 3.95, has been crystallized. DNA studies indicate that it is composed of 593 amino acid residues, including a signal peptide of 27 amino acid residues [K373].

Pleurotus ostreatus veratryl alcohol oxidase is a glycoprotein containing FAD, optimum pH 6.5 (broad), which forms veratraldehyde, with oxygen forming peroxide. A range of benzyl alcohols and cinnamyl alcohols are oxidized [F867].

Polystictus versicolor aryl alcohol oxidase is found in the media surrounding the mycelia. It acts on several benzyl alcohols and 2-hydroxymethylnaphthalene, but other alcohols are only marginally active [K878].

Pseudomonas fluorescens enzyme, a dimer, monomeric molecular weights 10 000 and 58 000, is a flavoprotein requiring an oxidizing agent, such as ferricyanide. It oxidizes *p*-hydroxybenzyl alcohols as well as forming coniferol alcohol from eugenol [J890].

Pseudomonas putida grown on 3,5-xylenol contains two NAD^+-dependent alcohol dehydrogenases, molecular weights 122 000 and 145 000. When grown on *p*-cresol a single NAD^+-dependent alcohol dehydrogenase develops, molecular weight 75 000. They all have an optimum pH of 9.5 or higher, and oxidize a range of substituted benzyl alcohols with minor differences in specificity. The xylenol-induced enzymes that oxidize benzyl alcohol, *m*- and *p*-hydroxybenzyl alcohols undergo spontaneous inactivation, and are protected by dithiothreitol. Inactivation by *p*-chloromercuribenzoate is partly prevented by substrate [A1366, A3837].

Pseudomonas putida 4-ethylphenol methylenehydroxylase (see Ethylbenzene dehydrogenases, above) oxidizes 1-(*p*-hydroxyphenyl)ethanol to *p*-hydroxyacetophenone [F381].

Pseudomonas syringae D-phenylserine dehydrogenase, molecular weight 31 000 and optimum pH 10.4, requires $NADP^+$ [H91].

Rhodopseudomonas acidophila *p*-hydroxybenzyl alcohol dehydrogenase (E.C. 1.1.1.90), molecular weight 27 000 and pI 7.4, has an optimum pH 6.5 for oxidation and pH 9 (broad) for the reverse reaction. Substrates include cinnamyl alcohol, phenylethanol and a series of benzyl alcohol analogues substituted in the *m*- and *p*-positions, but not *o*-analogues [Dl97].

Thauera benzyl alcohol dehydrogenase, which is a homotetramer, molecular weight 160 000, requires NAD^+ [H610].

A benzyl alcohol dehydrogenase has been detected in a Bacterium [A730].

Aromatic aldehyde and ketone reductases (aryl alcohol oxidase, E.C. 1.1.3.7; c.f. aryl-alcohol dehydrogenase ($NADP^+$); E.C. 1.1.1.91)

R′.CO.R → R′.CHOH.R, where R is H or an alkyl group and R′ an aryl or an aralkyl group.

Four or possibly 5 isozymes of aldehyde reductase in human brain reduce indole-3-acetaldehyde and *p*-nitrobenzaldehyde, with pI 5.3 (this isozyme appears to be E.C. 1.1.1.2), 6.0, 6.3, and the fourth fraction shows two values at 7.0 (minor) and 7.9. They require NADPH, although one isozyme can utilize NADH. Menadione, daunorubicin, *p*-hydroxyphenylacetaldehyde and *p*-hydroxymandelaldehyde are substrates for at least 2 of the isozymes. [B569].

Human erythrocyte 4-nitroacetophenone reductase, optimum pH about 7, is not cytochrome c. It requires NADPH, but not NADH. It is unstable at 50°, and is moderately unstable at 4° and is inhibited by *p*-nitrobenzaldehyde, *p*-chloromercuribenzoate and N-ethylmaleimide, and slightly by methanol. It is claimed to differ from other side chain keto reductases. A similar enzyme is found in rat [A15].

Beef enzyme is widely distributed throughout the brain [A1908]. It requires NADH; NADPH is a poor co-substrate. The optimum pH for reduction is 6.8, and 10 for the reverse reaction. Some aliphatics as well as *p*-nitrobenzaldehyde are substrates [A614].

Pig brain contains two isozymes, one low- and the other high-affinity. Both reduce 3,4-dihydroxy- and 4-hydroxy-3-methoxyphenylacetaldehydes as well as *l*-*p*-hydroxyphenylglycolaldehyde and D-3,4-dihydroxyphenylglycolaldehyde; the high affinity isozyme also reduces 5-hydroxyindole-3-acetaldehyde [A1287]. Another study found the molecular weight of the cytosolic enzyme to be 29 000 and pI 5.8. It utilizes NADPH in the reduction of benzaldehydes, *p*-hydroxymandelaldehyde, indole-3-acetaldehyde and some aliphatic aldehydes (especially lactaldehyde and glyceraldehyde; acetaldehyde is very poor), but it is ineffective in reducing ketones [Al679].

Monkey (apparently rhesus) brain enzymes have a similar specificity to that of pig brain enzyme. Both isozymes require NADPH; one is low affinity and high activity and the other high affinity and low activity [A1908].

Rat liver aldehyde reductase isozymes, pI 6.5 and 6.9, reduce 3,5-dihydroxyphenylacetaldehyde and *p*-nitrobenzaldehyde [B659]. An enzyme tentatively identified as E.C. 1.1.1.2 has an optimum pH of 6–8 for the forward reaction, whereas the optimum for the reverse reaction (on daunorubicinol) is above pH 10. Both aliphatic and aromatic aldehydes are reduced, the best being 4-carboxybenzaldehyde; adriamycin is reduced, but only poorly. Barbital, warfarin and phenobarbital are inhibitors, but is activated by NaCl, with peak activity enhanced by 50 per cent above the base-line activity at ionic strength 0.4. With 50 mM sodium sulphate there is 40 per cent activation, which declines to zero at ionic strength 0.3–0.4, with inhibition at higher concentrations [A2007]. A rat liver aldehyde reductase, optimum pH 6.5, reduces many benzaldehydes, as well as quinones and phenylglyoxal. It differs in

specificity from other aldehyde reductases in that it reduces *o*-quinones; it is the only one found in this study that reduces aflatoxin B_1-dialdehyde, a very poor substrate [H759].

Rat liver cytosol contains a highly specific 2-carboxybenzaldehyde reductase, molecular weight 64 000; the 3- and 4-carboxy analogues are not substrates. It requires NAD(P)H and a thiol for activity [G239].

Rat aflatoxin B_1 aldehyde reductase 2 is found as multiple forms, with molecular weights in the range 36 800 and 38 000. They also act on other aldehydes and quinones [K546].

A rabbit liver cytosolic enzyme, molecular weight 33 000 and optimum pH 6.2, reduces the oxo group of loxoprofen and requires NADPH. It also reduces benzaldehydes, acetophenones and various other oxo-compounds. A similar activity that reduces loxoprofen is found in guinea pig [D125]. Another study with rabbit liver cytosol found four isozymes, designated F_1, F_2, F_3 and F_4. F_2 is an aldehyde reductase, whereas the others are aromatic aldehyde/ketone reductases. F_1 and F_3 are monomeric with molecular weights 38 000 and 29 000 respectively. F_4 appears to be trimeric, molecular weight 78 000, and monomeric molecular weights 24 000 and 26 000. Substrates include 3- and 4-benzoylpyridines and *p*-nitroacetophenone [B431]. Flavonoids are inhibitory [K560]. A further publication reports molecular weights that differ appreciably from these values; it also describes a benzaldehyde-reducing enzyme that does not reduce acetophenones, whereas two acetophenone-reducing enzymes also reduce some benzaldehydes [B386]. Seven isozymes were detected in one study. Two are aldehyde reductases, the major having pI 6.0–6.3 and the minor 7.8. A major enzyme, pI 4.9, is active towards *p*-nitrobenzaldehyde and *p*-nitroacetophenone, but not naloxone or naltrexone. Four others, including one major enzyme, which reduce naloxone and naltrexone as well as other carbonyl compounds, were named dihydromorphinone reductases, pIs 5.4–5.5, 6.5, 6.6 and 6.9–7.2 [A3950]. Rabbit and chicken dihydromorphinone reductases require NADPH, and are found mainly in liver cytosol, although some activity is present in kidney and lung [A2290].

An enzyme in rabbit, rat and guinea pig liver that reduces substituted benzoylpyridines is found in both microsomes and cytosol (the latter not in rat), and requires NADPH. Cytosolic enzyme is inhibited by heavy metals, *o*-phenanthroline and azide among other compounds, whereas the microsomal enzyme is inhibited by Hg^{2+}, *p*-chloromercuribenzoate and N-ethylmaleimide [A2834].

Sheep heart enzyme reduces a range of phenylglycolaldehydes and oxidizes *p*-hydroxybenzaldehyde, and requires NADP as co-substrate [A57].

Cucumis sativus (cucumber) cytoplasmic indole-3-acetaldehyde reductase (E.C. 1.1.1.191) is highly specific and requires NADPH [F462]. Another study identified 3 indole-3-acetaldehyde reductase isozymes. Two, molecular weights 17 000 and 52 000 and optimum pH 5.2, require NADPH. A NADH-specific enzyme (E.C. 1.1.1.190) has a molecular weight of 332 000 and optimum pH 7.0. They all reduce phenylacetaldehyde and (poorly) *trans*-cinnamaldehyde. Some aliphatics are poor substrates, but benzaldehydes are not reduced [A2432].

A mung bean monomeric enzyme, molecular weight 36 000 and optimum pH 6.2–7.5, reduces eutypine irreversibly, and a series of benzaldehydes and cinnamaldehyde with NADPH as cofactor; it appears that no tests were made on the reversibility with these other substrates [J910].

Populus euramericana stem cinnamyl alcohol dehydrogenase, molecular weight 36 000 and pI 5.6, requires NADPH for the reduction of coniferaldehyde, *p*-coumaraldehyde and sinapaldehyde, and is inhibited by 1,l0-phenanthroline and sulphydryl-binding compounds [D54].

Both spruce and Glycine max contain cinnamyl alcohol: $NADP^+$ dehydrogenases (E.C. 1.1.1.195) that reduce coniferaldehyde, *p*-coumaraldehyde and sinapaldehyde. Both are dimers, monomeric molecular weight about 35 000 [B922]. Another study on the Glycine

enzyme found a molecular weight of 40 000 for a zinc-containing isozyme that reduces coniferaldehyde. It requires NADPH, and is inhibited by thiol-binding reagents [B95].

Swede enzyme, which is composed of three isozymes, is part of the system for forming coniferyl alcohol from ferulate. It requires NADPH (NADH is inactive) for the reduction of coniferaldehyde, and is reversible [A216]. Forsythia enzyme is very similar [A848].

Candida guilliermondii contains a phenylacetaldehyde reductase that requires NAD(P)H [A2483].

Corynebacterium phenylacetaldehyde reductase requires NADH. It also reduces nuclear substituted phenylacetaldehydes, phenacyl chloride, acetophenone, propiophenone and 4-phenylbutan-2-one stereoselectively to the (*S*)-alcohol (phenacyl chloride yields the (*R*)-isomer with the same spatial geometry). In the reverse reaction the (*S*)-alcohols are substrates [J893].

Geotrichum candidum reduces acetophenones [H749].

Lactobacillus kefir acetophenone reductase, optimum pH 7.0, which is protected by Mg^{2+}, requires NADPH, but NADH is inactive. The optimum pH for reduction is 7.0, and for oxidation 8.0. Propiophenone, a range of acetophenones, and some (but not all) other analogues tested, as well as benzaldehyde, are substrates. The product from acetophenone is (*R*)-(+)-1-phenylethanol, which is a substrate for the reverse reaction, although (*S*)-1-phenylethanol is not [Gl48].

Phycomyces blakesleeanus indole-3-acetaldehyde reductase is a tetramer, monomeric molecular weight 38 000, pI 5.4 and optimum pH 6–8. It requires NAD(P)H as cofactor [F846].

A Pseudomonas guaiacylglycerol β-guaiacyl ether dehydrogenase reduces the α-oxo analogue of this compound [G357].

Tryptophol oxidase

Tryptophol → indole-3-acetaldehyde

Cucumber enzyme is inhibited by the reaction product, and this inhibition is reversed by oxygen but not by the substrate. Several auxins are inhibitory [A835, A957]; this undoubtedly prevents over-production of IAA.

Phaseolus vulgaris, molecular weight 56 000, requires oxygen, and forms peroxide as a second product [H554].

Phycomyces blakesleeanus enzyme, molecular weight 56 000 and optimum pH 6–8, forms indole-3-acetaldehyde and possibly peroxide. It is activated by FAD and inhibited by Hg^{2+}, iodoacetate, and by 4 μM indole-3-acetaldehyde [E443].

Mandelate dehydrogenases and oxidases

R.CHOH.COOH → R.CO.COOH

Rhodotorula graminis L-(+)-mandelate dehydrogenase is a tetramer, monomeric molecular weight 59 100, that contains one mol each of haem and FMN per subunit. The optimum pH is 7.9, and pI 4.4. It acts on mandelate and a series of nuclear-substituted analogues [H90] and is stereospecific [G904]. Both D- and L-dehydrogenases are inducible. L-Dehydrogenase, optimum pH 7.0, requires dichlorophenolindophenol as reductant, and may be membrane-bound; activity is enhanced by phenazine methosulphate. D-Dehydrogenase, optimum pH 9.0, is not membrane-bound, and requires NAD^+ [D475].

Acinetobacter calcoaceticus enzymes, specific for each stereoisomer are found in cytoplasmic membranes. After solubilization, the D-dehydrogenase has a molecular weight of 59 700, optimum pH 8.0 and pI 5.5 [D870] and are very similar to the corresponding D- and L-lactate dehydrogenases (E.C. 1.1.2.4 and 1.1.2.3 respectively) [D674]. A novel enzyme found in a mutant strain but not in the wild-type organism, acts solely on the D-isomer. It is membrane-bound, and its pH and temperature dependence are similar to those of the L-dehydrogenase (the activity found in most strains). Inhibitors include L-mandelate [A1649, C801].

Aspergillus niger D-mandelate oxidase (not a dehydrogenase), optimum pH 7.6, is particulate and very unstable. It is specific for the D-isomer

of several mandelates. Neither NAD nor $NADP^+$ are involved, and metal ions are not activators. It appears to require cytochrome c and molecular oxygen, which cannot be replaced by other oxidizing agents, and peroxide is not formed as a second product. Heavy metal ions are inhibitors [A1204].

Pseudomonas putida (*S*)-mandelate dehydrogenase oxidizes mandelate and indole-3-glycollate, and acts very slowly on plenyllactate, indole-3-lactate and some aliphatic analogues [K95]. It is membrane-bound, with a binding segment of about 39 residues [K230].

Rhizobium leguminosarum enzyme is induced by 4-hydroxymandelate [F224].

A Bacterium (unidentified) enzyme, optimum pH 9.5, oxidizes D-VMA to the corresponding benzoylformate, but D-mandelate is not a substrate [J256]. Another study has identified a L-dehydrogenase in a Bacterium [A730].

Indole-3-acetaldehyde reductase (E.C. 1.1.1.190 and 1.1.1.191)

Indole-3-acetaldehyde → tryptophol

Human brain enzyme acts on indole-3-acetaldehyde [B569]. Rat liver enzyme [A2007] and pig brain enzyme [A1679] also reduce other aldehydes (see above).

Brassica campestris (Chinese cabbage), molecular weight 32 000 and optimum pH 6–7 requires NADPH. Other substrates are benzaldehyde and phenylacetaldehyde, but not 3-formylindole. It has also been found in B. napus, B. oleracea, Arabidopsis thahana and Sinapis alba [F931].

Cucumis sativa (cucumber) enzyme, which requires NADPH, is cytoplasmic and is specific for indole-3-acetaldehyde [F462].

Mung bean enzyme, a dimer, monomeric molecular weight 39 000, requires NADPH. It also reduces benzaldehyde and phenylacetaldehyde [J207].

Phycomyces blakesleeanus enzyme, molecular weight 38 000, pI 5.4 and optimum pH 6–8 requires NAD(P)H [F846].

This reduction has also been detected in Orobanche gracilis, O. lutea, O. ramosa [C181], Zygosaccharomyces [A923] and pea [A755].

Benzoylformate reductase

Benzoylformate → mandelate

This activity has been found in rats [J287], with a preponderance (10:1) of the (*R*)-isomer formed [F496].

Pseudomonas polycolor and Micrococcus freundii catalyse this reaction; this enables racemic mandelate to be converted into the (*R*)-isomer, because these organisms contain an enzyme that converts (*S*)-mandelate into benzoylformate, but is inactive towards (*R*)-mandelate [H668].

S. faecalis enzyme is dimeric, molecular weight 72 000, pI 4.9 and optimum pH 4.5, also reduces phenylpyruvate and some aliphatics, but not *p*-hydroxyphenylpyruvate or *p*-hydroxybenzoylformate. The optimum pH for the reverse reaction is 9.2 [E271].

Hydroxyphenylpyruvate reductase (E.C. 1.1.1.237)

Coleus blumei enzyme, which requires NADH reduces *p*-hydroxyphenylpyruvate and 3,4-dihydroxyphenylpyruvate to the corresponding lactates [E660].

Aromatic α-ketoacid reductase ((*R*)-aromatic lactate dehydrogenase; 1.1.1.222, diiodophenylpyruvate reductase; E.C. 1.1.1.96)

1. Reduction

Dog heart enzyme is a cytosolic dimer, monomeric molecular weight 40 000, pI 5.4, which requires NADH. Activity is also found in brain, kidney and liver, and is considered to be associated with an isozyme of malate dehydrogenase. The best substrate is 3,5-diiodophenylpyruvate, with good activity towards phenylpyruvate and indole-3-pyruvate [A2917].

In vivo studies have demonstrated this activity in rat [A2961, A3327]; reduction is catalyzed by

lactate dehydrogenase (E.C. 1.1.2.3) and aromatic alpha-keto acid reductase [A3327]. Highest activity is found in heart, and (in reducing order) in kidney, muscle and liver. 3,4-Dihydroxyphenylpyruvate is 10 times as active as 3-methoxy-4-hydroxyphenylpyruvate. Oxamate (a lactate dehydrogenase inhibitor) does not inhibit liver mitochondrial enzyme [A2983].

In a range of animals cytoplasmic malate dehydrogenase (E.C. 1.1.1.37) has been found to be identical with aromatic alpha-keto acid reductase (with *p*-hydroxyphenylpyruvate as substrate), with lactate dehydrogenase accounting for a minimal proportion of the total activity found in these species. The studies were carried out on flight muscle of Falco, Milvago, Herpetotheres, Phalcobanes, Spiziapteryx and Polyhierax, Palaemonedes (a marine invertebrate), and frog liver and muscle. The activity in Fundulus grandis (a marine fish) is identified as lactate dehydrogenase [E561].

Coleus blumei enzyme has an optimum pH between 6.5 and 7.0, requires NAD(P)H, and reduces the physiologically important pyruvates *m*- and *p*-hydroxy-, 3,4-dihydroxy- and 4-hydroxy-3-methoxyphenylpyruvates [E660, G289].

Candida guilliermondi enzyme requires NAD(P)H [A2483].

Candida maltosa enzyme is a tetramer, molecular weight 250 000–280 000, monomeric molecular weight 68 000. It requires Mn^{2+} and NAD(P)H for reduction; the reaction is reversible, with optimum pH 6.5 for reduction, and 9.5 for oxidation. Substrates studied are phenylpyruvate, *p*-hydroxyphenylpyruvate, indole-3-pyruvate and the corresponding lactates [D975].

Lactobacillus casei D-hydroxyisocaproate dehydrogenase reduces phenylpyruvate to D-phenyllactate [E587].

2. Oxidation (indolelactate dehydrogenase; E.C. 1.1.1.110)

Formation of phenylpyruvate from phenyllactate has been recorded in rat, Candida, Lactobacillus, Neisseria, Pseudomonas and Rhodotorula [B438, D975, E377, F92, G774, K95]. A similar reaction has been detected in rat for *m*-hydroxyphenyllactate and vanillactate [A2961]. In addition, *p*-hydroxyphenyllactate is oxidized by Neisseria gonorrhoeae [F92], and indole-3-lactate by Candida maltosa (see above) [D975].

Cinnamyl alcohol dehydrogenase (E.C. 1.1.1.195)

Aralia cordata enzyme is a heterodimer, molecular weight 72 000. The reaction is reversible, the reverse requiring NADPH. Substrates are coniferaldehyde, sinapaldehyde, coniferyl alcohol and sinapyl alcohol [G815].

Eucalyptus gunnii contains two isozymes; one is monomeric, molecular weight 38 000, and the other, molecular weight 83 000, is a heterodimer [G660].

Loblolly pine enzyme is a dimer, monomeric molecular weight 44 000. It reduces coniferaldehyde and sinapaldehyde [G484].

Nicotiana enzyme, which is composed of two isozymes, molecular weights 42 500 and 44 000, requires NADP [G458].

Spruce (Picea abies) enzyme is a dimer, molecular weight 42 000. Substrates are coniferaldehyde, *p*-coumaraldehyde, coniferyl alcohol and *p*-coumaryl alcohol with NADP(H) as co-substrate [G781].

Etiolated wheat seedlings contain three isozymes; the molecular weights of two of these are 40 000 and 45 000. Substrates are coniferaldehyde, *p*-coumaraldehyde and sinapaldehyde [H510].

Among those species studied, the enzyme is not found in Pteridophyta or monocotyledonous angiosperms (except Zea). It is mostly found in gymnosperms and dicotyledonous angiosperms. It is usually a single enzyme, except in a range of Salix species (three to eight isozymes, usually four). It is not the same as alcohol dehydrogenase; it requires NADP, whereas alcohol dehydrogenase requires NAD [A1732].

Benzyl 2-methyl-hydroxybutyrate dehydrogenase (E.C. 1.1.1.217)

Reduction of benzyl 3-oxo-2-methybutyrate to (2*R*,3*S*)- and (2*S*,3*S*)-benzyl 3-hydroxy-2-methylbutyrate in Candida albicans, Endomycopsis fibligera, Hansenula anomala, Lipomyces starkeyi, Pichia farinosa, P. membranaefaciens, Rhodotorula glutinis, Saccharomyces cerevisia and S. acidifaciens has been detected [K940].

Methyl 2-oxo-3-phenylbutyrate reduction

This reaction has been found in Candida albicans, Endomycopsis fibligera, Hansenula anomala, Kloeckera saturnus, Lipomyces starkeyi, Pichia farinosa, P. membranaefaciens, Rhodotorula glutinis, Saccharomyces cerevisiae, S. acidifaciens, S. delbruechii and S. fermentati. Different organisms form different ratios of stereoisomers [K883].

2-Hydroxy-6-oxo-6-phenylhexa-2,4-dienoate reductase (E.C. 1.3.1.40)

Pseudomonas cruciviae enzyme is composed of three isozymes. One, molecular weight 170 000, requires NADPH, and also reduces the methyl ester of the above compound (which forms 2,6-dioxo-6-phenylhexanoate) [E156].

Indanol dehydrogenase

(*S*)-l-Indanol ↔ 1-indanone

Human placenta oxidizes 1-indanol to 1-indanone, with $NAD(P)^+$ as cofactor. Most of the activity is present in microsomes, with some in mitochondria but little in the cytoplasm [D415].

Japanese monkey liver cytosolic enzyme, molecular weight 36 000 and pI 8.7, requires $NAD(P)^+$ for oxidation and NADPH for reduction; the amino acid composition has been determined. The specificity is broad for cyclic alcohols such as (*S*)-1-indanol, benzene-1,2-dihydrodiol and 1-hydroxytetralin, and for aldehydes and ketones in which the oxo-group is conjugated with the aromatic nucleus, such as benzaldehydes and acetophenones. The activity with (*R*)-1-indanol is much lower than with (*S*)-1-indanol [F241]. Four isozymes have been found, two major and two minor; classical indanol dehydrogenase is one of the major isozymes. Quantitative studies show that (*S*)-l-indanol and 1-acenaphthenol are the best substrates. One minor isozyme has a similar specificity, and differs mainly in that the pI is 7.9. The other major isozyme, molecular weight 38 000 and pI 6.2, shows a similar activity for each substrate studied. The product from benzene-1,2-dihydrodiol is catechol. The other minor isozyme that was studied does not oxidize (*S*)-1-indanol, but does oxidize dihydrodiols to catechols. The main activity for these enzymes is the reduction of nitrobenzaldehydes [F388].

Rabbit liver cytosolic enzyme is not separable from 3-hydroxyhexobarbital dehydrogenase, and like the monkey enzyme the specificity is broad [A2032].

Oestradiol 17α-dehydrogenase (E.C. 1.1.1.48)

Rabbit liver enzyme (see oestradiol 17β-dehydrogenase) oxidizes 17α-oestradiol and its 3-glucuronide [A157]. Chicken liver enzyme is marginally active towards 17α-oestradiol [B748].

Oestradiol 17β-dehydrogenase (E.C. 1.1.1.62)

17β-Oestradiol ↔ oestrone

Human ovary enzyme, optimum pH 8.1 and 6.9 for the forward and reverse reactions respectively, is cytosolic, with NADP(H), or less effectively NAD(H) as cofactors for reduction; 3-methoxyoestrone and 3-methoxy-17β-oestradiol are better substrates than the parent compounds [A3086].

Human endometrium enzyme utilizes $NAD(P)^+$; reduction is not stimulated by

NADPH [A732]. Its activity increases at the end of the proliferation phase of the oestrus cycle, reaches its maximum value by the mid-secretory phase and falls towards its original value at the end of this phase. It then remains constant at about 5 per cent of the maximum value throughout the proliferative phase [A1104].

Human enzymes, both foetal and maternal, have an optimum pH of about 9, and are very unstable at -20° [A 1551]. The reverse reaction, which is catalyzed by placental enzyme, is inhibited by ATP, especially with NADPH as cofactor. In contrast, ATP inhibition is more marked with NADH when 16α-hydroxyoestrone is the substrate [A1775]. Placental enzyme activity is not affected by prostaglandins [A374]. Kidney enzyme oxidizes 17β-oestradiol and its 3-sulphate and glucuronide conjugates [A1214]. Both human and rat erythrocyte enzymes reduce oestrone and its sulphate conjugate [A518].

Rabbit liver enzyme oxidizes 17α- and 17β-oestradiol and their 3-glucuronides. Soluble enzymes have been separated into three fractions. One, that oxidizes both 17α-compounds, has been further separated into five sub-fractions by isoelectric focussing, each of which exhibits different kinetics. The second fraction oxidizes 17β-oestradiol, and the third 17β-oestradiol-*β*-D-glucuronide [A157].

Sheep ovary 17β-hydroxysteroid: $NAD(P)^+$ dehydrogenase has a molecular weight of 70 000 and optimum pH 9.2 [A2389].

Rat liver microsomal enzyme reduces 16α-chlorooestrone; oestrone is inhibitory [A1749].

Chicken liver enzyme is composed of three isozymes, pI 6.0, 6.8 and 6.9, and optimum pH 9.9 for the forward reaction. Two isozymes have molecular weights of 43 000 and 97 000. The reaction requires $NADP^+$; the reverse reaction utilizes NADPH. 17α-Oestradiol is marginally active, but oestriol is not a substrate. *p*-Chloromercuribenzoate is inhibitory [B748].

Cochliobolus lunatus enzyme acts on oestrone and alkyl steroids as well as quinones, aldehydes and ketones [K378].

Flavanone reduction (E.C. 1.1.1.234)

Flavanone → hydroxyflavan

Cryptomeria japonica enzyme is cytosolic, molecular weight 133 000 and optimum pH 7. It requires NADPH with (+)-aromadendrin and (+)-dihydroquercetin as substrates [E758].

Matthiola incana flower enzyme, optimum pH about 6, requires NADPH; NADH is not so good. It reduces (+)-aromadendrin to 3,4-*cis*-3,4,4′,5,7-pentahydroxyflavan; it also reduces (+)-dihydroquercetin and (+)-dihydromyricetin [D782].

Dihydrokaempferol 4-reductase (E.C. 1.1.1.219)

Matthiola incana flower enzyme, optimum pH about 6, forms *cis*-3,4-leucopelargonidin from dihydrokaempferol. Other substrates are (+)-dihydroquercetin and (+)-dihydromyricetin [D782].

Codeinone reductase (E.C. 1.1.1.247)

Papaver somniferum enzyme, a monomer molecular weight 35 000 requires NADPH for reduction of (−)-codeinone and a range of morphinan ketones, but does not act on other aldehydes and ketones [K756, K757].

Naloxone reductase (E.C. 1.1.1.128)

Rat liver enzyme, molecular weight 34 000 and pI 5.9, which reduces naloxone to 6β-naloxol, is identical to 3α-steroid dehydrogenase. It also reduces benzaldehydes, acetophenones, quinones and non-aryl ketones [J744]. In guinea pig the 6α-isomer is formed [F579].

Daunorubicin reductase

Human liver contains four isozymes, three with optimum pH 6.0, and the fourth, possibly an

aldehyde reductase, optimum pH 8.5. Their molecular weights are in the range of 30 000–40 000 [C531]. Two isozymes of human brain aldehyde reductase reduce daunorubicin, pI 5.3 and 7.9 [B569].

Rabbit liver contains two reductases with optima at pH 6.0 and 8.5. Their properties indicate that they are ketone reductase and aldehyde reductase respectively [B402]. One, tentatively identified as E.C. 1.1.1.2, reduces daunorubicin less well than other substrates. Sodium chloride activates, with maximal activity at an ionic strength of 0.4, but it causes less activation at higher concentration. Sodium sulphate inhibits at ionic strength 1, but it activates at low concentration [A2007]. In one study only two of seven carbonyl reductases (E.C. 1.1.1.184) examined, pI 4.9 and 6.0–6.3, reduced daunorubicin [A3950].

Rat liver enzyme, molecular weight 39 000, pI 6.3 and optimum pH 8.5–9.0, is probably monomeric and requires NADPH. It also reduces some sugar aldehydes and straight chain aldehydes. The amino acid composition has been determined [A50, A1327].

Two classes of reductase found in both human and rabbit liver have optima at pH 6.0 and 8.5, whereas in mouse and rat liver the optimum pH is 8.5. These activities can be further separated by isoelectric focussing: Rabbit 'pH 6.0' enzyme: molecular weight 32 300, 3 isozymes, pI 4.8, 5.3 and 6.3; 'pH 8.5' enzyme: molecular weight 36 000, 2 isozymes, pI 5.9 and 6.3, with numerous minor forms in both classes. Human 'pH 6.0' enzyme: molecular weight 34 500; 'pH 8.5' enzyme, molecular weight 38 700; these are less clearly separated into isozymes than rabbit enzyme. Relative to rabbit, the activities in mouse, rat and man are very low. Adriamycin is also a substrate for human and rabbit enzymes, molecular weights 34 500 (man) and 32 800 (rabbit). In man, the isozymes are similar to daunorubicin reductases with four isozymes, all with pI 5.4, as well as a number of minor isozymes [B169].

Steffimycinone reductase

This reaction, which occurs in Streptomyces nogalacter, forms steffimycinol with an optimum at pH 7. It requires NADPH; NADH is inactive [A2759].

Salutaridine reductase (E.C. 1.1.1.248)

Papaver somniferum enzyme, molecular weight 52 000, pI 4.4 and optimum pH 6.0–6.5 (reverse reaction pH 9.0–9.5), forms (7*S*)-salutaridinol, a precursor of morphine. It is highly specific [K758].

Other ketone reductases

Rabbit liver enzyme, which is cytosolic, molecular weight 33 000 and optimum pH 6.2, requires NADPH. It reduces aryl ketones as well as alkyl ketones such as 2-(4-(2-oxocyclopentyl-methyl)phenyl)propionate [D125].

Aldehyde dehydrogenases (E.C. 1.2.1.3, 1.2.1.4, 1.2.1.5, 1.2.1.7, 1.2.1.28, 1.2.1.29, 1.2.1.39)

$$R.CHO \rightarrow R.COOH$$

Pig brain contains an enzyme that oxidizes the physiologically important aldehydes 5-hydroxyindole-3-acetaldehyde, 4-hydroxy-3-methoxy- and 3,4-dihydroxyphenylacetaldehydes, D-3,4-dihydroxyphenylglycollaldehyde as well as *d*- and *l*-*p*-hydroxyphenylglycollaldehyde [A1287].

Rat liver enzyme is found in mitochondria (three isozymes, pI 5.4, 5.6 and 6.9) and cytosol (five isozymes, pI 5.8, 6.05, 6.15, 6.6 and 7.4). All of them oxidize *p*-nitrobenzaldehyde and 3,4-dihydroxyphenylacetaldehyde [B659]. Cytosolic enzyme oxidizes phenylacetaldehyde, and is induced by phenobarbital, DDT, polychlorobiphenyls and other xenobiotics [A2973]. Another study found three peaks of activity towards *m*-nitrobenzaldehyde. One isozyme required NADPH and a second required NADH. Both were identified as E.C. 1.1.1.2, the

second being a 3α-hydroxysteroid dehydrogenase. The third required NADH, and was identified as alcohol dehydrogenase, E.C. 1.1.1.1 [A1688].

Cucumber enzyme oxidizes indole-3-acetaldehyde to indole-3-acetate. It is a metalloflavoprotein that does not require cofactors [A3378].

Achromobacter euridice phenylacetaldehyde dehydrogenase (E.C. 1.2.1.39), optimum pH 8.9, requires NAD^+ (NADH does not catalyze the reverse reaction) and a monovalent cation (K^+ is best). The reaction is irreversible and is highly specific; there is some action with indole-3-acetaldehyde, but other aldehydes show poor activity. It is unstable, but it is protected by substrates or 10 per cent acetone [K869].

Acinetobacter calcoaceticus benzaldehyde dehydrogenase II has a molecular weight of 51 654, with 484 amino acid residues, based on nucleotide sequencing [J621]. It is a tetramer, optimum pH 9.5 [E596]. The reaction is not reversible [E473].

Dehydrogenase I, which is involved in mandelate metabolism, is a tetramer, subunit molecular weight 56 000, optimum pH 9.5 and pI 5.5. It requires NAD^+; $NADP^+$ is less effective. It oxidizes a large range of benzaldehydes. There is an associated esterase activity with *p*-nitrophenyl acetate as substrate [F366].

A Flavobacterium constitutive benzaldehyde dehydrogenase requires NAD^+, whereas a dehydrogenase induced by phenylglycine requires phenazinemethosulphate [E355].

Pleurotus eryngii aryl alcohol dehydrogenase oxidizes benzaldehydes and cinnamaldehydes, but mostly at a slow rate [G668].

Pseudomonas coniferaldehyde dehydrogenase, apparently a homodimer, molecular weight about 86 000 and optimum pH 8.8, requires NAD^+. Other substrates are *trans*-cinnamaldehyde, sinapaldehyde and benzaldehyde, but not vanillin [J707].

Pseudomonas putida produces two different aldehyde dehydrogenases depending on whether it is grown on *p*-cresol or 3,5-xylenol. The former enzyme is stable at 4°, but the latter enzyme is somewhat unstable at 4°; stability is improved in 10 per cent ethanol [A30]. Rhodopseudomonas acidophila contains two aldehyde dehydrogenases, one of which preferentially acts on aliphatic, and the other on aromatic aldehydes. The latter is a dimer, molecular weight about 70 000, optimum pH 9.0 and pI 4.74. It oxidizes cinnamaldehyde and a series of benzaldehydes [G246].

Streptomyces aldehyde oxidase, molecular weight about 80 000, oxidizes vanillin [F225].

Benzaldehyde dehydrogenase I has been found in a Bacterium [A730].

Aryl-aldehyde oxidase (E.C. 1.2.3.9)

Streptomyces viridosporus enzyme oxidizes vanillin and a range of benzaldehydes, but is inactive towards phthalaldehyde and aliphatics. It requires oxygen; peroxide is a second product [C284].

3-Formylindole/indole-3-acetaldehyde oxidases (E.C. 1.2.3.7)

Citrus enzyme, molecular weight 200 000 and optimum pH 7.5, forms peroxide as well as indole-3-carboxylate; it is highly specific [H80].

Pea indole-3-acetaldehyde oxidase is composed of two isozymes that are not activated by pyridine nucleotides. The main has optimum pH 4.5, and the other optimum pH 7.0, with 3-formylindole as another substrate. It is not a dismutase [G446, G520]. Another report states that the optimum pH is 8.0; it requires oxygen [B861].

3.4 *Reductions of acids*

Aryl-aldehyde dehydrogenase (E.C. 1.2.1.30)

a. $Ar.COOH \rightarrow Ar.CHO$

Clostridium formicoaceticum reductase, a dimer, monomeric molecular weight 67 000, contains iron and tungsten. It reduces a range of benzoates [G416].

Neurospora crassa enzyme has an optimum pH of 7. Benzoate initially yields benzoyl AMP, which then produces benzaldehyde. In the presence of hydroxylamine, benzoate yields benzoylhydroxylamate. Many benzoates and cinnamates are substrates, but a large proportion of these are at best very poor substrates.

The reaction scheme suggested is:

$$\text{Aryl acid} + Mg^{2+} + \text{ATP} \leftrightarrow \text{pyrophosphate} + \text{enzyme.acyl AMP}$$

$$\text{Enzyme.acyl AMP} + \text{NADPH} \leftrightarrow \text{aldehyde} + \text{AMP} + NADP^{+}$$

[A750].

Nocardia enzyme, molecular weight 140 000 or 163 000 (depending on the measurement method), reduces benzoate, and requires ATP and NADPH [H955]. N. asteroides enzyme, a monomer, molecular weight 152 000, requires ATP, NADPH and Mn^{2+}; benzoyl AMP is an intermediate in the reduction of benzoate. The enzyme acts on substituted benzoates, preferentially on *meta*-substituted acids, but usually not on those with *ortho* substituents. Some longer chain acids are also substrates [G207].

b. $Ar.COOH \rightarrow Ar.CH_2OH$

Rat brain enzyme reduces dopac to 3,4-dihydroxyphenylethanol, optimum pH 7.5; it is unclear whether an alcohol dehydrogenase is part of the system. It is activated by Zn^{2+}, Mn^{2+}, Co^{2+} and Cu^{2+}, and EDTA is inhibitory. 3,4-Dihydroxymandelate, 4-hydroxy-3-methoxymandelate and 4-hydroxy-3-methoxyphenylacetate are not substrates [H798].

Cinnamoyl CoA reductase (E.C. 1.2.1.44)

$$\text{Cinnamoyl CoA} \rightarrow \text{cinnamaldehyde}$$

Eucalyptus gunnii enzyme (cinnamoyl CoA: $NADP^{+}$ oxidoreductase), molecular weight 38 000 and pI 7, acts on CoA conjugates of ferulic, sinapic and *o*-coumaric acids [H330].

Glycine max enzyme, molecular weight 38 000 and optimum pH 6.1, requires NADPH. Substrates include CoA conjugates of ferulic, sinapic, *p*-coumaric, 5-hydroxyferulic, caffeic and cinnamic acids. It is inhibited by thiol-binding reagents [A2576]. Spruce and Glycine enzymes are similar; in another study they were found to be dimeric, with the molecular weight of the native enzymes about 70 000. The reaction is reversible [B922].

Populus euramericana enzyme, a homodimer, monomeric molecular weight 40 000, pI 7.5, is found in the stem. Substrates include CoA conjugates of ferulic, sinapic and *p*-coumaric acids, with NADPH as co-substrate [D54].

3.5 *Deamination*

D-Phenylglycine dehydrogenase

Flavobacterium enzyme, which requires phenazinemethosulphate as cofactor, acts on a number of D-amino acids, but not on the L-isomers. The product formed from D-phenylglycine is phenylglyoxylate [E355].

D-Amino-acid oxidase (E.C. 1.4.3.3)

$$R.CHNH_2.COOH + O_2 + H_2O \rightarrow R.CO.COOH + NH_3 + H_2O_2$$

Mouse enzyme acts on phenylalanine and tryptophan [C219]. In one mouse strain some animals are devoid of activity; the genetics demonstrate the involvement of an inactive allele [C219a].

Pig kidney enzyme has a monomeric molecular weight of 38 000 or 39 600 using different methods [A151].

Rat kidney enzyme acts on D-dopa, and is inhibited by D-alanine and benzoate. The appearance of 3,4-dihydroxyphenylpyruvate predominates over formation of dopamine in

kidney (presumably formed by reverse transamination of 3,4-dihydroxyphenylpyruvate followed by decarboxylation), but only at high substrate concentrations [A1393].

Studies on human, African green monkey, rat, pig and mouse kidney found activity with phenylalanine and tryptophan, but in chicken and frog the tryptophan activity was missing [C114].

Fish enzymes (electric eel, rainbow trout, carp, crucian carp and catfish) act on phenylalanine but not on tryptophan [C219].

L-Amino-acid oxidase (E.C. 1.4.3.2)

$$R.CHNH_2.COOH + O_2 + H_2O \rightarrow$$
$$R.CO.COOH + NH_3 + H_2O_2$$

These enzymes are an important component of snake venoms, and their concentration is sufficiently high in some to enable the raw venom to be used as a reagent for measuring specific amino acids.

Cerastes vipera oxidase is a dimer containing FAD, molecular weight 122 000, monomeric molecular weights 61 000 and 64 000 and optimum pH 7.5; phenylalanine is a substrate. It is activated by Cu^{2+} and Mn^{2+}, and inhibited by EDTA [G417].

Trimeresurus (Taiwan habu snake) venom enzyme is dimeric, molecular weight 140 000 and pI 5.4, and contains two mol FMN/mol. Substrates are phenylalanine and tyrosine [E770]. Another study found pI 8.4 for habu snake enzyme. During purification the specificity changes, suggesting that there are several isozymes [A636].

Viper palaestinae enzyme is composed of three isozymes, molecular weight 130 000 and optimum pH 8.8 with kynurenine as substrate [A1044].

Neurospora crassa enzyme, molecular weight 300 000, and optimum pH 9.5 probably contains four FAD/mol; phenylalanine is a substrate [A404].

L-Phenylalanine dehydrogenase (L-phenylalanine: NAD^+ oxidoreductase, deaminating, E.C. 1.4.1.20)

$$\text{L-Phenylalanine} + NAD^+ \leftrightarrow \text{phenylpyruvate} + NH_4^+ + NADH$$

Sporosarcina ureae and Bacillus sphaericus enzymes have been crystallized. They are both probably homooctamers, molecular weights 305 000 and 340 000, pI 5.3 and 4.3, optimum pH 10.5 and 11.3 (oxidation), and 9.0 and 10.3 (reduction) respectively. S. ureae enzyme acts on phenylalanine (best) and on tyrosine, tryptophan, phenylalaninamide, phenylalanine methyl ester and L-phenylalaninol. B. sphaericus acts on phenylalanine and tyrosine, but poorly if at all on the other foregoing compounds [E445]. S. ureae enzyme aminates pyruvates [E423]; its molecular weight has also been reported to be 290 000 [D919].

Microbacterium enzyme, a homooctomer, monomeric molecular weight 41 000 and pI 5.8, requires NAD^+ [J534].

Thermoactinomyces intermedius enzyme is a hexamer, monomeric molecular weight 41 000, that acts reversibly on L-phenylalanine [G222].

Nocardia enzyme is monomeric, molecular weight 42 000 and optimum pH 10 with phenylpyruvate, *p*-hydroxyphenylpyruvate and indole-3-pyruvate as substrates; other pyruvates are not substrates. The enzyme does not act on D-phenylalanine or other amino acids [F394].

Rhodococcus enzyme, optimum pH 10.1 for the forward reaction and 9.25 for the reverse, acts on phenylalanine (best), tyrosine and tryptophan and the corresponding pyruvates [E451]. It requires NAD^+ or analogues; NADPH and analogues are inactive. The reaction sequence is binding of NAD^+ prior to phenylalanine; the products are released in the order ammonia, phenylpyruvate and NADH [K558].

Bacillus sphaericus enzyme acts on several phenylpyruvates with *para* substituents, and phenylpyruvate analogues with different side chain lengths. The products are the corresponding amino acids, which are formed quantitively [G168].

Activity has only been found in one out of many Brevibacterium strains tested [D90].

L-Tryptophan dehydrogenase and 2′,3′-dioxygenase (E.C. 1.4.1.19)

Pea (optimum pH 8.5), maize and tomato enzymes require NAD(P) for the reversible formation of indole-3-pyruvate [G483]. It is found additionally in Prosopis juliflora (mesquite) and wheat, but not in Brassica [D968].

Chromobacterium violaceum L-tryptophan 2′,3′-dioxygenase forms 2′,3′-dehydrotryptophan as the initial product, which can then isomerize to the imine, from which indole-3-pyruvate is formed by hydrolysis. The reaction, which is specific for the L-isomer, requires an unmodified indole nucleus and a carboxyl group. It also acts on some peptide hormones that contain tryptophan residues as well as other tryptophan analogues [H664]. The enzyme is polymeric, molecular weight 68 0000, with monomeric molecular weights 74 000 and 14 000, pI 4 and a broad optimum pH 3–8. It is a haem-containing mixed function oxidase, which forms peroxide from oxygen. N-substituted tryptophans (which cannot isomerize) form 2′,3′-dehydro analogues of the substrates. Tryptamine, N-substituted tyrosine and phenylalanine are not substrates [H248]. Reaction with N-benzyloxycarbonyltryptophan involves a *syn* elimination [A2770].

In Pseudomonas N-acetyl-L-tryptophanamide forms N-acetyl-2′,3′-dehydrotryptophanamide in two steps, the first of which is enzymatic, and forms 5-(3-indolyl)-2-methyl-2-oxazoline-4-carboxamide. This then forms 2′,3′-dehydrotryptophanamide non-enzymatically with a time lag; at a lower pH, β-hydroxytryptophanamide is formed. The latter compound is further oxidized to β-oxotryptophanamide [A3617, C511]. Other products are indole-3-glycolaldehyde and probably indole-3-glyoxal [A3009].

Monoamine oxidases (MAO) (E.C. 1.4.3.4)

$$R.CH_2.NH_2 + O_2 + H_2O \rightarrow R.CHO + NH_3 + H_2O_2$$

These enzymes play an important part in the physiological control system for the catecholamine neurotransmitters in animals. Studies on these enzymes have led to the development of drugs that affect the amount of catecholamine available for neurotransmission, and, in consequence, valuable treatments for neurologically-induced illness have been developed as a result of the enormously extensive studies on this enzyme system. Of the many thousands of studies on monoamine oxidases it is possible to include in this review only a few that address basic enzyme properties.

a. Mitochondrial MAO.

MAO activity, which is associated with the inner mitochondrial membrane, is separated into two forms, distinguishable by inactivation by low concentrations of clorgyline at 10^{-8} M (MAOA) and deprenyl at 10^{-6} M (MAOB); these are 'suicide' inhibitors for MAO. In general, serotonin is oxidized by MAOA, and phenethylamine by MAOB [A1613, A1909, A2727, A2588]. Neither inhibitor is cleanly associated with MAOA or B; both inhibitions overlap in a concentration-dependent manner. Both clorgyline and pargyline (also an A inhibitor) and deprenyl initially inhibit reversibly, and this is followed by an irreversible phase. The conversion rate of clorgyline-inhibited MAOB (rat liver) into irreversibly inactivated enzyme is much slower than for MAOA. Deprenyl-inhibited MAOB is slowly converted into an irreversibly inactivated form, whereas there is no irreversible inactivation of MAOA by deprenyl [A1670, C46].

After solubilising human frontal lobe MAO with octylglucoside, MAOA and B were separated by chromatography on DEAE-Sepharose CL-6B [C682].

Studies using dopamine specifically labelled with deuterium in the α-position have demonstrated that the *R*- and not the *S*-deuterium is

removed [D606]. α,α-D_2-Phenethylamines (phenethylamine, tyramine and *m*-tyramine) are oxidized by rat liver microsomal enzyme at 25% of the rate for unlabelled compounds; the β,β-D_2-analogues show a slight enhancement in activity [B660].

Kinetic studies suggest that the substrate amino group hydrogen bonds to an amino group in the enzyme. Introduction of a β-or *p*-hydroxyl group leads to a sharp drop in binding free energy, accompanied by a shift from B to A type substrates, possibly with a shift in orientation of the bound substrate [A1957].

Human MAOB acts on phenethylamine, dopamine and tyramine [F754]. By using clorgyline to inhibit MAOA and deprenyl to inhibit MAOB, studies on liver, kidney and cerebral enzyme have found that serotonin and 3-methoxytyramine are substrates for MAOA and phenethylamine for MAOB, whereas dopamine, tyramine and tryptamine are substrates for both MAOA and B [A2967, E55].

Phenethylamine is oxidized by human lung MAOA and B, whereas serotonin only by MAOA [A3957].

Dopamine is oxidized mainly by MAOB in dopamine-rich human brain areas, whereas MAOA contributes significantly to dopamine oxidation in most other tissues [A3688].

Monoamine oxidase activity is almost unaltered from normal in a range of areas in postmortem human parkinsonian brain [A381].

Human placental MAOA oxidizes phenethylamine and serotonin [A3957], as well as kynuramine, MPTP and a large range of MPTP analogues substituted in the phenyl ring [F395].

Activity of human platelet enzyme, which is almost exclusively MAOB [A1901] fluctuates during the oestrous cycle, with a maximum about the time of ovulation, and then drops by about 23 per cent to a minimum 5–11 days later [A367]. Activity is evenly distributed throughout human heart [A756]. A particulate enzyme in blood, thought to be mitochondrial, has an optimum pH between 6 and 8.8 depending on substrate, apparently without correlation with A and B status [A2010].

Rat liver enzyme can be distinguished into two distinct activities by the action of clorgyline and aryl nitriles [A367]. It is inhibited by the thiol-binding compounds nitroprusside and 5,5′-dithiobis(2-nitrobenzoate). Neither arsenite nor thiols are inhibitory [A238]. Hydroxylamine rapidly inhibits activity towards tyramine and benzylamine within one minute, whereas after one hour the activity towards tyramine, but not benzylamine is increased [A 1760]. It migrates electrophoretically as several bands, but after treatment with perchlorate, which releases lipid without change in activity, only one band is found [A 1039]. Using tyramine as substrate K_m for MAOA and B are different [B661]. Both MAOA and B oxidize tryptamine, N-methyltryptamine, serotonin and 5-methoxytryptamine, whereas N-methylserotonin, bufotenine and N,N-dimethylserotonin are selective for MAOA, and N,N-dimethyltryptamine is selective for MAOB [B653].

Another study found that rat brain MAOA is heat stable, whereas B is labile. A and B are partially separated by sucrose density gradient centrifugation [A1227, A1309, Al841]; more MAOB is found in high-density mitochondria [A1909]. Both A and B are fairly evenly distributed throughout brain [A2386]. Brain enzyme is inhibited reversibly by β-propiolactone and β-nitropropionate [A1800], by apomorphine [A2069] and atropine (also heart enzyme) [A1898]. The specificity of A and B are similar to human enzyme (above) [A1324]. Brain mitochondrial enzyme has an optimum pH of 7.5 for dopamine and tyramine, 8.2–8.5 for serotonin and tryptamine, and 9.1 for kynuramine. Similar results were obtained with beef brain mitochondrial enzyme [A1285]. Brain MAOA oxidizes dopamine better than MAOB [A2484]; *m*- and *p*-tyramine are substrates for both isozymes, whereas *o*-tyramine is substrate only for MAOB [A3667]. The ratio of B to A in synaptosomal mitochondria is about 1/2 that for extrasynaptosomal mitochondria from whole brain; the ratio is lower in striatal mitochondria than in cerebellar, and in cortical mitochondria it is lower still [A2487]. One study, however, suggested that both isozymes are probably

extraneuronal [A3619]. Rat skeletal muscle contains both MAOA and B; A is more heat labile than B [A1798].

Rat brain enzyme activity increases sixfold to the adult level in the first 10 days following parturition [A2490].

Spinal cord transection in rat has no effect on cord MAOA or B activity [A562].

3-(N-Cyclopropyl)-5-phenylethylamino-1,2,4-oxadiazole is specific inhibitor for rat liver MAOA. Substitution with methyl or chloro in the *p*-position of the phenyl ring does not alter selectivity. Other substrates substituted on the *m*-position partially or completely lose their selectivity for MAOA [A794].

Rat A and B arterial isozymes are partially soluble. After treatment with 6-hydroxydopamine 70 per cent of MAOA activity was lost, whereas B was unaffected [A1045]. Rat lung shows both MAOA and B activities [A2161, A3863]. Another study found MAOB in pancreas as well as in lung, liver, kidney and brain [A2835].

Rat placental MAO activity increases threefold from day 15–20 of gestation, and then declines by 50 per cent at term [A2469].

Rat heart enzyme is mainly MAOB at three weeks post partum, a mixture of A and B at eight weeks and only A in the adult [A3665].

Studies on partially lysed MAOA and B from rat hepatoma indicate that the peptide chains are different in these isozymes [A3683].

In rat, a series of oxo analogues of phenylethanolamines are converted into mandelic acids, with phenylglyoxals as the initial products. The reaction is much faster than with the corresponding phenylethanolamines [J287]. Further studies (Goodwin, B.L., Ruthven, C.R.J., unpublished) with human placental MAO showed that MAOA oxidizes these β-oxophenethylamines.

Beef liver MAOB acts on benzylamine, MPTP and a large number of MPTP analogues substituted on the phenyl ring [F395]. These results (and the results for human MAOA) suggest that MAO is involved in MPTP-induced parkinsonism, and if parkinsonism is caused by the action of an environmental amine, the involvement of MAOB might explain the claimed beneficial effects of deprenyl in parkinsonism; MPTP does not appear to be the enviromental toxin [K948].

A study on beef brain cortical enzyme, using clorgyline, pargyline, harmaline and deprenyl as inhibitors suggested that the inhibition pattern is too complex to be simply due to MAOA and B. A two-stage inhibition is postulated, involving a rapid reversible step at two different binding sites, followed by a slow irreversible phase [A2181]. Treatment of this enzyme with cyanoacetyl hydroxyethylhydrazide induced the ability to oxidize histamine, cadaverine and analogues; this was prevented by pre-treatment with clorgyline, but not with deprenyl [A19l6].

Guinea pig brain activity increases 2.5-fold in the first 35 days following parturition, to 50 per cent of the adult level [A2490].

In hamster the ratio of MAOB to A activity varies from tissue to tissue. The ratio in brain is about 0.03, and in heart, lung, liver and spleen it is higher, but less than 1. In rat, the ratio is also consistently less than 1 in these tissues, but the ratio between tissues is different from that found in hamster. In rabbit the ratio for the above tissues is close to 1 [A2588].

Japanese monkey platelet enzyme is mostly B, with three components, molecular weights about 60 000, pI 5.5, 6.5 and 7.0, whereas liver enzyme has pI 6.5. They can be solubilized with Triton X-100 [F758].

Mouse lung mitochondria, after fractionation by sucrose density gradient centrifugation, are separated into fractions with more MAOB than A in the higher density mitochondria [A1895]. Enzyme activity in the eye decreased after day one post-partum, increased to a peak at day five and then fell to the adult level at 14 days [A946]. In brain, it increased from day one to the adult level at two weeks except in cerebellum, where a slight increase continued until after week six [A1105]. Using tryptamine as substrate, brain and liver enzymes are inhibited by a range of β-carbolines, especially harmine and harmaline [A2178].

Pig brain enzyme shows a time-dependent inhibition by several N-substituted propargylamines, although this study found that

not all compounds with this structure are inhibitory [A74]. A pig liver mitochondrial enzyme that acts on benzylamine (a benzylamine oxidase?) is a polymer with molecular weight about 1 200 000 containing about eight Cu and subunit molecular weight 146 000 [A1033]. Pig dental pulp membrane-bound enzyme (presumably mitochondrial) oxidizes a range of amines, particularly phenethylamine and tryptamine [B206]. Pig heart enzyme oxidizes serotonin, tyramine and benzylamine, it is inhibited by clorgyline, and is considered to be heterogeneous [A2587]. The development pattern differs from organ to organ. Liver enzyme activity falls by 40 per cent at birth, and then increases threefold to the adult level at one month. Kidney and spleen activities rise steadily from 10 days pre-partum until 70 days post-partum. Heart activity reaches a maximum near birth, and then declines by 80 per cent over two months. Brain activity declines slightly near birth, and then increases slightly to the adult level; adrenal enzyme shows a similar pattern [A1569].

Rabbit lung and brain enzymes are inhibited reversibly by imipramine, DMI and DDMI [A94]. The ratio of MAOA to B in heart, kidney, lung, liver, spleen and brain is about 1 [A2588], and both A and B are found in platelets [A2326].

Terbutaline and orciprenaline are not substrates for rat and human liver MAO [A724].

The ratio of chick CNS MAOA and B depends on site, using phenethylamine and serotonin as markers. The highest ratio is found in spinal cord and lowest in cerebrum [A2386]. Brain enzyme activity is detectable at 14 days incubation, and increases steadily until 2 days post-hatching [A1413].

Squid brain enzyme can be differentiated into A and B [E147].

b. Benzylamine oxidase (E.C. 1.4.3.6).

In man, the enzyme is found in all vascular tissues, localized in smooth muscle [B537]. Serum activity is reduced in burns and cancer patients [A2965]. It appears to be present in lung and placenta; however, benzylamine oxidation is considered to be catalyzed by MAOB in liver [A3957].

Human plasma and rat lung enzymes are not inhibited by deprenyl at 10^{-4} M (both MAOA and B are inactivated at this concentration) or by clorgyline, but semicarbazide, procarbazine and carbidopa are inhibitory. It is found (high activity) in aorta and lung, with slightly less in colon, ileum stomach, portal vein and duodenum, with low activity in some other tissues, including serum. Rat enzyme also oxidizes dopamine and phenethylamine, but these are not substrates in man [A2835, A3690].

Beef aorta enzyme is separable into two fractions; the major is particulate (probably not mitochondrial), and the minor cytosolic. N-Methylbenzylamine is a substrate only for the particulate enzyme. Carbonyl-binding reagents, especially pargyline are inhibitory [A574]. It is proposed that the mechanism for beef liver enzyme is ping-pong, with an imine intermediate being hydrolyzed to ammonia and aldehyde, with reduced flavoenzyme reacting with oxygen to form peroxide [A967].

Pig plasma enzyme is a dimer, monomeric molecular weight 95 000. Water of hydration bound to enzyme Cu^{2+} rapidly exchanges [A1025]. Heart enzyme has a molecular weight of 97 000, the same as plasma enzyme. It, also, is inhibited by carbonyl-binding reagents, and contains two Cu/mol [J833].

Pig dental pulp enzyme (soluble) oxidizes benzylamine, tryptamine and (less well) tyramine, but serotonin and phenethylamine are very poor substrates. This distinguishes it from MAOA and B [B206].

Rat brain contains a soluble enzyme that oxidizes kynuramine, but is not inhibited by deprenyl or clorgyline; this may be benzylamine oxidase [C186].

Rabbit enzyme that oxidizes mescaline appears to be similar to benzylamine oxidase [A1666].

c. Microorganism MAO.

Arthrobacter globiformis contains a soluble, Cu^{2+}-dependent enzyme (E.C. 1.4.3.6) that oxidizes phenethylamine. The peptide chain contains a 2,4,5-trihydroxyphenylalanyl residue as its quinone; this acts as cofactor in the

reaction. It is formed spontaneously from a specific tyrosyl residue by the action of Cu^{2+} [H298]. The enzyme is a homodimer, molecular weight 141 000, with optimal activity and stability at pH 6.5. The products are presumably aldehydes, with peroxide as a second product. Other substrates include 3-phenylpropylamine, tyramine, dopamine, octopamine, tryptamine and 4-phenylbutylamine, but not benzylamine or aliphatic amines; carbonyl-binding reagents are inhibitors [F626, H912].

E. coli contains a phenethylamine oxidase with the above quinone cofactor, which is formed spontaneously by incubation of the enzyme at 30° and pH 6, especially at low enzyme concentration [H422].

Micrococcus luteus enzyme is a homodimer containing FAD, monomeric molecular weight 49 000 by standard methods; DNA studies indicate a molecular weight of 49 100, with 443 amino acid residues. Substrates include tyramine, adrenaline, dopamine and noradrenaline. It is inhibited by reagents specific for MAOA and B [K420].

MAO is membrane bound in some bacterial species, but is not present in others. It has been detected in Klebsiella, Escherichia, Salmonella, Pseudomonas, Brevibacterium and Micrococcus, and is induced by tyramine. Substrates include tyramine, dopamine, and (except in Micrococcus) octopamine and noradrenaline [B225].

d. Unspecified enzymes.

Helix pomatia enzyme is found in crop and nervous system, and a little in the heart [A657].

Hymenolepis diminuta enzyme is membrane-bound. It oxidizes (in decreasing order) dopamine, adrenaline, noradrenaline, tryptamine, tyramine and octopamine, but not serotonin or benzylamine. Inhibitors include cupferron, α,α-dipyridyl, iodoacetamide, pargyline, nialamide and iproniazid, but not azide, hydroxylamine or semicarbazide [A3815].

Tetrahymena pyriformis MAO oxidizes tryptamine, dopamine and serotonin. The activity increases in the pH range 6.5–7.8 [A3131].

Spermine: oxygen oxidoreductase (deaminating; E.C. 1.4.3.3)

Sheep plasma enzyme acts on benzylamine and nuclear-substituted benzylamines, tyramine, tryptamine and serotonin [A535].

Monoamine dehydrogenases

Rat brain enzyme, which has also been called ephedrine-neotetrazolium chloride reductase (neotetrazolium chloride is the hydrogen-receptor co-substrate), is mainly mitochondrial, but some is cytosolic, with a dialysable heat-labile cofactor; $NADP^+$ activates it. Substrates include ephedrine, adrenaline, tryptamine, serotonin, tyramine and noradrenaline, optimum pH 7.5. It is inhibited irreversibly by cyanide, but not by MAO inhibitors such as iproniazid or pargyline; iron chelators, such as *o*-phenanthroline and α,α-dipyridyl, are inhibitory. The nature of the reaction is not specified in Chemical Abstracts, but it appears to act on the amino groups, probably to form carbonyl compounds [A1053, A2489, A2490, A2802].

An Alcaligenes faecalis enzyme called aromatic amine dehydrogenase acts on tyramine and a range of phenethylamines to form aldehyde and ammonia, but not peroxide. The protein chain contains a crosslinked tryptophan tryptophanylquinone group, which is part of the redox system [H367, H421].

Pseudomonas aromatic amine dehydrogenase (aralkylamine dehydrogenase, E.C. 1.4.99.4) is an inducible tetramer composed of two pairs of monomers, molecular weights 46 000 and 8000 and optimum pH 7.5–8.0, depending on substrate (tyramine, serotonin, tryptamine, phenethylamine, benzylamine and, best, dopamine); the products are ammonia and aldehydes. Traces of iron and copper are found, but these may be artifacts. The amino acid composition has been determined [C517, K709].

Octopamine hydro-lyase (E.C. 4.2.1.87)

Pseudomonas aeruginosa enzyme is soluble and forms *p*-hydroxyphenylacetaldehyde [K709].

Synephrinase (E.C. 4.2.1.88)

Arthrobacter synephrinum enzyme, optimum pH 8.0 is cytosolic. It converts *p*-sympatol into *p*-hydroxyphenylacetaldehyde and methylamine, apparently anaerobically. It requires Mg^{2+} or Ca^{2+}, and is further activated by thiols. Tyramine, N-methyltyramine and hordenine are not substrates [A2915].

Nocardia also demonstrates this activity [E615].

Diamine oxidase (E.C. 1.4.3.6)

p-Dimethylaminomethylbenzylamine is oxidized by human kidney enzyme. A study on inhibitors revealed that a series of dimethylsulphonium and trimethylammonium compounds with a hydrocarbon chain consisting of up to 12 methylene units, trimethylsulphonium, tetramethylammonium and ammonium compounds as well as phenelzine are competitive inhibitors, whereas pargyline is an uncompetitive inhibitor. A series of isothiuronium and guanidinium compounds with a chain consisting of up to 12 methylene units, 5-methylisothiuronium, guanidine, methylguanidine, hydralazine, iproniazid, nialamide and other compounds are noncompetitive inhibitors [A1686].

An enzyme in pig kidney that is claimed to be diamine oxidase acts on *p*-substituted benzylamines and many aliphatic amines [A3693]; it may be identical with benzylamine oxidase (R. Lewinsohn, personal communication).

3.6 *Oxidative removal of substituents on amino groups*

N-Demethylation

$$R_1R_2NR_3 \rightarrow R_1R_2NH$$

Aminopyrine N-demethylase activity is lower in red-winged blackbird than in rat; this difference parallels lower levels of P450 in bird microsomes [A358]. In male rat, activity increases 20-fold in the first 10 weeks post-partum, most of which occurs in the first four weeks. In female rat, activity is three times higher at birth than in the male, and it increases a further threefold in the following five weeks [A736]. The results of another study on rat liver differed considerably from this in detail [A71]. In rabbit, the activity increases sharply from a low level at about 20 days post-partum, and then remains level or declines slightly to the adult level [A1980].

Aminopyrine is demethylated by catalase and cumene hydroperoxide by a free-radical mechanism. It is suggested that the active site for this reaction differs from the one involving hydrogen peroxide [B378].

d-Benzphetamine is demethylated as the preferred substrate by all six P450 fractions separated electrophoretically in one study on human liver [C798].

p-Chloro-N-methylaniline demethylase is found in chick embryo liver and human foetal liver, adrenal, brain and lung [B8l5].

N,N-Dimethylaniline is demethylated by rat P450, horseradish peroxidase, beef liver catalase, human placental and Glycine max lipoxygenases, lactoperoxidase and haemoglobin, whale myoglobin and chloroperoxidase. Using substrate labelled with deuterium on one methyl group an isotope effect is observed with all these enzymes, the extent of which is specific for each enzyme. High isotope effects found with most of the haemoproteins tested are considered to indicate a rate-limiting step of hydrogen atom abstraction from the α-carbon (in this case defined as the methyl group), whereas deprotonization of the α-carbon is postulated for a low isotope effect, as observed with P450 and chloroperoxidase [C814]. Lipoxygenases also act on a range of other N-methylated anilines, with the formation of formaldehyde, but without any evidence for the formation of N-oxides as intermediates. Glycine enzyme has an optimum pH of 6.5 [K419].

N-Ethyl-N-methylaniline is dealkylated to both monodealkylated products. NADH enhances dealkylation, but not N-oxidation; dealkylation of the corresponding N-oxide is very feeble. These

results, combined with the effects of selective inhibitors indicate that most of the dealkylation occurs directly, rather than via the N-oxide [A310].

Ethylmorphine N-demethylase is found in quokka, kangaroo, bettong, bandicoot, and possum (marsupials), as well as in rat [A2420]. Activity of rat and mouse liver enzymes is increased by EDTA and decreased by Fe^{2+}; this probably correlates with inactivation by lipid peroxides [A89].

Imipramine demethylase activity found in rat hepatocyte microsomes is suppressed by SKF 525-A, a P450 inhibitor [K168]. Glycine lipoxygenase catalyzes demethylation, with peroxide as oxidant; apparently a free radical is an intermediate, and formaldehyde is released. A number of imipramine analogues are also demethylated [K359].

Human haemoglobin can dealkylate N-methylaniline and benzphetamine [D135].

N-Methylephedrine is demethylated by rat liver microsomes. The enzyme is inhibited by CO or SKF 525-A, but not by methimazole or by pre-incubation [F501].

Rat liver P450 N-demethylates 15 different compounds, utilizing either O_2 and NADPH, or hydrogen peroxide. There is no correlation between the reaction rates corresponding to these mechanisms for the different compounds used; it is therefore considered that these are independent reactions [C669].

In rat, guinea pig and mouse N-demethylase activity is correlated with P450 activity [A627].

With some tertiary amines demethylation occurs in two stages, with the amine N-oxide as intermediate. This is described under the enzymes involved.

Demethylation of N-methylated amides

Rat liver microsomes demethylate N,N-dimethylbenzamide to form N-methylbenzamide and formaldehyde, with the corresponding N-hydroxymethyl compound as an intermediate. Several *para*-substituted N,N-dimethylbenzamides are also substrates [G683].

Amides from hippurates

Human bifunctional peptidylglycine α-amidating monooxygenase requires ascorbate, copper and oxygen, with hippurates as substrates. Salicyluric acid initially forms N-salicyl-α-hydroxyglycine, which then forms salicylamide and glyoxylate [K660].

Lipoxygenase (E.C. 1.13.11.12)

Glycine max enzyme, optimum pH 6.5, dealkylates aminopyrine by a free radical reaction, forming formaldehyde and peroxide. This is claimed to be a novel reaction [J526].

Formyltetrahydrofolate dehydrogenase (E.C. 1.5.1.6)

Pig liver enzyme, optimum pH 7.5, requires NADP; NADPH is ineffective. Tetrahydrofolate is formed, with the release of carbon dioxide from the formyl moiety [K877].

Pteridine/folate fission

Pseudsomonas acidovorans enzyme, named pteridine 6-methylaminohydrolase, acts on pteroate or folate (it is unclear which compounds were tested) to cleave the C–N bond linking the pteridine and aminobenzoate moieties. Structural considerations indicate that this is an oxidative reaction, with formation of *p*-aminobenzoate [A971].

Dealkylation of quaternary bases

N-Methylnaltrexone is demethylated by rat, dog, man and mouse [F486].

N-Debutylation

Man and monkey debutylate bupivacaine, but the reaction was not further studied [A255, J881, K14].

N-Oxide dealkylation

$$R_1R_2R_3NO \rightarrow R_1R_2NH$$

a. Aryl N-oxides (dimethylaniline-N-oxide aldolase; E.C. 4.1.2.24)

N,N-Dimethylaniline and *p*-cyano-N,N-dimethylaniline N-oxides are demethylated by bacterial $P450_{CAM}$ and rabbit liver $P450_{LM2}$ [D40]. Cytochrome c is also able to catalyse this reaction [B185].

b. Alkyl N-oxides

This reaction is observed *in vivo* in mammalia with N-oxides of tricyclic drugs such as imipramine [A3656], but is not well documented. It is complicated in that reduction to the parent drug followed by demethylation without involvement of the N-oxide may contribute to the observed results, although in man the urinary excretion of DMI is very much greater after dosing with imipramine-N-oxide than after imipramine (personal unpublished observation).

3.7 *Oxidations and reductions involving nitrogen atoms*

Tyrosine N-monooxygenase (E.C. 1.14.13.41)

Sorghum bicolor enzyme, which catalyzes this reaction is a P450. This is a key step in the formation of dhurrin [A3175, A3335, G228, H331, K711].

Oxidation of amino to nitro groups

$$R.NH_2 \rightarrow R.NO_2$$

Chlorphentermine is oxidized to 1-(*p*-chlorophenyl)-2-methyl-2-nitropropane in rabbit and man; it appears that the corresponding hydroxylamine is an intermediate [A177].

Oxidation of hydroxylamines to oximes

Rat liver microsomes oxidize N-hydroxyamphetamine to phenylacetone oxime. The enzyme is probably not P450, and oxygen is probably not the oxidizing species [B664].

Amidoxime formation from amidine

Rabbit liver microsomes convert benzamidine into benzamidoxime [E238, F230, G798]; the reaction has also been observed in rat [G990].

Conversion of imines into oximes

$$R.\,C = NH.\,CH_3 \rightarrow R.\,C = NOH.\,CH_3$$

Rabbit liver microsomes act on some acetophenone imines, including 2,6-di-, 2,4,6-tri-, 2,3,5,6-tetra- and 2,3,4,5,6-pentamethylacetophenone imine as well as 2,6-dichloroacetophenone imine. The reaction is also observed in hamster, rat, mouse, guinea pig and ferret. The product is mainly the *anti*-oxime and usually a small proportion (< 10 per cent) of the *syn*-isomer [D955].

Rabbit enzyme, which acts on 2,6-dimethyl-acetophenone imine and 2,6-dichloroaceto-phenone imine, is found in liver, with lesser amounts in lung [C243].

Oxime reduction to hydroxylamines

Rat liver microsomal (not P450) and cytosolic oxime reductases which act on acetophenone oxime require NADPH [A1452].

Oxime oxidation to nitro compounds

Both rat and rabbit liver oxidize 1-phenyl-2-propanone oxime to 2-nitro-1-phenylpropane [A1982, A3315].

Oxo formation from oxime

Rabbit liver aldehyde oxidase acts on the oximes of acetophenone, salicylaldehyde and benzamidine to form the corresponding oxo compounds [E358].

Aldoxime and nitrile formation from tyrosine

Triglochin maritima and Sorghum bicolor P450 both oxidize L-tyrosine to *p*-hydroxyphenylacetaldoxime. It is postulated that the reaction sequence is:

L-Tyrosine → N-hydroxy-L-tyrosine → N, N-dihydroxy-L-tyrosine → 3-(*p*-hydroxyphenyl)-2-nitrosopropionate;

the latter then decarboxylates and rearranges to the oxime. Further reaction steps lead to the formation of *p*-hydroxyphenylacetonitrile and *p*-hydroxymandelonitrile [H423, K216, K711]; the first of these steps has been confirmed directly in Sorghum, and the formation of dhurrin and *p*-hydroxymandelonitrile from the aldoxime confirms the side-chain hydroxylation reaction [A2914, J504]. Other potential precursors of *p*-hydroxymandelonitrile, such as *p*-hydroxyphenylacetamide, 1-nitro-2-(*p*-hydroxyphenyl)-ethane, *p*-hydroxyphenylacetaldoxime, tyramine and N-hydroxytyramine are ineffective in Sorghum [A3335].

Salicylhydroxamate reductase

Rat liver enzyme is a heterodimer, molecular weight 140 000–150 000 and pI 5.4. The product is salicylamide. Another substrate (poor) is N-hydroxy-2-acetamidofluorene [H16]. Both guinea pig and rabbit liver aldehyde oxidases catalyze this reaction, with an electron donor. Anthranilhydroxamate is another substrate [C897].

Aldehyde formation from N-nitrosoamine

Mouse liver microsomes form benzaldehyde from N-methyl-N-nitrosobenzylamine, with NADPH. The enzyme has also been found in mouse forestomach, as well as oesophagus, forestomach and liver of rat (in all cases, female) [B131].

N-Oxide formation with tertiary alkylamines

$$R_1R_2R_3N \rightarrow R_1R_2R_3NO$$

Rat liver and brain imipramine N-oxidase is a microsomal flavoprotein. After solubilization 2 isozymes were found, molecular weights 57 000 and 61 000, with optimum pH 8.5; the activity was rapidly lost at 45° [J174]. It is postulated that it is different from the dimethylaniline-oxidizing enzyme [C196]. N-Methylephedrine is oxidized by a rat liver flavoprotein, and inhibited by methimazole or by pre-incubation, but not by CO or SKF 525-A [F501]. Further studies on the liver enzyme found that two systems were involved, and its activity was lost rapidly by pre-incubation at pH 8.5, with little loss at pH 7.5. A high-affinity enzyme was inhibited by methimazole, an inhibitor of the flavin-containing monooxygenase, whereas a low-affinity enzyme was inhibited by SKF 525-A, suggesting that it is a P450 [K168].

Mouse and pig liver microsomal enzymes, which have an optimum pH of about 9, contain FAD and require NAD(P)H. Substrates include imipramine, as well as N,N-dimethyl- and N,N-diethylaniline [D446].

Methylphenyltetrahydropyridine N-monooxygenase (E.C. 1.13.12.11)

Mouse microsomal enzyme acts on MPTP to form the N-oxide [E979].

N-Oxide reductase

Rat liver reduction of the N-oxides of imipramine, cyclobenzaprine and brucine is observed in cytosol, mitochondria and microsomes, and requires NAD(P)H and menadione (or any of a range of quinones). It has been suggested that the cytosolic enzyme is DT-diaphorase plus a haem protein. The first reaction is considered to be the reduction of a quinone by a quinone reductase, followed by a non-enzymatic reduction of the N-oxide by the quinol, mediated by the haem group of haemoproteins [J563].

A rat liver mitochondrial enzyme, bound to the inner membrane, requires NAD(P)H to reduce imipramine-N-oxide as well as aromatic N-oxides. The activity is also found in microsomes, but the relative reaction rates for the substrates are different from those in mitochondria. It is inhibited by oxygen, and mitochondrial enzyme is partially inhibited by carbon monoxide [A1913].

Rat liver microsomes reduce octoclothepine-N-oxide to octoclothepine anaerobically (oxygen inhibits), with NADPH as co-substrate. It is also inhibited by carbon monoxide [B935]. Imipramine and tiaramide N-oxides are substrates, and the reaction requires NADH. It is inhibited by oxygen or carbon monoxide; the enzyme appears to be a P450 [A1847]

Rat liver xanthine oxidase or crude liver extract reduce benzydamine-N-oxide, optimum pH 9 for the xanthine-dependent reduction or pH 7 for the crude extract; there are at least two enzymes in the crude extract. There is a requirement for NAD(P)H or FMN [B307].

Rat blood reduces the N-oxides of imipramine, brucine and cyclobenzaprine, with menadione or other quinols as electron acceptor, and NAD(P)H as coenzyme. The enzyme appears to be haemoglobin [J876].

Rat, mouse, hamster, pig and rabbit liver cytosolic aldehyde oxidase as well as rabbit liver microsomes reduce the N-oxides of imipramine and cyclobenzaprine. Rabbit microsomal enzyme requires NAD(P)H. Cytosolic enzyme is not activated by NAD(P)H, but several compounds, including aldehydes, N′-methylnicotinamide and especially 2-hydroxypyrimidine are effective; with the latter compound the reaction rate is much greater than with microsomes [D218].

Reflux of N-oxides at pH 14 can remove the oxygen moiety [H894].

3.8 *O-Dealkylation*

e.g. 4-Methoxybenzoate monooxygenase (O-demethylating) (E.C. 1.14.99.15)

$$\mathrm{Ar.O.CH_2.R} \rightarrow \mathrm{ArOH} + \mathrm{RCHO}$$

Human haemoglobin can demethylate *p*-anisidine, anisole, *p*-methoxyphenol and *p*-nitroanisole [D135].

Rat liver microsomes demethylate *o*-, *m*- and *p*-methoxyphenols and *o*-, *m*- and *p*-anisoles. Studies with $^{18}O_2$ show a high oxygen incorporation with *o*- and *p*-methoxyphenols, and low incorporation with *m*-methoxyphenol. This suggests that demethylation of *o*- and *p*-methoxyphenols involves a quinone-type intermediate, with elimination of the entire methoxy moiety [J201]. 7-Ethoxycoumarin deethylase is composed of two isozymes, one low and the other high affinity [D666]. An activity confined to microsomes that is inhibited by carbon monoxide demethylates 2-methoxyoestrone and 2-methoxyoestradiol; it has a requirement for NADPH, suggesting a P450 involvement. Each compound appears to be demethylated by a separate isozyme [B668]. Hepatocyte microsomal enzyme demethylates 2,6-dichloro-4-nitroanisole with a broad optimum between pH 6.0–7.5 [A2855]. 1,3-Dichloro-2-methoxy-5-nitrobenzene demethylase, which is inhibited by vinyl chloride, may be composed of two isozymes. It is not induced by pre-treatment with 3-methylcholanthrene, i.e., it is not a P448 [A3495].

Rabbit liver microsomes demethylate *p*-nitroanisole and *p*-nitrophenetole. With NADPH as co-substrate (optimum pH 7.4) carbon monoxide inhibits, but with NADH as co-substrate (optimum pH 6.0) carbon monoxide is not inhibitory; cyanide inhibits neither demethylation, demonstrating that cytochromes

are not involved in the hydrogen transport system [A2545].

Rabbit 7-ethoxycoumarin deethylase activity begins to increase from a low level at day nine post partum in liver and at day 16 in small intestine. At 30 days the activity is at least as great as that in the adult [A1980].

7-Alkoxycoumarin dealkylation has been detected in mouse, guinea pig, rabbit, dog and monkey, with methyl, ethyl and propyl as the alkyl groups; it exhibits a requirement for NADPH and oxygen. 7-Butoxycoumarin is also dealkylated in rat; induction studies indicate that this involves a different enzyme [C160].

Activity of guinea pig, rat and mouse liver microsomal enzyme activity is correlated with P450 activity [A627].

Erythrocyte lysates from bear, beef, cat, dog, guinea pig, man, mouse, rabbit, pigeon, rat and sheep demethylate normetanephrine to noradrenaline, and at least in rat dopa, dopamine and adrenaline are formed from the corresponding 3-O-methyl compounds [A3063].

Red-winged blackbird liver microsomal enzyme acts on *p*-nitroanisole; the measured activity is lower than in rat, and follows a lower P450 content [A358].

Bacillus oxidizes *p*-hydroxyphenoxyacetate to quinol with the incorporation of oxygen from molecular oxygen [A3639].

Chaetomium piluliferum and Xerocomus badius (fungi) enzymes, optimum pH 5 and 7 respectively act on 3- and 4-methoxybenzoate, veratrate and 3,4-dimethoxycinnamate, with oxygen and NADH as co-substrates [K896].

Pseudomonas fluorescens *meta*-demethylating system is composed of two enzymes, one, a non-haem Fe-containing monooxygenase, is a dimer, molecular weight 118 000, and the other a NADH-dependent reductase, molecular weight 80 000 [A3627].

Pseudomonas putida demethylating system is composed of two enzymes, one a Fe-containing monooxygenase, molecular weight 120 000, and the other a Fe–S-containing NADH-dependent reductase, molecular weight 42 000 and optimum pH 8.0. Both are highly unstable in the presence of oxygen. The system demethylates *m*- and *p*-methoxybenzoate; use of uncoupling substrate analogues results in formation of peroxide [A903, A2952, K800]. P. putida Fe–S-containing reductase, pI 4.72, contains about 30 per cent carbohydrate; its amino acid composition has been determined. The Fe–S moiety is plant ferredoxin type, i.e., it contains S^{2-}. The enzyme has been given the trivial name Putidamonooxin I [A2954]; the two components have been called putidamonooxin and NADH-putidamonooxin oxido-reductase [K800]. The monooxygenase contains protein, iron and labile sulphur in the ratio 1:3.3:3.3 (the expected value is 1:4:4). Inhibition is brought about by Cu^{2+}, Hg^{2+}, *p*-chloromercuribenzoate and bathophenanthrolinedisulphonic acid [K801]. The optical absorption is altered by substrate. It has been postulated that this is a previously unreported enzyme type [A2955]. A Pseudomonas enzyme has been described that acts on *p*-methoxybenzoate and is specific for the *para* isomer [A563].

7-Ethoxyresorufin deethylase

Human liver enzyme is a P450 [J299]; many studies have found that 7-ethoxyresorufin can be used as a specific probe for CYP1A2. Activity is also found in lymphocytes [J245].

Rat liver microsomal enzyme dealkylates ethyl-, benzyl- and pentylresorufins [D421]. Liver, kidney and lung activity is associated with just one P450, at that time designated as P448. It is induced by the carcinogens benzo[*a*]pyrene and 1,2,5,6-dibenzanthracene, but not by benzo[*e*]pyrene and anthracene [C748]. Enzyme is also found in lung [J904] and intestine [A2127].

Alligator activity is much lower than in rat [J855].

Channel catfish liver microsomes dealkylate alkylresorufins with methyl, ethyl and benzyl, but not pentyl alkyl groups. After treating animals with 3-methylcholanthrene, all these compounds are dealkylated [E209].

This activity has been found in many other species, including dog, cat, rabbit, guinea pig, hamster, mouse, quail and trout [A2129, C562].

Carbon monoxide-dependent O-demethylase

Clostridium thermoaceticum enzyme demethylates methoxybenzenes and methoxybenzoates. Nitrogen or hydrogen cannot replace carbon monoxide, which is postulated to act on CoA to form acetyl CoA with the released methyl group [K457].

2,4,5-Trichlorophenoxyacetate oxygenase

Pseudomonas cepacia enzyme is a two-component system, one of which is a red protein and the other is a tetramer composed of two pairs of identical subunits, molecular weights 49 000 and 24 000. The reaction requires oxygen and NADH to form 2,4,5-trichlorophenol and glyoxylic acid [H644].

3.9 *Oxidations and reductions of non-aromatic ring systems*

Indane hydroxylation

Pseudomonas putida toluene dioxygenase (E.C. 1.14.12.11) hydroxylates a range of substituted indanes in the 1-position. About 70 per cent of the oxygen comes from water [E567, K207]. Naphthalene dioxygenase (E.C. 1.14.12.12) yields (+)-(1*S*)-indanol and (+)-*cis*-(1*R*,2*S*)indanediol as well as further oxidation products [H580].

Rhodococcus strains form *cis*-(1*S*,2*R*)-indanediol, with one exception, which forms the *trans*-(1*R*,2*R*)-isomer [K305].

In rat 1- and 2-hydroxylation occurs as well as the formation of *cis*- and *trans*-indane-1,2-diol [E533, F617].

1*H*-4-Oxoquinoline monooxygenase

Pseudomonas putida enzyme is a trimer, molecular weight 126 000, which requires oxygen and NADH. It is specific for 1*H*-4-oxoquinoline, which it hydroxylates at position 3 [G812].

Flavanone 2-hydroxylase

Licorice flavone synthase II acts on naringenin to form 2-hydroxynaringenin as a first step in flavanone formation [K290].

Flavanone 3-hydroxylase (E.C. 1.14.11.9)

Petunia hybrida enzyme, optimum pH 6.5–7.0, requires Fe^{2+}, ascorbate and α-oxoglutarate. It oxidizes naringenin to dihydrokaempferol, eriodictyol to dihydroquercetin and 3′,4′,5,5′,7-pentahydroxyflavanone to dihydromyricetin [D772]. In another study the enzyme was found to have a molecular weight of 74 000 and optimum pH 8.5. It oxidizes (2*S*)-naringenin to (2*R*,3*R*)-dihydrokaempferol and (2*S*)-eriodictyol to (2*R*,3*R*)-dihydroquercetin, but (2*R*)-naringenin is not a substrate [E72].

Tulipa anther enzyme oxidizes naringenin to dihydrokaempferol [F162].

This reaction has also been observed in Haplopappus gracilis [A200] and Petroselinum crispum [B957].

Matthiola incana requires oxygen, Fe^{2+}, ascorbate and α-oxoglutarate, forming dihydrokaempferol, succinate and carbon dioxide; eriodictyol is a second substrate [B679].

Isoliquiritigenin 3-hydroxylase

Dahlia variabilis petal enzyme, optimum pH 7.5, appears to be a cytochrome P450. The product is butein [J626].

Dihydrofolate reductase (tetrahydrofolate dehydrogenase; E.C. 1.5.1.3)

Calf and rat brain enzyme activities, which are low relative to rat liver, are inhibited by methotrexate [A3366].

Pig enzyme, molecular weight 20 000 and pI 8.6, is inhibited by methotrexate [A2480].

Calf and rat brain enzyme activities, which are low relative to rat liver, are inhibited by methotrexate [A3366].

Rabbit brain enzyme is found in cortex, stem, cerebellum and striatum, with highest activity in cerebellum, and a three-fold activity range between tissues [A3401]. Liver and brain enzymes, optimum pH 4.8, require NADPH. Brain activity is 15 per cent of that for liver. Both activities are abolished by methotrexate [A2011].

In dihydrofolate-deficient immature domestic poultry chicks, activity is doubled by folate or oestradiol, but these effects are not additive [A1680].

Drosophila menanogaster enzyme, molecular weight in the range 17 000–22 000, is monomeric, with optima at pH 4.8 and 8.5 [K458].

Daucus carota enzyme is cytosolic and appears to be a homotrimer, molecular weight 183 000, monomeric molecular weight 58 400 and optimum pH 5.9; it requires NADPH. It does not cross-react with antibodies against the human enzyme [K199].

Glycine max enzyme requires NADPH for activity; NADH is poor. It is inhibited by phosphate, but Cu^{2+} with phosphate activates. It is inhibited by N-ethylmaleimide, glutathione or aminopterin, and several iron-chelating compounds inhibit in the presence of phosphate, but diethyldithiocarbamate activates [A2343].

Helianthus enzyme, optimum pH 5.9–7.2 (buffer dependent) requires $NADPH_2$; the activity increases with increasing callus age [K461].

E. coli contains two isozymes, molecular weights 18 500. The activity of one is nearly constant in the pH range 4–9, whereas the other shows high activity at pH 4, but decreases almost to zero at pH 9 [A3113].

Lactobacillus leichmannii enzyme, molecular weight 20 000, Stokes radius 0.34 nm and optimum pH 7.4 is composed of 168 amino acid residues; the terminal amino acids have been determined and the presence of one active thiol has been detected. It is unstable above 35°. There are complex relationships between KCl and urea concentrations and the kinetics of the reaction. The reaction rate is greater at pH 6.5 than at 8.5, and the reaction rate is nearly linear with time. 1M KCl inhibits especially at pH 6.5, with non-linear reaction rates. Urea (4M) inhibits strongly, especially at pH 8.5. Urea and KCl together inhibit less at pH 6.5 and more at pH 8.5 than urea alone. Methotrexate (40 nM) is inhibitory in all situations, and the presence of urea and KCl together dramatically increases its effect [A6, K484].

The complete amino acid sequence of a Streptococcus faecium mutant has been determined [A2222].

Flavin mononucleotide reductases (NAD(P)H: flavin oxidoreductase; E.C. 1.6.8.1)

Human erythrocyte NADPH dehydrogenase reduces FMN, FAD, riboflavin, as well as methylene blue and dichlorophenolindophenol [A3008].

Benecka harveyi, a luminous bacterium, contains two isozymes; one (molecular weight 30 000) requires NADH, and the other (molecular weight 40 000) NADPH [A2305, A3095]. Another study found that the former isozyme is monomeric, molecular weight 24 000, and that NADPH is a poor co-substrate. FAD is another substrate [A3209].

Eubacterium enzyme, molecular weight 260 000 and optimum pH 6.8, has an absolute requirement for NADH. It reduces FMN, riboflavin, as well as methylene blue, menadione and dichlorophenolindophenol [B426].

Acetylindoxyl oxidase (E.C. 1.7.3.2)

Zea enzyme, optimum pH above 9, is found in leaf of etiolated seedlings and shoot sap (only after dialysis), and requires oxygen [K902].

Cannabinoid ring hydroxylases

Extensive studies with cannabinoids have demonstrated that hydroxylations occur at various positions in the molecule; however, few studies appear to have been carried out at an enzyme level. The literature on this subject is very extensive, and the references given are purely illustrative.

Cannabinoid 6α-hydroxylation

This reaction has been detected in rabbit, guinea pig, man, mouse and Thamnidium [A108, A1391, B742, C2, E7, F819].

Cannabinoid 6β-hydroxylation

This reaction has been detected in man, monkey, guinea pig and Thamnidium [B458, B742, C2, H418].

Hydroxylations of the side chains are described elsewhere.

Codeine 14β-hydroxylase

Pseudomonas putida carries out this reaction; codeinone is also a substrate [K311].

Desacetoxyvindoline hydroxylation

Catharanthus roseus enzyme, molecular weight 45 000 is probably monomeric, and is composed of three isozymes, pI 4.6, 4.7 and 4.8. Hydroxylation occurs at the 4-position, to form deacetylvindoline [H5].

3,9-Dihydroxypterocarpan 6a-hydroxylase

Glycine max P450 D6aH, molecular weight 55 000, catalyzes the reaction; it requires NADPH, and dilauroylphosphatidylcholine is the best activator found in a study to identify its lipid requirement [F242].

Geissoschizine dehydrogenase (E.C. 1.3.1.36)

Catharanthus roseus enzyme is highly specific and requires $NADP^+$; other oxidoreductive cofactors are inactive. It catalyzes the removal of the 21α hydrogen, to form a quaternary base [K700].

2′-Hydroxydaidzein reductase (E.C. 1.3.1.51)

Glycine max enzyme, optimum pH 7.0, is monomeric, molecular weight 34 700; it reduces the 2,3-bond. Other substrates include 2′-hydroxyformononetin and 2′-hydroxygenistein [K702].

Hyoscyamine (6*S*)-dioxygenase (E.C. 1.14.11.11)

Hyoscyamus enzyme, molecular weight 38 000–40 000, is found exclusively in roots. It is thought to be involved in the pathway for scopolamine formation [G135]. H. niger enzyme, molecular weight 41 000 and optimum pH 7.8, requires α-oxoglutarate and is activated by Fe^{2+}, catalase or a reducing agent, such as ascorbate. Other substrates include a series of tropine esters [E350].

Hyoscyamus niger root enzyme requires Fe^{2+}, oxygen and α-oxoglutarate (which yields carbon dioxide and succinate), and is stimulated by ascorbate. It is also found in Datura fastuosa (but not other Datura species), Atropa belladonna and Duboisia leichhardtii [K885].

Morphine 6-dehydrogenase (E.C. 1.1.1.218)

Morphine → morphinone

Hamster liver cytosolic enzyme, molecular weight 38 000, optimum pH 9.3 and pI 5.6, requires NAD^+; $NADP^+$ is a poor co-substrate. Substrates include morphine, codeine, normorphine, 1-indanol, 1-acenaphthenol, 4-chromanol and thiochroman-4-ol [K443].

Rabbit liver cytosoic enzyme, molecular weight 36 000, pI 6.4 and optimum pH 9.4, requires

$NAD(P)^+$, with NAD^+ preferred. Codeine, ethylmorphine, normorphine, 1-indanol and phenylglycol are also substrates. The enzyme also reduces polynuclear quinones with NAD(P)H as coenzyme, but not *p*-quinones [H920].

Pseudomonas putida enzyme, molecular weight 32 000 and optimum pH 9.5 oxidizes morphine and codeine, and reduces codeinone with NADPH as coenzyme [G181].

Morphinone reductase

Codeinone → hydrocodone

Pseudomonas putida enzyme, molecular weight 80 000 contains one mol of FMN. A second substrate is morphinone [H892]. It requires NADH for the reduction of the double bond conjugated with the oxo group. The reaction sequence is:

Formation of a charge-transfer intermediate with NADH;
Reduction of the flavin moiety;
Formation of reduced enzyme-codeinone complex;
Flavin re-oxidation;
Hydrocodone release [J635].

Protopine 6-monooxygenase (E.C. 1.14.13.55)

Eschscholtzia californica forms dihydrosanguinarine from protopine; 6-hydroxylation is considered to be the first reaction step [F699].

Pterocarpan hydroxylase

Ascochyta rabei (a fungus) enzyme, molecular weight 58 000, requires FAD, NAD(P)H and oxygen. It oxidizes medicarpin and maackiain at the 1α carbon to form the corresponding 1α-hydroxy-1,4-dien-3-ones [G213].

Vinorine hydroxylation

Rauwolfia serpentina enzyme is a P450 enzyme, optimum pH 8.3, which hydroxylates vinorine to vomilenine with oxygen and NADPH as co-substrates. This is a key step in the formation of ajmaline [H414].

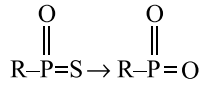
Vitamin K_1-2,3-epoxide reductase (tertiary alcohol-forming)

Beef liver microsomal enzyme, molecular weight 25 000 appears to be a homodimer which requires dithiothreitol and 3-((3-cholamidopropyl)dimethylammonio)-1-propanesulphonic acid and is inhibited by high concentrations of glycerol. The reaction products are 2,3-dihydro-2- and 3-hydroxy-2-methyl-3-phytylnaphthoquinone [D683].

Zearalenone reductase

Liver enzyme (microsomal), molecular weight 230 000, optimum pH 4.5 and 7.4 has been detected in (in reducing order) cow, mouse, pig, rat, rabbit and guinea pig; the figures shown are for rat. Hamster optima, pH 5.5 and 8.0 with NADH, are raised by 0.5 pH unit by substitution with NADPH. The products are both 6α- and 6β-zearalenol. Except with guinea pig enzyme, where neither product predominates at any pH, the β-isomer predominates at neutral pH, whereas the α-isomer predominates at acidic pH [C719, C858].

3.10 *Sulphur replacement*



Parathion, for instance, is a substrate for this class of reaction, with paraoxon as product. Little is known about the reaction.

The reaction has been observed in mouse liver [D858], rabbit [A1995], rat liver [A881] and microorganism [A2435], but not in lobster hepatocytes [A2567].

3.11 *Dehydroxylation*

Rat kidney dehydroxylates oestriol, with oestrone as the final product [A2549, A3644].

Rat and rabbit convert octopamine into *p*-hydroxyphenylacetate; antibiotics do not affect the reaction, unlike aryl dehydroxylation [A373].

3.12 *Side chain halogenation*

Bjerkandera acts on benzoate and *p*-hydroxybenzoate to form veratryl chloride. This is claimed to be the first report of a benzylic halide natural product [J482].

3.13 *Oxidative rearrangement*

Acetophenone oxygenase

A Pseudomonas putida arylketone monooxygenase, molecular weight 70 000, catalyzes a Baeyer-Villiger type oxidation, converting acetophenones into phenyl acetates. It contains one mol FAD and requires oxygen and NADPH; NADH is inactive. Its N-terminal sequence has been determined. Substrates include acetophenone, *p*-hydroxyacetophenone and *p*-hydroxypropiophenone; benzophenone and cyclohexylacetone are not substrates [K698]. Arthrobacter and Alcaligenes also exhibit the same reaction; monochloroanisoles are additional substrates [A2380, G107].

A similar reaction has been reported with *p*-hydroxypropiophenone in Pseudomonas [K698].

Alcaligenes enzyme acts on *o*-, *m*- and *p*-chloroacetophenone to form the corresponding phenyl acetates [G107].

Arthrobacter enzyme requires one mol each of NADPH and molecular oxygen for the reaction [A2380].

4. Formation and degradation of side-chains

4.1 *Side-chain formation*

Nuclear C-methyl incorporation

1. Benzene and toluene

Human bone marrow supplemented with S-adenosylmethionine converts benzene into toluene, which in turn yields *o*-, *m*- and *p*-xylenes [F853]. This may account for the apparent hydroxymethylation of benzene (Sloane, N.H., *Biochim. Biophys. Acta* (1965), **107**, 599; Sloane, N.H., Heinemann, M., Biochim. Biophys. Acta (1970), **201**, 384).

2. Polunuclear hydrocarbons

Rat is able to incorporate a methyl group at positions 7 and 12 of benzanthracene and possibly its metabolites. Incorporation was not observed with a range of non-carcinogenic analogues [F534]. The enzyme has been located in rat lung cytosol. Incorporation of a second methyl group occurs with both monomethylated benzanthracenes to yield 7,12-dimethylbenzanthracene, with S-adenosylmethionine as the methyl donor [F742, G491]. With rat liver cytosol chrysene forms 6-methylchrysene [G118].

3. Natural products.

Euglena gracilis γ-tocopherol methyltransferase (c.f E.C. 2.1.1.64), molecular weight 150 000 and optimum pH 7.5, incorporates a methyl group into both γ-tocopherol and β-tocopherol, in both cases forming α-tocopherol [G754].

In Streptomyces antibioticus 3-hydroxyanthranilate 4-C-methyltransferase (E.C. 2.1.1.97), a key enzyme in the formation of actinomycin, yields 3-hydroxy-4-methylanthranilate. The enzyme, molecular weight 36 000, which is stimulated by EDTA or mercaptoethanol, has negligible activity towards a range of substrate analogues [E725, F934]. The co-substrate is S-adenosylmethionine [E676]. The optimum pH lies between 6 and 8, depending on the buffer [E542].

C-Formylation

Rat brain and liver mitochondria incorporate a formyl group at the 5-position of 2,3,4,5-tetrahydro-1-(1-phenylcyclohexyl)pyridinium, with N^5-formyltetrahydrofolate as co-substrate [G209].

Incorporation of carboxyl group into phenols without hydroxyl removal

Phenol is a substrate for this reaction type [G923]; bacteria form *p*-hydroxybenzoate reversibly from phenol and carbon dioxide (E.C. 4.1.1.61), optimum pH 6.5–7.0. A two-stage mechanism has been suggested [F468].

Desulfococcus forms gentisate from quinol and carbon dioxide [H293].

Incorporation of carboxyl group into aniline

Rhodococcus erythropolis cells incorporate carbon dioxide into aniline (optimum at pH 7–7.5) to form anthranilate [D273]. Fratearia also catalyses the reaction [D595].

Incorporation of carboxyl group into polynuclear hydrocarbons

Microorganisms act on naphthalene to form 2-naphthoate with incorporation of carbon dioxide. Phenanthrene is also carboxylated, but the position is unclear [K253].

Incorporation of carboxyl group with hydroxyl removal

Phenol is converted into benzoate by microorganisms; the reaction sequence has not been clarified [F177, G281]. Substituted phenols with an *ortho* substituent yield *m*-substituted benzoates, with elimination of a hydroxyl group. Substrates include catechol, as well as phenols *ortho* substituted with halides, amino or carboxyl groups [G917].

A bacterial consortium acts on phenol to form benzoate, apparently involving *para* carboxylation as well as a dehydroxylation step [G424].

Bacterium forms benzoate from quinol and bicarbonate; it was postulated that gentisate was an intermediate [H110]. Another study found that the reaction occurs in species that dehydroxylate *p*-hydroxybenzoate [G167].

Other microorganisms, including those found in pig manure form benzoate from phenol, apparently without *p*-hydroxybenzoate as an intermediate [F515, H842].

The reverse reaction is described under ***p*-Hydroxy- and 3,4-dihydroxybenzoate decarboxylases** (below).

Tyrosine phenol-lyase (E.C. 4.1.99.2)

e.g, L-Serine + phenol ↔ L-tyrosine

Citrobacter freundii enzyme has a broad optimum from pH 6.8 to above 9 and acts on phenol to generate L-tyrosine, with S-(*o*-nitrophenyl)-L-cysteine as co-substrate [F38]. C. intermedius enzyme forms tyrosine from phenol, glycine and formaldehyde, but only in the presence of an aldolase (E.C. 4.1.2.13) [B693].

Erwinia herbicola enzyme has an optimum pH of about 8 for amino acid synthesis, and is denatured by high concentrations of phenol or catechol [A851]. The enzyme also acts on L-dopa, and the reverse reaction has been observed with phenol, catechol, resorcinol and pyrogallol. In intact cells D-tyrosine is converted into L-tyrosine, presumably by side-chain removal and reconstruction [A708].

Escherichia intermedia enzyme acts on resorcinol to form 2,4-dihydroxy-L-phenylalanine, with S-methyl-L-cysteine as co-substrate, which can be replaced by L-tyrosine; presumably the enzyme releases L-serine from L-tyrosine, which then condenses with resorcinol. The configuration with both D- and L-tyrosine is retained at C-3 [A2242, E401]. Phenols that are substrates include phenol, *o*- and *m*-cresol, *o*- and *m*-chlorophenol, catechol, resorcinol, pyrogallol and hydroxyquinol [B292]. The enzyme requires pyridoxal phosphate as cofactor; its N-oxide and 2′-hydroxypyridoxal phosphate are not so good as cofactors [A155].

Leptoglossus phyllopus enzyme, which is found in the ventral abdominal gland interconverts phenol and L-tyrosine [A2260].

Symbiobacterium thermophilum enzyme, optimum pH 7 and pI 4.8 is heat stable. It is activated by K^+ and NH_4^+, but not by Na^+ or Mg^{2+}, with both D- and L-tyrosine as substrates. It converts catechol into L-dopa, with pyruvate and ammonia as co-substrates [G603].

Activity has been found in Pseudomonas, Xanthomonas, Alcaligenes, Achromobacter, Escherichia, Aerobacter, Erwinia, Proteus, Salmonella and Bacillus, but generally only in a small proportion of the strains tested. In this study it was not found in numerous other bacterial genera, fungi, Actinomycetes or yeasts [A692].

Catechol is a substrate for enzyme found in Erwinia, Symbiobacterium and Citrobacter [e.g. E959, G603, J512], and leads to a potentially viable method for the commercial production of L-dopa.

Tryptophan synthase; (E.C. 4.2.1.20)

Indole + L-serine → L-tryptophan

Enzymes from Daucus carota and Nicotiana tabacum utilize as additional substrates 4-, 5- and 6-fluoroindole, 5-hydroxy-, 5-methoxy- and 5-methylindole. Several other substituted indoles are at best poor substrates [B874].

In Juglans regia the enzyme is associated with a particulate fraction that is not mitochondrial, with optimum pH 7–8 [A818].

The reaction has also been studied in Zea mays [H126].

In Enterobacteriaceae genera the activity (using pyruvate and ammonia instead of serine) has been found only in some strains and species of Escherichia, Kluyvera, Enterobacter, Erwinia and Proteus. Other genera tested and found inactive include Pseudomonas, Azotobacter, Aeromonas, Rhizobium, Alcaligenes, Salmonella and Clostridium. Between four and 475 strains of each genus were tested [A781].

Vibrio enzyme requires pyridoxal phosphate, and can use S-methylcysteine in place of cysteine, optimum pH 8.0 [B85].

E. coli enzyme, optimum pH 9, yields 5-hydroxytryptophan from 5-hydroxyindole [A430].

Salmonella typhimurium enzyme, which requires pyridoxal phosphate for activity, is a complex of two pairs of different subunits [K275]. This and E. coli enzymes catalyze the reverse reaction, but only slowly [E101].

The reverse reaction has been described under Tryptophanase.

L-Tryptophan 2-C-methyltransferase (E.C. 2.1.1.106)

Streptomyces laurentii enzyme, optimum pH 7.8 (sharp) transfers the methyl group from L-methionine to the nucleus of L-tryptophan to form L-2-methyltryptophan with retention of configuration. Indole-3-pyruvate and D-tryptophan (poor) are also substrates, but not indole [K752].

L-Tryptophan 4-dimethylallyltransferase (E.C. 2.5.1.34)

This compound, which is a key intermediate in the formation of ergot alkaloids, is formed from L-tryptophan in Claviceps paspali [A3599].

Aspulvinone dimethylallyltransferase (E.C. 2.5.1.35)

Aspergillus terreus enzyme, molecular weight 240 000–270 000 (monomer 45 000) and optimum pH 7.0 acts on aspulvinone E or aspulvinone G and dimethylallyl pyrophosphate to form a series of dimethylallyl-substituted analogues [K829].

Trihydroxypterocarpan dimethylallyltransferase (E.C. 2.5.1.36)

Glycine enzyme acts on 3,6a,9-trihydroxypterocarpan and dimethylallyl pyrophosphate to form 2- and 4-dimethylallyl-3,6a,9-trihydroxypterocarpan [K905]. The enzyme is found after elicitor treatment (Phytophthora megasperma) [K904].

Formation of ubiquinone, tocopherol and analogues by prenylation

In man 2,3-dimethoxy-5-methyl-*p*-quinone (ubiquinone 0) is precursor to ubiquinones 30, 45 and 50, and 'menadione diphosphate' is precursor for vitamins $K_{2(20)}$, $K_{2(45)}$ and $K_{2(50)}$ [A774].

Rat liver and brain mitochondria contain 4-hydroxybenzoate: polyprenyl transferase (c.f. E.C. 2.5.1.31), with polyprenyl pyrophosphates containing 8–10 isoprene units as the second substrate. *p*-Aminobenzoate is also a substrate. Inhibitors (not very effective) include serotonin, dopamine, noradrenaline, aspirin and other salicylates. Maximum activity is found in heart, and it is also found in kidney and spleen [A147].

Homogentisate is the substrate from which many prenylated compounds are formed.

3-Octa- and 3-nonaprenyltoluquinols are formed in Euglena gracilis and sugar beet, with octaprenyl- and nonaprenyl pyrophosphates as co-substrates respectively; γ-tocopherol is another product [A201, A1584, G754]. Plastoquinones, α- and γ-tocopherol are formed in spinach and lettuce chloroplasts, with phytyltoluquinone as a possible intermediate [A2522, D902].

Saccharomyces (baker's yeast) contains a mitochondrial 4-hydroxybenzoate: polyprenyl transferase with an optimum at pH 7 that synthesizes the corresponding 2-polyprenylphenols with two, three, four, five, eight, nine and 10 isoprene units. Formation of the triprenyl product requires *trans, trans*- farnesyl pyrophosphate. The synthesis is stimulated by Mg^{2+} and inhibited by phosphate [A147].

An E. coli enzyme system acts on *p*-hydroxybenzoate and polyprenylpyrophosphates to form 3-octaprenyl- and 3-nonaprenyl-4-hydroxybenzoates [A1524].

Benzaldehyde side chain carboligation

Pseudomonas putida benzoylformate decarboxylase (which requires thiamine pyrophosphate) exhibits a second reaction in which benzaldehydes form (*R*)-benzoins [K424].

4.2 *Decarboxylation reactions of phenolic groups without hydroxylation*

***p*-Hydroxy- and 3,4-dihydroxybenzoate decarboxylases** (E.C. 4.1.1.61 and E.C. 4.1.1.63 respectively)

Clostridium hydroxybenzoicum enzyme, a homohexamer, subunit molecular weight 57 000, pI 5.1 and optimum pH 5.6–6.2, reversibly decarboxylates *p*-hydroxybenzoate and protocatechuate to form phenol and catechol respectively [H576].

a. p-Hydroxybenzoate decarboxylase

A microorganism enzyme, molecular weight 420 000 (subunit molecular weight 119 000) and pI 5.6 acts on *p*-hydroxybenzoate to yield phenol [K573].

A bacterial enzyme, optimum pH 6.5–7.0 reversibly decarboxylates *p*-hydroxybenzoate specifically; it requires Mn^{2+} and phosphate, and is rapidly inactivated by oxygen [F468].

A mixture of microorganisms decarboxylates several benzoates reversibly [G632].

b. 3,4-Dihydroxybenzoate decarboxylase

Clostridium hydroxybenzoicum enzyme, molecular weight 270 000 and optimum pH 7.0 appears to be a homotetramer, and is absolutely specific for protocatechuate. The reaction is reversible, in favour of the acid. No coenzyme is required. A second enzyme was separated in the same study; the N-terminal sequences of these enzymes were different [J184].

6-Methylsalicylate decarboxylase (E.C. 4.1.1.24)

This activity, which forms *m*-cresol is found in Valsa friesii [A1049].

Orsellinate decarboxylase (E.C. 4.1.1.58)

Gliocladium roseum enzyme catalyzes the formation of orcinol and carbon dioxide; the enzyme is activated by azide [K908].

Pyrocatechuate decarboxylase (E.C. 4.1.1.46)

$$\text{Pyrocatechuate} \rightarrow \text{catechol} + CO_2$$

An enzyme in Aspergillus niger is a homotetramer, monomeric molecular weight 28 000 and optimum pH 5.2 [E417]. Another study found the native molecular weight to be 150 000, but with

the same optimum pH. It is inhibited by cyanide and borohydride [B83]. A. oryzae enzyme, which does not require cofactors, appears to have a histidyl residue at the active centre [J206].

Bacterium decarboxylates pyrocatechuate as well as gallate, protocatechuate and *m*-hydroxybenzoate [C396].

Trichosporon cutaneum is a dimer, molecular weight 66 000. Other substrates include 2,3,5- and 2,3,6-trihydroxybenzoates [B790].

Gentisate decarboxylase (E.C. 4.1.1.62)

Klebsiella aerogenes enzyme, optimum pH 5.9, which is soluble, does not require oxygen and releases carbon dioxide [K943].

Gallate decarboxylase (E.C. 4.1.1.59)

Pantoea (formerly Enterobacter) agglomerans enzyme, a homohexamer, molecular weight 320 000, requires Fe (which makes it unique among similar decarboxylases), and is inhibited by Fe^{2+}-binding reagents. It is highly specific, forming pyrogallol and carbon dioxide [J859].

A bacterium has been described that decarboxylates gallate and several other benzoates [C396].

3,4-Dihydroxyphthalate decarboxylase (E.C. 4.1.1.69)

Protocatechuate is formed from 3,4-dihydroxyphthalate in Micrococcus; no enzymology has been described [K753].

4,5-Dihydroxyphthalate carboxylyase (E.C. 4.1.1.55)

$$4,5\text{-Dihydroxyphthalate} \rightarrow \text{protocatechuate} + CO_2$$

Pseudomonas fluorescens enzyme is probably a hexamer, molecular weight 420 000, monomeric molecular weight 66 000 and optimum pH 6.8. It is inhibited by *p*-chloromercuribenzoate [D538]. P. testosteroni enzyme, which is induced by phthalate, appears to be a tetramer, molecular weight 150 000 and monomeric molecular weight 38 000. It also forms *m*-hydroxybenzoate from 4-hydroxyphthalate [A3332].

***p*-Cresol formation from *p*-hydroxyphenylacetate**

Clostridium difficile enzyme, which is unstable, requires amino acids (serine or threonine) or the corresponding pyruvates as cofactor, or dithionite [D917].

4.3 *Decarboxylation reactions of side-chains*

Auxin oxidases

Zea mays enzyme is composed of two isozymes, molecular weights 32 500 (main) and 54 500, with a requirement for Mn^{2+} and *p*-coumarate. The product with IAA is indole-3-methanol [F798]. This product is also found in wheat [D150] and Pinus sylvestris [D597]. Lupinus alba forms, in addition, 3-hydroxymethyloxindole, 3-methyleneoxindole and 3,3′-bisindolylmethane [F847]. Horseradish peroxidase also forms indole-3-methanol, 3-formylindole, 3-methyleneoxindole and 3-hydroxymethyloxindole from IAA [C525, D234, F961].

3-Methyleneoxindole formation (indoleacetate oxidase)

$$\text{Indole-3-acetate} \rightarrow \text{3-methyleneoxindole}$$

Arachis contains four peroxidase isozymes with indoleacetate oxidase and polyphenol oxidase activities. Each isozyme has a different optimum pH for each type of substrate; the optima for indoleacetate oxidase are 7.2–7.6 [A2519].

Bean (Phaseolus vulgaris) etiolated seedling root oxidase activity is increased by treating the

plants with naphthenate (identity unspecified), cyclohexanecarboxylate and cyclopentylacetate; there is no *in vitro* effect with these compounds [A220].

Three commercial sources of horseradish peroxidase contain a total of 42 isozymes by isoelectric focussing, and the oxidase-peroxidase ratio is essentially identical for all these isozymes [A3293]. Other studies have failed to separate peroxidase and indole oxidase activities in peroxidase preparations from horseradish and Betula (yellow birch) leaves (20 and 13 isozymes respectively) [A3428, A3429].

Studies on Nicotiana indicate that the reaction is entirely mediated by peroxidases. At least four isozymes are found by electrophoresis, and indoleacetate oxidase is separated from monophenol monooxygenases [A221].

Oat coleoptile peroxidase is separable by electrophoresis into eight isozymes, six of which exhibit indole-3-acetate oxidase activity [A1135].

Peach seed enzyme, optimum pH 4.5–5.0, requires Mn^{2+} and 2,4-dichlorophenol [A655].

Wheat enzyme is a peroxidase, which requires Mn^{2+} and a phenolic cofactor without addition of peroxide. With peroxide, ferulate and *p*-coumarate are also oxidized. A coloured free radical appears to be the first product [A219].

4-Hydroxymandelate oxidase (E.C. 1.1.3.19)

Pseudomonas convexa enzyme, molecular weight 155 000 requires Mn^{2+}, oxygen and FAD or FMN in oxidatively decarboxylating 4-hydroxymandelate to form *p*-hydroxybenzaldehyde. It is inhibited by thiols, EDTA, cyanide and 8-hydroxyquinoline [A2681].

3,4-Dihydroxymandelate decarboxylation with tyrosinase

Mushroom enzyme forms protocatechualdehyde from 3,4-dihydroxymandelate. It has been postulated that the mechanism involves quinone formation, followed by tautomerization to a quinone methide, with oxidative decarboxylation [D865, E963].

Benzoylformate (phenylglyoxylate) decarboxylase (E.C. 4.1.1.7)

$$R.CO.COOH \rightarrow R.CHO$$

Pseudomonas putida decarboxylates *p*-hydroxyphenylglyoxylate to form *p*-hydroxybenzaldehyde [E669]. The enzyme requires thiamine pyrophosphate with phenylglyoxylate, *p*-methylphenylglyoxylate, *p*-chloromethylphenylglyoxylate and *p*-fluoromethylphenylglyoxylate as substrates. *p*-Bromomethylphenylglyoxylate is inhibitory; it reacts with the cofactor to yield bromide and (*p*-methylbenzoyl)thiamine pyrophosphate which in turn forms *p*-toluate. A small proportion of *p*-chloromethylphenylglyoxylate exhibits the same side-reaction [E714]. Other substrates are phenylglyoxylate and *m*-hydroxyphenylglyoxylate [E771].

Acinetobacter calcoaceticus, a tetramer, monomeric molecular weight 58 000 and optimum pH 5.9, requires thiamine pyrophosphate, which is firmly bound. It appears to be highly specific [D809].

Moraxella enzyme acts on *o*-hydroxyphenylglyoxylate to form salicylaldehyde [G356].

This activity has also been observed in Acinetobacter, Bacterium and Flavobacterium [A730, D487, E355].

L-Arylamino acid decarboxylases (E.C. 4.1.1.28)

$$R.CHNH_2.COOH \rightarrow R.CH_2NH_2$$

1. Phenylalanines and tryptophans

Animal enzymes have developed genetically with specificities that enable the non-protein amino acids L-dopa, the precursor of the catecholamine neurotransmitters and 5-hydroxytryptophan, the precursor of the neurotransmitter serotonin, to be readily decarboxylated. These enzymes have little activity towards the amino

acids tyrosine, tryptophan and phenylalanine, which are ingested in large amounts and are utilized extensively for protein synthesis. The ready decarboxylation of these amino acids would swamp the organism with amines that would interfere with neurotransmission, as well as possibly compromising the availability of amino acids for protein synthesis.

Human phaeochromocytoma enzyme appears to be a dimer, monomeric molecular weight 50 000 and pI 5.7. Substrates are L-dopa, 5-hydroxy-L-tryptophan and L-*threo*-3,4-dihydroxyphenylserine [D793, G452]. Human kidney enzyme is a dimer, molecular weight 100 000. Phenylalanine, tyrosine and tryptophan are not substrates [G104].

The presence of the enzyme in human brain has been a matter of controversy. For instance in one study only a few P.M. brains showed any activity, and these were considered to show activity only because the enzyme had been carried there by blood as a result of trauma [A3753]. This was clearly erroneous, since the brain needs to synthesize these neurotransmitters. In P.M. parkinsonian brain dopa decarboxylase activity is reduced about 10-fold in those areas that normally show high activity, especially caudate nucleus, putamen, substantia nigra and putamen. Only a small decrease has been found in other brain regions, and an increase has been detected in cerebellar cortex [A381]. In aromatic L-amino acid decarboxylase deficiency, a rare autosomal recessive, a catecholamine deficiency is observed, with associated symptoms [K380].

Rat kidney enzyme is a homodimer, monomeric molecular weight 48 000, and pI 6.7. The amino acid composition has been determined. It is immunologically identical with enzyme found in striatum, adrenal medulla, pineal and liver. The optimum pH for L-dopa is 7.0, 5-hydroxytryptophan 7.7, tyrosine 8.2, tryptophan 8.6 and phenylalanine 8.2. The V_{max} for the last three substrates is low, and K_m is much higher than physiological concentrations [E735]. In agreement with this, there is little evidence for tyrosine decarboxylation in rat or mouse liver under more moderate conditions [A2559].

Rat brain enzyme, molecular weight 115 000 and pH 6.4–6.5, contains firmly bound pyridoxal phosphate. Substrates are L-dopa and 5-hydroxytryptophan, but not tryptophan or tyrosine. The reaction products serotonin and dopamine are inhibitory, as are N-ethylmaleimide, dodecyl sulphate, Cu^{2+}, Fe^{2+} and Ni^{2+}. In dilute solution of either pyridoxal phosphate or the amino acid substrate, an excess of the second substrate is inhibitory [A2378]. Liver enzyme is inhibited by serotonin and dopamine (competitive), and by α-methyl-*m*-tyrosine (competitive for dopa but non-competitive for 5-hydroxytryptophan). Dopamine binds better at pH 6.8 than at 7.8, serotonin binds with equal firmness under these conditions, whereas α-methyl-*m*-tyrosine and α-methyldopa bind less firmly at pH 6.8 [A2105].

A tyrosine decarboxylase, optimum pH 8.0, well distributed through rat brain and kidney as well as human kidney; is thought to be 'ordinary' L-amino acid decarboxylase, based on the ratio of activity with 5-hydroxytryptophan as substrate and on antibody tests. It is stimulated by a series of cyclic organic solvents such as benzene, toluene, cyclohexane and cyclopentane, as well as by phenol. A series of other amino acids are decarboxylated, but information about relative reaction rates was not given [C566]. Rat kidney activity increases fivefold between two days post-partum and six-eight weeks, whereas brain activity remains constant until about five weeks [A2195].

In vivo studies with rats show that although *o*- and *m*-tyrosine and 3-hydroxy-4-methoxyphenylalanine readily yield decarboxylation products, a series of methoxyphenylalanines are not significantly decarboxylated [A2961, J411].

Pig kidney enzyme has a molecular weight of 86 000 and pI 5.0 according to one study [F197]. In another study, the molecular weight was found to be 112 000, with subunit molecular weights 57 000, 40 000 and 21 000 with dopa, 5-hydroxytryptophan, tryptophan and tyrosine as substrates [A1906]. It converts L-dopa substituted with deuterium on the α-carbon into *S*-[α-D]-dopamine whereas L-dopa in D_2O yields *R*-[α-D]-dopamine [D606]. About 0.02 per cent

of L-dopa and *m*-tyrosine, and 2 per cent of α-methyl-*m*-tyrosine and α-methyldopa undergo a subsidiary reaction at pH 6.5. For L-dopa the subsidiary products are 3,4-dihydroxyphenylacetaldehyde and pyridoxamine phosphate, which, in the absence of further pyridoxal phosphate cofactor, inactivates the enzyme. The proportion of substrate undergoing this subsidiary reaction relative to decarboxylation is independent of pH in the range 6.5–9 [A2425]. Another study on this alternative reaction found that α-methyldopa uses molecular oxygen and yields phenylacetone and ammonia as products, and 5-hydroxytryptophan forms 5-hydroxyindole-3-acetaldehyde. The amount of these subsidiary products formed greatly exceeded the amount of pyridoxal phosphate present, indicating that it is not simply a decarboxylation-dependent transamination with pyridoxal phosphate as amino acceptor. Nor is it an oxidative deamination [B780].

Beef adrenal medulla enzyme is present in the cytoplasm of all cells [A1409], molecular weight 50 000, with at least five components with pI in the range 4.9–5.3 [G452].

Mouse enzyme has an optimum pH of 6.6 [A1297]. Both D- and L-phenylalanine are decarboxylated, but not by prior conversion of the D-to the L- isomer. Decarboxylation of D-tyrosine is not inhibited by L-tyrosine decarboxylase inhibitors [A3612]. In eye the activity of the enzyme acting on 5-hydroxytryptophan rises rapidly in the first three days after birth, and then declines to the adult level at day seven [A946]. In brain, the activity reaches the adult level in cerebellum, medulla and pons two weeks after birth, in the mesencephalon and diencephalon at four weeks and in the cerebral hemispheres after six weeks [A1067].

The enzyme is found in islet cells from hamster, rabbit and guinea pig [A1911].

Embryo chick brain enzyme is detected at 14 days incubation, but with very low activity in cerebellum. Activity increases 10-fold just before hatching [A1413]. In pineal, 5-hydroxytryptophan decarboxylase is inactive at 12 days incubation, and at hatching the activity is 50 per cent of the activity found 16 days post-hatching. In cerebrum the pattern of development is similar, except that it appears two days earlier [A160].

Skipjack tuna liver enzyme, which acts on 5-hydroxytryptophan, has a molecular weight of 110 000 [H683].

In leech, the enzyme is present in nerves [A659].

Mytilus edulis and Elliptio complanata dopa decarboxylases are inhibited by α-methyldopa, N^1-(DL-seryl)-N^2-(2,3,4-trihydroxybenzyl) hydrazine and hydrazinomethyl-3,4-dihydroxyphenylalanine [A1084].

Aedes aegypti (mosquito) enzyme, molecular weight 112 000 [B738] is induced by β-ecdysone, and this effect is enhanced by β-ecdysone administered together with dibutyryl cyclic AMP, but cyclic AMP on its own has no effect [A1027].

Calliphora vicuna larval dopa decarboxylase, molecular weight 90 000–96 000 is composed of two subunits, molecular weights 40 000 and 46 000. 5-Hydroxytryptophan, tryptophan, tyrosine and phenylalanine are not substrates. Al^{3+} and Mn^{2+} are activators, whereas Cu^{2+} and Hg^{2+} are inhibitory. N-Acetyldopamine, the product that is used in the formation of polymers, is also inhibitory [A2151].

Ceratitis capitata enzyme was found to have very similar properties to the human enzyme (see above) [G104].

Periplaneta americana decarboxylates L-dopa, L-tyrosine, 5-hydroxytryptophan and *m*-tyrosine. Two isozymes are found; one, molecular weight 120 000 acts on dopa and the other, molecular weight 100 000, on tyrosine. Both have an optimum pH of 7.5 [E448].

Barley (Hordeum vulgare) enzyme, optimum pH 7.3, is specific for L-isomers. Substrates include dopa, *o*-, *m*- and *p*-tyrosine. Competitive inhibition is observed between the substrates, and caffeate and *p*-coumarate are also competitive inhibitors. Other inhibitors include hydroxylamine, semicarbazide, Fe^{2+}, Cu^{2+} and Hg^{2+}. The enzyme is also found in Triticum aestivum, Zea mays and Cytisus scoparius [A1210].

Papaver somniferum contains two decarboxylases which require pyridoxal phosphate (like other decarboxylases). They act on L-tyrosine or,

better, L-dopa, with a broad optimum, pH 7.5–8.5 [H557]. Another study found the optimum pH to be 7. Substrate inhibition is observed with pyridoxal phosphate and L-dopa at 1 mM, and by cyanide, semicarbazide, hydroxylamine and *p*-chloromercuribenzoate [A3143].

Tomato shoot enzyme decarboxylates L-tryptophan and 5-hydroxytryptophan; D-tryptophan, L-phenylalanine and L-tyrosine are not substrates. It requires pyridoxal phosphate and has an optimum pH of 8.0. Inhibition is brought about by pre-incubation with 2 mM Fe^{2+}, Fe^{3+}, Ca^{2+}, Co^{2+} and Zn^{2+}, but not by Mg^{2+} or Mn^{2+} [A536].

Bacillus tryptophan decarboxylase, molecular weight 150 000 and optimum pH 7, requires pyridoxal phosphate [D555].

Lactobacillus brevis tyrosine decarboxylase, optimum pH 5.0, requires pyridoxal phosphate; L-dopa is a less good substrate. It is stabilized by substrate and coenzyme, and is inhibited by glycerol, mercaptoethanol and tyramine [K277].

Purified Micrococcus percitreus enzyme, a dimer, molecular weight 101 000, subunit molecular weight 48 000, and optimum pH 9.0, requires pyridoxal phosphate. Compounds found to be substrates are tryptophan, 5-hydroxytryptophan, phenylalanine, *o*- and *p*-tyrosine (*m*-tyrosine is a poor substrate), dopa and its 2,4-dihydroxy analogue, 2- and 3-methyltyrosine, 2- and 3-chlorotyrosine, 3,5-dibromotyrosine, 5-fluorotryptophan, 5-methyltryptophan and 3-hydroxykynurenine. Substitution with a methyl group on the α-carbon almost or totally eliminates activity [A336, C62].

S. faecalis enzyme requires pyridoxal phosphate [G332]. Substrates include tyrosine and dopa, and after pre-treatment of cells with toluene *m*-tyrosine is a substrate [A537]. The enzyme is a dimer, molecular weight 143 000 and pI 4.4; a second component, pI 4.5, is eliminated by removal of pyridoxal phosphate and other low molecular weight compounds [F197]. Another study found pI 3.2 and 4.5 for isozymes [A3573].

Tyrosine decarboxylase (E.C. 4.1.1.25) is found in one or more strains of Acinetobacter, Bacillus, Candida, Citrobacter, Cryptococcus, Enterococcus, E. coli, Hafnia, Lactobacillus, Pseudomonas, Proteus, Saccharomyces, Serratia, Shigella, Staphylococcus aureus, Torulopsis and Yersinia [H302].

2. Phenylserines

$$R.CHOH.CHNH_2.COOH \rightarrow R.CHOH.CH_2NH_2$$

Pig kidney enzyme, optimum pH 8.5, decarboxylates L-*threo*-3,4-dihydroxyphenylserine to yield noradrenaline. It is specific for the L-isomer, requires pyridoxal phosphate and is inhibited competitively by L-dopa, L-5-hydroxytryptophan, and to some extent by D-dopa. D-*threo*-3,4-Dihydroxyphenylserine inhibits competitively at low concentration, but non-competitively at high concentration. It is inactivated above 40° [A2593].

Rat heart decarboxylates L-*threo*-3,4-dihydroxyphenylserine; the enzyme is specific for the L-isomer, and requires low concentrations of pyridoxal phosphate; high concentrations are inhibitory. The optimum pH is 8.5 [A3882].

Rat and human enzymes appear to be the same as the normal amino acid decarboxylase [C566].

A crude decarboxylase preparation from a species that Chemical Abstracts does not specify has an optimum pH of 7.8–8.2. L-*threo*-3,4-Dihydroxyphenylserine and (a poorer substrate) D-*threo*-3,4-dihydroxyphenylserine are substrates [A3177].

L-Phenylalanine oxidase (deaminating and decarboxylating) (E.C. 1.13.12.9)

L-Phenylalanine → phenylpyruvate

L-Phenylalanine → phenylacetamide

Pseudomonas enzyme is a dimer, molecular weight about 140 000, which contains two mol of FAD. The amino acid composition has been determined. It catalyzes two reactions; one is the formation of phenylpyruvate with a sharp optimum at pH 11 and a broad plateau between pH 4 and 9 with elimination of ammonia and water. The other is the formation of

phenylacetamide with elimination of carbon dioxide, which shows a broad optimum between pH 5 and 9. Molecular oxygen is incorporated into the carbonyl of the amide. The enzyme is specific for L-isomers, and tyrosine, *o*-, and *m*-tyrosine, *p*-fluorophenylalanine and tryptophan are additional substrates. *m*-Tyrosine is the only substrate where deamination is the major pathway; with some others the reaction is almost exclusively amide formation. It is inhibited by Hg^{2+}, but milder inhibitors such as Fe^{2+} and Cu^{2+} markedly reduce the proportion of substrate undergoing the deamination reaction; otherwise the proportion of phenylalanine deaminated is about 20 per cent of the total [C444, C546, D246].

Tryptophan 2-monooxygenase (E.C. 1.13.12.3)

Tryptophan → indole-3-acetamide

Coprinus enzyme, molecular weight 420 000 and optimum pH 9.0, appears to be a hexamer, each monomer binding one FAD non-covalently. This reaction is a minor pathway with L-tryptophan oxidase (see below) [K563].

The reaction has been observed in Poncirus trifoliata, Azospirillum brasiliense, Xanthomonas campestris, Streptomyces, Bradyrhizobium, Pseudomonas savastanoi and P. campestris [E435, E578, F788, G760, G776, H384].

Tryptophan oxidases

Arabidopsis thaliana enzyme formation of indole-3-acetate involves a single enzyme complex, molecular weight 160 000–180 000. It requires oxygen, but this is not incorporated into the product; indole-3-acetonitrile may be the intermediate [K605].

Coprinus enzyme, molecular weight 420 000, optimum pH 7.0 and stability range pH 6.0–10.5, appears to be a hexamer, each monomer binding one FAD non-covalently. The main reaction forms indole-3-pyruvate and indole-3-acetate; a smaller amount (10 per cent) of indole-3-acetamide is formed. Slight activity is found with L-phenylalanine and L-tryptophan [K563].

Tryptophan 2′-dioxygenase (E.C. 1.13.99.3)

Pseudomonas enzyme, molecular weight 280 000 is a haemoprotein; it is not a catalase or peroxidase. L-Tryptophan forms indole-3-glycolaldehyde (or possibly indole-3-glyoxal); a number of indoles are also substrates, but decarboxylation is not a pre-requisite for activity [A3009]. Another study on an enzyme, molecular weight 250 000, optimum pH about 4 and pI 4.8 with an apparently different specificity contained iron; its amino acid composition was determined. There are indications that α-hydroxylation is the first reaction step in a sequence that may include decarboxylation [A3007].

Phenylpyruvate decarboxylase (E.C. 4.1.1.43)

R.CO.COOH → R.CHO

Acinetobacter calcoaceticus enzyme, a tetramer, monomeric molecular weight 56 800 and optimum pH 7.0, requires thiamine pyrophosphate. The product is phenylacetaldehyde; the enzyme appears to be highly specific [D809].

Candida guilliermondii enzyme requires thiamine pyrophosphate and Mg^{2+} [A2483].

Thauera aromatica also catalyzes this reaction [J397].

***p*-Hydroxyphenylpyruvate decarboxylase**

R.CO.COOH → R.COOH

Arthrobacter enzyme forms *p*-hydroxyphenylacetate from *p*-hydroxyphenylpyruvate without formation of the aldehyde. The enzyme, optimum pH about 7.5, requires thiamine pyrophosphate, FAD, glutathione and Mg^{2+} or Mn^{2+} [A3208].

Indole-3-pyruvate decarboxylase (E.C. 4.1.1.74)

$$R.CO.COOH \rightarrow R.CHO$$

The reaction has been found in Bragyrhizobium elkanii [J189], E. coli [H348] and Azospirillum lipoferum [F49]. Enterobacter cloacae enzyme has been reviewed [K792].

Indole-3-pyruvate ferredoxin oxidoreductase

$$R.CO.COOH \rightarrow R.CO.CoA$$

Pyrococcus furiosus enzyme is a tetramer composed of two pairs of subunits, molecular weights 23 000 and 66 000, optimum pH 8.5–10.5, with one thiamine, a cluster of 4 $[4Fe\text{-}4S]^{2+,\,1+}$ and one $[3Fe\text{-}4S]^{0,\,1+}$ units, and a requirement for CoA. The products from indole-3-pyruvate, phenylpyruvate and *p*-hydroxyphenylpyruvate are the corresponding acetyl CoA compounds. It is only active at high temperature (90°), and is inhibited by oxygen [H306].

Mandelates formed from phenylpyruvates

$$R.CH_2.CO.COOH \rightarrow R.CHOH.COOH$$

This reaction has been detected in rat with phenylpyruvate as substrate [G829].

Amycolatopsis orientalis converts *p*-hydroxyphenylpyruvate into *p*-hydroxymandelate; molecular oxygen is incorporated into both CO_2 and the benzylic hydroxyl. This appears to be one of the steps in the formation of vancomycin [K499].

Decarboxylation of cinnamic acids

$$R.CH{=}CHCOOH \rightarrow R.CH{=}CH_2$$

Bacillus subtilis enzyme is a dimer, molecular weight 45 000, with a broad optimum at about pH 5. Substrates include ferulate, *p*-coumarate and caffeate [J623]. B. pumilis enzyme is a dimer, molecular weight 45 000 and optimum pH 5.5. Substrates are *p*-coumarate and ferulate [H346].

Pseudomonas fluorescens enzyme is a dimer, molecular weight 40 000 and optimum pH 7.3. Substrates are *p*-coumarate and ferulate, but not *o*- and *m*-coumarate [H364].

Polyporus circinata enzyme has an optimum at pH 6.1. *p*-Coumarate and caffeate are substrates, but not cinnamate or some other aromatic acids. The products are the corresponding styrenes [A2690].

Cladosporium phlei enzyme acts on *p*-coumarate to yield *p*-hydroxystyrene; caffeate and ferulate are also substrates, with a slight preference for the *cis*-isomers. The acrylate side-chain and the *p*-hydroxyl group are essential for activity. The enzyme is stable at −20°, but is rapidly inactivated at 35°; the temperature coefficient for inactivation appears to be unusually large. Thiols protect the enzyme from inactivation by iodoacetate and *p*-chloromercuribenzoate. Maleate and some cinnamates are inhibitory, but chelators, fumarate and acrylate are not [A2675].

Saccharomyces cerevisiae decarboxylates 3,4-dimethoxycinnamate to yield 3,4-dimethoxystyrene. Substrate labelled with deuterium at position 2 on the side-chain totally retains the label conformation [A2157].

Klebsiella oxytoca enzyme acts on *p*-coumarate, caffeate, ferulate and 2,4-dihydroxycinnamate, but only on the (*E*)- (i.e., *trans*) isomers [J853].

Lactobacillus plantarum enzyme is a homotetramer, molecular weight 93 000 and optimum pH 5.5–6.0; it does not require metal ions for activity. Substrates are *p*-coumarate and caffeate, but not ferulate [H897].

Candida lambrica enzyme has an optimum at pH 6.5 [K70].

This reaction has been observed in a large range of microorganisms. A major study on the decarboxylation of ferulate, isoferulate, *o*- *m*- and *p*-methoxycinnamate, *o*- *m*- and *p*-coumarate, caffeate, 5-methoxyferulate, *p*-methylcinnamate, *o*- *m*- and *p*-chlorocinnamate and 2,6-dichlorocinnamate was carried out by a series of unspecified microorganisms. Ferulate

decarboxylation was used as a marker to identify the reaction in Aspergllus carneus, A. ochraeus and A. terreus, Bacillus pumilus, Candida intermedia, Corynespora cassiicola, Curvularia affinis, C. clavata and C. lunata, Fusarium coerulum, F. dimerum, F. eumartii, F. moniliforme, F. oxysporum, F. roseum, F. solani and F. tritinctum, Hansenula anomala, H. beckii, H. capsulata, H. henricii and H. minuta, and Saccharomyces cerevisiae [F390], Aspergillus niger, Bacillus megaterium and B. subtilis, Mycobacterium, Nocardia, Penicillium frequentans, Pseudomonas putida, Rhizopus arrhizus, Rhodotorula rubra and Streptomyces rimosus [G895]. Other active species include Brettanomyces anomalus, Cladosporium herbarum, Erwinia uredovora, Klebsiella oxytoca, Rhizoctonia solani, Rhodotorula rubra and R. minuta [G797, H356, K70].

In some instances the reaction product is an ethylbenzene analogue [e.g. E263, H52, H356]; the corresponding styrene is a probable intermediate.

Arylmalonate decarboxylase (E.C. 4.1.1.76)

Alcaligenes bronchisepticus enzyme, molecular weight 24 000 and optimum pH 8.5, decarboxylates α-aryl-α-methylmalonates, where the aryl group may be phenyl, phenyl substituted with halide, methyl or methoxy groups, or by naphthyl groups [G716]. The enzyme contains 240 amino acid residues, with a corresponding molecular weight of 24 737 [K794].

E. coli enzyme, which is stereospecific, forms (*R*)-α-fluorophenylacetate from α-fluorophenylmalonate [K232, K576].

Phaseolus hydroxycinnamate side chain oxidase

P. mungo enzyme, molecular weight about 30 000–40 000 and optimum pH 7.5 apparently decarboxylates *p*-coumarate; the identity of the product is not stated in Chemical Abstracts. The enzyme requires cysteine, and is inhibited by iron and copper chelators [D591].

Tropate dehydrogenase

Pseudomonas enzyme, which forms phenylacetaldehyde from tropate, has an optimum pH 9.5 and requires NAD^+ [H829].

Precarthamin decarboxylase

Carthamus tinctorius enzyme, molecular weight 33 000, activation energy 19.7 kcal/mol and optimum pH 5.0, forms carthamin; it is found in immature flowers. It is inhibited by divalent cations and reducing agents [K557, K579].

Decarboxylation with bromination

Glycine max seed coat peroxidase, with bromide and peroxide as co-substrates, converts 3,4-dimethoxycinnamate into *trans*-ω-bromo-3,4-dimethoxystyrene [K439].

Ethanolamine incorporation with decarboxylation

Debaryomyces polymorphus replaces the carboxyl group in maesanin (a quinone) with an ethanolamino group to form a substituted aniline [K388].

4.4 *Other reactions involving side-chain shortening and removal*

Polynuclear hydrocarbon demethylation

Rat lung cytosol demethylates 7-methyl- and 7,12-dimethylbenzanthracene [G491]. Liver cytosol demethylates 5- and 6-methylchrysene [G118].

Tryptophanase and tryptophan indole-lyase (E.C. 1.13.11.11 and 4.1.99.1)

$$\text{L-Tryptophan} \rightarrow \text{pyruvate} + NH_3 + \text{indole}$$

In E. coli the reaction, optimum pH 8.5 is

reversed by high concentrations of pyruvate and ammonium ion [A430]. D-Tryptophan is also a substrate, but only in high concentrations of $(NH_4)_2HPO_4$ [J250].

Salmonella typhimurium and E. coli tryptophan synthase (E.C. 4.2.1.20), free from any tryptophanase (the latter catalyses the reaction rapidly) slowly catalyzes the reaction. It is not inhibited by (3*R*)-2,3-dihydro-L-tryptophan, a tryptophanase inhibitor, but is inhibited by (3*S*)-2,3-dihydro-L-tryptophan, a tryptophan synthase inhibitor. Another substrate is S-(*o*-nitrophenyl)-L-cysteine, which yields *o*-nitrothiophenol, but the reaction rate is slower than with tryptophanase [E101].

Proteus rettgeri enzyme synthesises tryptophans from indole, 5-methylindole, 5-hydroxyindole and 5-aminoindole [B292].

Gut flora, protozoa and Clostridium catalyze the reaction [A2571, D477, G485].

Debenzylation of tetrahydroisoquinolines

Nelumbo nucifera peroxidase releases vanillyl alcohol from orientaline, and *p*-hydroxybenzyl alcohol from N-methylcoclaurine and armepavine [D566].

(+)-Usnate deacetylation

Mortierella isabellina enzyme, molecular weight 76 000 and optimum pH 7, forms (+)-2-deacetylusnate and acetate from usnate; it is claimed to be a hydrolytic reaction. It is activated by divalent cations (Co, Ni, Mn, Mg, and Zn), but a large number of potential inhibitors do not act on this enzyme. It is specific for the (+)-isomer, and it does not act on several analogues [A2521].

Kynureninase (kynurenine hydrolase, hydroxykynureninase; E.C. 3.7.1.3)

L-Kynurenine → anthranilate

Human liver enzyme, which requires pyridoxal phosphate, is both cytosolic and mitochondrial. Both forms have similar properties, with molecular weight 130 000 and pI 5.9. They act on kynurenine, or, better, 3-hydroxykynurenine [D272].

Mouse liver enzyme is inhibited by Zn^{2+} and activated by Mn^{2+} [A97]. The affinity for 3-hydroxykynurenine is much greater than for kynurenine. 3-Hydroxyanthranilate is inhibitory [A854].

Activity is found in liver, lung and brain (in decreasing order of activity) from rabbit, rat, gerbil and mouse [J830].

Rat liver enzyme does not act on 5-hydroxykynurenine; 3-hydroxykynurenine is a better substrate than kynurenine. Several substituted hydrazines are inhibitory, and interaction with the pyridoxal phosphate coenzyme is thought to be the mechanism [A2546, A2664].

Suncus murinus liver enzyme, a dimer, molecular weight 110 000, optimum pH 8.5 and pI 6.4, requires pyridoxal phosphate, with kynurenine and 3-hydroxykynurenine as substrates. Traces are found in other organs [F175].

Neurospora crassa enzyme kynureninase I, which has been crystallized, is inducible [K227], molecular weight 105 000. It is inhibited by hydroxylamine, phenylhydrazine, semicarbazide and borohydride; all but the latter inactivation are reversed by pyridoxal phosphate. EDTA and divalent ions are not inhibitory. L-3-Hydroxykynurenine is a better substrate, whereas N-formyl-L-kynurenine is less effective; this contrasts with enzyme from Pseudomonas marginalis for which both compounds are less effective substrates than kynurenine [A2766]. The inducible enzyme has an optimum pH 8.5 and pI 4.90 [B26]; the latter is a homodimer, and contains one mol of pyridoxal phosphate [C245]. Kynureninase II is constitutive [K227], molecular weight 110 000, optimum pH 8.5 and pI 4.75. L-3-Hydroxykynurenine is a better substrate than kynurenine [B26].

Both constitutive and inducible enzymes are found in Mucor ambiguus and M. javanicis, Gibberella fujikuroi, Neurospora sitophila and N. tetrasperma, Aspergillus niger, A. oryzae and

A. wentii, Fusarium oxysporum, Penicillium notatum, P. purpurogenum and P. urticae. Only a constitutive enzyme is found in Rhizopus oryzae [B26].

Rhizopus stolonifer enzyme acts on 3-hydroxykynurenine and kynurenine. Enzyme in Penicillium roqueforti, Pseudomonas fluorescens and A. niger are induced by tryptophan [A3659].

A Streptomyces parvulus enzyme, molecular weight 82 000, acts on kynurenine, and second enzyme, molecular weight 56 000, acts on 3-hydroxykynurenine [B335].

Studies on induction in Penicillium roqueforti, A. niger, Pseudomonas fluorescens and Rhizopus stolonifer indicate that different enzymes act on kynurenine and 3-hydroxykynurenine [A2150].

Pseudomonas marginalis enzyme acts on kynurenine in the presence of pyridoxal phosphate and benzaldehyde to form 2-amino-4-hydroxy-4-phenylbutyrate. This is considered to arise from the trapping of an amino acid β-carbanion that would normally form alanine in the absence of benzaldehyde. Benzaldehyde can be replaced by *o*- and *p*-nitrobenzaldehyde, 3- and 4-formylpyridine and poorly by vanillin, but not by aliphatic aldehydes as trapping agents [D449]. P. fluorescens enzyme acts on β-methyl-L-kynurenine [K233].

Benzaldehyde lyase (benzoin aldolase) (E.C. 4.1.2.38)

Benzoin → benzaldehyde

Pseudomomas fluorescens enzyme, molecular weight 80 000 (monomer 53 000) and optimum pH 7.5–8.5, requires thiamine pyrophosphate and a divalent cation to form benzaldehyde, irreversibly. Anisoin is the only substrate analogue tested with activity [F221].

Hydroxynitrilase (E.C. 4.1.2.39)

Hevea brasiliensis (rubber) enzyme acts on acetone cyanhydrin and mandelonitrile to form cyanide and the corresponding oxo-compound; a similar reaction is observed with cassava [K795].

This reverse reaction with this enzyme is described in section 4.5.

Aldehyde formation from benzonitrile

Sorghum forms *p*-hydroxybenzaldehyde from *p*-hydroxyphenylacetonitrile; *p*-hydroxymandelonitrile is considered to be the enzymatic product of a peroxidase-type reaction on *p*-hydroxyphenylacetonitrile; it then breaks down spontaneously to the aldehyde. The reaction requires oxygen, and is stimulated by peroxide and Mn^{2+}, but cyanide is inhibitory, presumably reversing the spontaneous breakdown step. The same reaction was observed with horseradish peroxidase [A3471].

Phenylserine aldolase (E.C. 4.1.2.26)

A human brain enzyme converts L-*threo*-3,4-dihydroxyphenylserine into protocatechualdehyde and glycine. The enzyme, optimum pH 8.4, is mainly cytosolic and requires pyridoxal phosphate. The *erythro*-isomer is less active, and the D-isomers are not substrates [E371]. The activity is also found in rat [H231].

Benzoates from phenethylamines

A mouse enzyme that requires oxygen and NAD(P)H to convert mescaline into 3,4,5-trimethoxybenzoate, shows highest activity in brain. The reaction is not inhibited by monoamine, or by diamine oxidase inhibitors [A117].

β-Oxidation

$R.CH_2.CH_2.COOH \rightarrow R.COOH$

A large number of studies have detected metabolic products that imply the degradation of side-chain carboxylic acids, with the side chain reduced in length by a multiple of two carbon atoms.

In Trichosporon cutaneum an intermediate in this reaction, *p*-hydroxyphenylhydracrylate is converted into *p*-hydroxybenzaldehyde; ATP and CoA are required [B34]. Flavobacterium converts phenylhydracrylate into phenylacetaldehyde [E679].

A number of studies with cannabinoids have demonstrated degradation of the alkyl side chain by Nocardia, involving removal of two carbon units, presumably with initial oxidation of the terminal methyl group [e.g A3010].

Pseudomonas fluorescens 4-hydroxycinnamoyl CoA hydratase/lyase is a homodimer, molecular weight 63 000, (monomeric molecular weight calculated to be 31 010 from the gene sequence), pI 5.2 (calculated as 5.63 from gene sequence) and optimum pH 8.5–9.5. The product is a benzaldehyde; the reaction sequence is postulated to involve the formation of phenylhydracryloyl CoA, with acetyl CoA elimination. Substrates are the CoA conjugates of ferulate, caffeate and *p*-coumarate, but not cinnamate, sinapate or *o*-coumarate. It is inactivated by iodoacetamide [K92].

Skatole formation

Gut flora convert L-tryptophan into skatole [G485]. With rumen organisms up to twice as much tryptophan is converted into skatole as into indole [D477].

Double bond fission by lipase

Lipase and peroxide convert isoeugenol into vanillin [K626].

Lignin degrading peroxidase (diarylpropane oxygenase)

Phanerochaete chrysosporium enzyme, molecular weight 42 000 requires peroxide. It acts on 1,2-bis(3,4-dimethoxyphenyl)propanediol to form veratraldehyde and 1-(3,4-dimethoxyphenyl) ethanediol; the latter is further degraded to veratraldehyde and 3,4-dimethoxy-ω-hydroxyacetophenone. Other studies found a molecular weight of 41 000 for a major isozyme, and 39 000 and 43 000 for two minor isozymes. It contains Fe, probably as haem, and the main isozyme contains 6 per cent carbohydrate. A number of analogues of the above compounds are substrates [C401, D467, D655]. This enzyme is essential for the organism's ability to degrade wood.

Lignostilbene α, β-dioxygenase (E.C. 1.13.11.43)

Pseudomonas enzyme, optimum pH 8.5 and molecular weight 94 000, is a homodimer containing Fe. It requires oxygen for the inter-phenyl double bond fission of 1,2-bis(4-hydroxy-3-methoxyphenyl)ethylene to form vanillin. *p*-Hydroxystyrene is another substrate; other analogues may have marginal activity [K754].

Noscapine fission

In rat, rabbit and man noscapine is converted into cotarnine, hydrocotarnine and meconine. The reaction involves a novel C–C bond fission between two ring systems; the products demonstrate, in one instance only, hydroxylation of the heterocyclic ring at the site of fission [A3719].

C-Glucoside removal

Gut flora remove the 8-C-β-D-glucopyranosyl group from puerarin [J525]. This reaction is also observed in rat [H408].

Human gut flora remove the C-glucoside group of aloesin; this was claimed to be the first report of this reaction type [G226].

Gut flora remove the C-glucoside group present in barbaloin [F44].

Oxidative de-esterification

Rat and dog remove the isopropyl group from barnon. It was suggested that the reaction was oxidative, with formation of acetone [A3057].

In rat dimethyl 2,6-dimethyl-4-(*o*-nitrophenyl)-3,5-pyridinedicarboxylate is mono-demethylated; there is no hydrolytic cleavage, and the reaction appears to oxidative [F540].

Tea catechol oxidase, optimum pH 5.7, oxidatively degallates (−)-epigallocatechin gallate and (−)-epicatechin gallate to release gallate; it is not an esterase [A972].

Anthracycline glycoside reductase

Rat liver P450, optimum pH 7.4 removes the glycoside moiety of aclacinomycin A reductively, utilizing NAD(P)H as co-substrate, with 7-deoxyaklavinone and 7-deoxyaklavinone dimer as products; the reaction removes the oxygen at the 7-position. Two other compounds, designated MA 144M1 and M144N1 are claimed to be substrates; their identities are not disclosed in Chemical Abstracts [B229].

Aeromonas enzyme, molecular weight 35 000, requires NADH and is inhibited by oxygen but not by cyanide or EDTA. It cleaves steffimycin to 7-deoxysteffimycinone [A2754]. The same reaction is found in Aeromonas hydrophila, E. coli and Citrobacter freundii [A2756, A2759].

Streptomyces steffisburgensis enzyme, which requires NADH, cleaves daunomycin, daunomycinol and adriamycin to the corresponding 7-deoxy aglycones [A2755, A2757].

Many studies in animals with daunorubicin and analogues have demonstrated the formation of 7-deoxyaglycones; presumably a similar reaction occurs.

Daunorubicin/adriamycin oxidative deglycosylation

Cows' milk xanthine oxidase forms semiquinone free radicals from these compounds, which then yield the corresponding 7-deoxyaglycones [B370].

2,4′-Dihydroxyacetophenone dioxygenase (E.C. 1.13.11.41)

Alcaligenes enzyme acts on the above compound to form formate and *p*-hydroxybenzoate; molecular oxygen is incorporated into both products [E173].

Phloretin hydrolase (E.C. 3.7.1.4)

Phloretin is converted into phloretate and phloroglucinol in rat and microorganisms [D159].

2-Hydroxy-6-oxo-6-phenylhexa-2,4-dienoate hydrolase (E.C. 3.7.1.8)

Burkholderia cepacia enzyme, a homotetramer, monomeric molecular weight 32 000, forms benzoate and 2-hydroxypenta-2,4-dienoate from 2-hydroxy-6-oxo-6-phenylhexa-2,4-dienoate. A similar reaction is observed with compounds in which the phenyl group is replaced by an alkyl group or the phenyl group is in position 5, and with a range of analogues halogenated on the nucleus and the side chain. The reaction is stated to be a hydrolysis, and is involved in the degradation of polychlorinated biphenyls [J710, K522].

Pseudomonas cruciviae enzyme (grown on biphenyl – the substrate is a biphenyl metabolite), molecular weight 160 000 and monomeric molecular weight 29 000, has an optimum at pH 4.7 [E85].

Transmethylations

a. Methylenetetrahydrofolate-tRNA (uracil-5-) methyltransferase (E.C. 2.1.1.74)

S. faecalis enzyme transfers the methyl group from methylenetetrahydrofolate to form tetrahydrofolate; the reaction requires $FADH_2$ [K837].

b. 5-Methyltetrahydropteroyltriglutamate-homocysteine methyltransferase (E.C. 2.1.1.14)

E. coli enzyme, molecular weight 84 000 is polymeric and requires Mg^{2+} (Mn^{2+} is less effective); it forms methionine and tetrahydropteroyltriglutamate. 5-Methyltetrahydrofolate is not a substrate [K807, K842].

c. 5-Methyltetrahydrofolate-homocysteine methyltransferase (E.C. 2.1.1.13)

E. coli enzyme, molecular weight 150 000 for urea-resolved apoenzyme (native molecular weight appears to be 205 000), contains bound cobalamin and requires Mg^{2+}, ATP, FAD and NADH; it forms methionine and tetrahydrofolate. The Stokes radius is 5.42 nm [K804, K807].

Enzyme from green string bean, barley sprout and spinach acts additionally on 5-methyltetrahydropteroyltriglutamate [K802].

d. Tetrahydropteroylglutamate methyltransferase

Rat liver enzyme, optimum pH 6.7, acts on 5-methyltetrahydropteroylglutamate and 5-methyltetrahydropteroylpentaglutamate with L-homocysteine as co-substrate to form methionine and the demethylated glutamates [A2502].

Phaseolus vulgaris enzyme, molecular weight 40 000 and optimum pH 6.5, catalyzes the reaction anaerobically [A3085].

Tyrosine phenol-lyase is described in 4.1.

4.5 *Chain lengthening reactions*

Hydroxynitrile lyases (oxynitrilase; mandelonitrile lyase and hydroxymandelonitrile lyase, E.C. 4.1.2.10 and 4.1.2.11 respectively)

e.g. Mandelonitrile ↔ benzaldehyde + HCN

Sorghum bicolor and almond catalyze the formation of hydroxynitriles from benzaldehydes to form (*S*) and (*R*) isomers respectively. A range of benzaldehydes, substituted in the *p*-position, are substrates [H208, J194]. The molecular weight of Sorghum enzyme is 95 000 [G263].

Ximenia americana enzyme is composed of two isozymes, one of which is minor. The other, molecular weight 38 000, optimum pH 5.5 and pI 3.9, is a glycoprotein, and unlike Prunus enzyme it does not appear to be a flavoprotein. Only one isomer of mandelonitrile, (presumably (*R*)) is substrate [F265].

(*R*)-Oxynitrilase is found in apple, apricot, cherry, plum, and almond kernel. Substrates studied were benzaldehyde, 3,4-isopropylenedioxybenzaldehyde, 3,4-dimethoxybenzaldehyde, 4-acetoxy-3-acetoxymethylbenzaldehyde, and benzaldehydes substituted in the *p*-position with acetoxy, *tert*-butylcarbonyloxy, phenoxy, isopropyl or hydroxyl groups. In most cases the enantiomeric purity of the product is in excess of 90 per cent. Almond enzyme acts on all these substrates, and apple on all but *p*-acetoxybenzaldehyde. Only benzaldehyde is substrate for all species studied; of the remaining species only cherry and apple enzymes act on substituted benzaldehydes [J302].

Almond enzyme acts on cinnamaldehyde, 1-(formylmethoxy)naphthalene, acetophenone, 2-acetyl-6-methoxynaphthalene and pentachlorobenzaldehyde. Almond, peach and loquat all act on cinnamaldehyde and some benzaldehydes [K6, K320]. Prunus amygdalus enzyme, used in conjunction with an organic solvent yields oxynitriles with high enantomeric purity (presumably (*R*)) from benzaldehyde, *m*-phenoxybenzaldehyde and phenylacetaldehyde as well as from some aliphatic aldehydes [E353].

Prunus serotina leaf and stem enzyme hydrolyzes (*R*)-mandelonitrile; Prunus enzyme acts on benzaldehyde [H343, H781].

Phlebodium aureum (fern) enzyme exists as three polymeric forms, molecular weights about 170 000, all with monomeric molecular weight 20 000 and optimum pH 6.5. They act on benzaldehyde and are (*R*)-specific. Unlike many analogous enzymes from other species it is not a flavoprotein. Iodoacetamide, diethylpyrocatechuate and Ag^{+} are inhibitors;

they are more susceptible to inhibition than P. amygdalus enzyme [H781].

An (*S*)-oxynitrilase (source uncertain) differs from (*R*)-oxynitrilase in that it acts on aromatic aldehydes, whereas (*R*)-oxynitrilase acts on both aromatic and aliphatic aldehydes. Its substrates are benzaldehydes, substituted in the *para* position with H, methyl, chloro or hydroxyl groups, or in the *meta* position with chloro, bromo, hydroxyl, methoxy or phenoxy groups. In most cases the product is enantiomerically at least 90 per cent pure, except for *p*-chlorobenzaldehyde which yields the racemic mixture [F680].

D-Phenylserine formation

Arthrobacter acts on glycine and benzaldehyde to form D-phenylserine. The reaction requires mercaptoethanol, pyridoxal phosphate and Mn^{2+} [G140].

Propiophenone formation

Acinetobacter calcoaceticus acts on benzoylformate and acetaldehyde to form (*S*)-2-hydroxypropiophenone [H403].

2-Hydroxypropiophenone formation

Pseudomonas putida benzoylformate decarboxylase acts on aryl aldehydes and acetaldehyde with thiamine diphosphate as coenzyme, to form 2-hydroxypropiophenones. A large number of benzaldehydes are substrates, with low activity for *o*-substituted benzaldehydes [K524].

Acetophenone formation from benzoate

Streptomyces levoris converts *p*-aminobenzoate into *p*-aminoacetophenone [C350].

Benzalacetone synthase

Raspberry converts *p*-coumaroyl CoA and malonyl CoA into *p*-hydroxyphenylbutan-2-one, via *p*-hydroxyphenylbut-3-en-2-one [J26].

Benzylsuccinate synthase

Thauera aromatica enzyme, molecular weight 220 000 is composed of four subunits, molecular weights 94 000, 90 000, 12 000 and 10 000; the substrates are toluene and succinate, and more than 95 per cent of the product is the (+)-isomer [J817]. The enzyme is very sensitive to oxygen [J651]. Another report states that the co-substrate is fumarate [J191].

Azoarcus enzyme is anaerobic, and uses fumarate as co-substrate. Besides toluene, it acts on xylenes, monofluorotoluenes and benzaldehyde. Studies with several toluene analogues found that the hydrogen abstracted from the toluene methyl group is retained in the succinyl moiety [K238].

The reaction is also found in Desulfobacula toluolica [J847].

L-Phenylacetylcarbinol formation

Candida utilis forms this compound from benzaldehyde and pyruvate by the action of pyruvate decarboxylase. The product is used in ephedrine synthesis [H771, J192].

Zygosaccharomyces bisporus enzyme acts on pyruvate and aldehydes. Benzaldehyde forms 1-hydroxy-1-phenyl-2-propanone; phenylacetaldehyde is another substrate [K611]. Candida and Saccharomyces exhibit the same reaction [J192].

Side-chain C-methyltransferases

Streptomyces flocculus forms (2*S*,3*R*)-β-methyltryptophan from L-tryptophan and *S*-adenosylmethionine [D183].

Streptomyces griseus indolepyruvate C-methyltransferase (E.C. 1.1.1.47), molecular

weight 55 000–59 000 (by different methods) and optimum pH 7.5–8.5 is stable at 0°, but activity is lost on freezing or heating; it does not require cofactors. It introduces a methyl group into the side chain to form (*S*)-3-methylindolepyruvate, with S-adenosylmethionine as co-substrate. It is inhibited by thiol-binding reagents and iron-zinc chelators, as well as by indolmycin, the product of the reaction sequence. Phenylpyruvate and *p*-hydroxyphenylpyruvate are also substrates [A2281, A2307, K847]. Evidence has been presented that the same enzyme is responsible for the methylation of tryptophan and indolepyruvate. Streptonigrin is reckoned to be the final product of this reaction sequence [D148].

C-Glucoside formation

Fagopyrum esculentum UDP-glucose: 2-hydroxyflavanone-6 (or 8)-glucosyltransferase, molecular weight 41 000 and optimum pH 9.8, acts on 2,4′,5,7-tetrahydroxyflavone and 2,5,7-trihydroxyflavanone, but not on analogues lacking the 7-hydroxyl group [E614].

C-Glucuronide formation

In mouse Δ^6-tetrahydrocannabinol forms the corresponding C-4′-glucuronide [A3724], in man feprazone forms a C-4-glucuronide [A3916], and sulphinpyrazole (species unclear) forms C-4-glucuronide [A3243].

L-Phenylalanine from phenylacetate, and allied reactions

This reaction has been detected in Ruminococcus albus [C793], in rumen bacteria and protozoa [H960]. Another study with rumen microorganisms found in addition that *p*-hydroxyphenylacetate forms L-tyrosine and IAA forms L-tryptophan [A1164].

Indole-3-butyrate formation

Zea mays enzyme, molecular weight 31 000 and optimum pH 4.8, catalyzes this reaction, with IAA as substrate. It requires acetyl CoA and ATP as cofactors [G758, H694].

5. Conjugation and substitution reactions

5.1 *Ester formation* A. Carboxylate esters

Acetyl CoA: benzyl alcohol acetyltransferase

Clarkia breweri flower enzyme acts on benzyl alcohol to form benzyl acetate [J521, K240].

Mandelonitrile ester formation

Pseudomonas forms O-acetylmandelonitriles from *m*-methoxy- and 3,4-dimethoxymandelonitriles, with vinyl acetate as co-substrate [H303].

O-Acetylmandelic acid formation

Commercial lipase forms this ester from mandelic acid and vinyl acetate [K310].

Chloramphenicol O-acetyltransferase (E.C. 2.3.1.28)

This enzyme has been purified by affinity chromatography from a chloramphenicol-resistant E. coli strain [A164]; acetyl CoA is the co-substrate.

In Klebsiella the 3-acetate is the major product, whereas some 1-acetate is formed [A460].

Streptomyces griseus forms both the 1- and 3-acetates as well as the propionate, isobutyrate, butyrate and isovalerate at the 3-position [A2476].

The activity has been detected in duck [G945].

Oestradiol esters

Beef placental acyl CoA: oestradiol-17β acyltransferase, optimum pH 5.0 forms oleoyl, palmitoyl, palmitoleoyl, linoleoyl, linolenoyl and possibly arachidonoyl 17β esters with oestradiol [E431, E968].

Acetyl CoA deacetylvindoline 4-O-acetyltransferase

A plant enzyme, molecular weight 50 000, forms vindoline [J701].

Acetyl CoA deacetylvindoline 17-O-acetyltransferase (E.C. 2.3.1.107)

Catharanthus roseus enzyme is found in vindoline-containing plant parts [K931].

Acetyl CoA: 10-hydroxytaxane O-acetyltransferase

Taxus chinensis enzyme is monomeric, molecular weight 71 000, pI 5.6 and optimum pH 9.0 and is specific for the 10β-isomer. Other substrates are 10-deacetylbaccatin III as well as other analogues that lack an aryl moiety [K91].

Indoleacetylglucose inositol O-acetyltransferase (E.C. 2.3.1.72)

Zea mays acts on indole-3-acetylglucose and *myo*-inositol to form indole-3-acetyl-*myo*-inositol and glucose [B433, K746].

N-Hydroxyarylamine O-acetyltransferase

Hamster enzyme acetylates the hydroxyl group of N-hydroxy-2-acetamidofluorene [G757].

The enzyme is cytosolic, molecular weight 33 000, and requires acetyl CoA. It also shows arylhydroxamate N,O-acetyltransferase (E.C. 2.3.1.118) and arylamine N-acetyltransferase activities [E110].

The activity is also found in rat liver [C70, G811]; all the three above activities are found associated with the rat enzyme, molecular weight 32 000 [H566]

Aromatic hydroxylamine O-acetyltransferase (E.C. 2.3.1.56)

N-Hydroxy-4-acetamidobiphenyl + N-hydroxybiphenyl → N-hydroxy-4-aminobiphenyl + N-acetoxy-4-aminobiphenyl

Rat enzyme, optimum pH 7.5, is found in liver with lesser amounts in kidney, small intestinal mucosa, spleen and mammary tissue. The reaction involves the transfer of an acetyl group from N-hydroxy-2-acetamidofluorene or N-hydroxy-4-acetamidobiphenyl to 4-hydroxylaminobiphenyl or 2-hydroxylaminofluorene, forming the corresponding acethydroxamic acids. It is activated by NAD(P)H or cysteine [K747].

Esterification by transacetylation and transformylation

Hamster liver N,O-acetyltransferase converts N-hydroxy-2-acetamidofluorene into N-acetoxyaminofluorene. Other substrates are N-hydroxy-2-acetamidofluorene substituted at the 7 position with bromo, acetyl, ethyl or ethoxy groups [H106]. It is a glycoprotein, molecular weight 60 000 and pI 5.4. It also deacetylates the product as well as hydrolyzing *p*-nitrophenyl acetate [G744].

Dog liver N,O-acyltransferase is a glycoprotein trimer, monomeric molecular weight about 60 000, and about 20 000 of this is glycoside. The pI of the aglycone enzyme is 5.6, and 5.4–5.6 for the native enzyme, which appears to be heterogeneous. The substrate is N-hydroxy-2-formamidofluorene [H247].

Rat liver enzyme acts on N-hydroxy-2-formamidofluorene and N-hydroxy-2-acetamidofluorene. Four isozymes have been found, molecular weights 60 000, 61 000, 180 000 and 60 000, with pI 5.0, 5.5, 6.0 and 6.5 respectively. The largest isomer is a trimer. These enzymes also catalyze deacetylation reactions [G735].

Rat liver arylhydroxamate N,O-acetyltransferase (E.C. 2.3.1.118), molecular weight 38 500, pI 4.5 and optimum pH 7.0, is oxygen-labile. This enzyme activates the substrates to bind with tRNA [D447].

Acetyl CoA: salutaridinol-7-O-acetyltransferase (E.C. 2.3.1.150)

Papaver somniferum enzyme, molecular weight 50 000, pI 4.8 and optimum pH 6–9, acts on salutaridinol with acetyl CoA as co-substrate. This is a key reaction in the formation of opium alkaloids; the reaction product spontaneously eliminates the acetate moiety with the formation of an epoxide ring to position 5, forming thebaine [J1, K784, K786].

Glycoside esterification

Chenopodium rubrum hydroxycinnamoyltransferase acts on both (*R*)- and (*S*)-amaranthin, with sinapoylglucose, feruloylglucose, caffeoylglucose and *p*-coumaroylglucose as acyl donors (celosianin II is a typical product); the glycoside is esterified at the 2″ position [G255].

Gentiana triflora anthocyanin 5-aromatic acyltransferase (E.C. 2.3.1.153), molecular weight 52 000 and pI 4.6 is monomeric. Substrates are delphinidin- and cyanidin-3,5-diglucosides which form the corresponding 5-O-glucoside-6″-O-hydroxycinnamates; *p*-coumaroyl CoA and caffeoyl CoA are co-substrates [K788].

Silene dioica petal hydroxycinnamoyl CoA: anthocyanidin 3-rhamnosyl(1 → 6)glucoside

4‴-hydroxycinnamoyl transferase, molecular weight 56 000 and optimum pH 7.6–7.8, condenses *p*-coumaroyl or caffeoyl CoA with cyanidin or pelargonidin 3-rhamnosyl (1→6)glucosides and cyanidin 3-rhamnosyl (1→6)glucoside-5-glucoside [B411].

Zinnia elegans enzyme, which requires acetyl CoA, acts on cyanidin and pelargonidin 3-glucosides to form acetylglucosides [G996].

E. coli acetyl CoA: galactoside 6-O-acetyltransferase (E.C. 2.3.1.18) acts on *p*-nitrophenyl-β-D-galactoside, to form the 6-O-acetylgalactoside [A731].

O-Malonyltransferases

Malonyl CoA + flavonoid-O-β-glucoside → CoA + O-malonylflavonoid-O-β-glucoside

Petroselinum crispum isozymes, molecular weight 50 000 and optimum pH about 8, require malonyl CoA. One isozyme (E.C. 2.3.1.115) acts effectively on 7-glucosides of apigenin, luteolin, diosmetin, naringenin and on apiin, but 3-glucosides are poor substrates, with malonyl CoA as co-substrate. A number of non-flavonoid glucosides are also substrates. The other isozyme (E.C. 2.3.1.116) acts on 3-glucosides of kaempferol, quercetin and isorhamnetin, but poorly on 7-glucosides; they are immunologically distinct [D684, K725, K727].

Chickpea (Cicer) malonyl CoA: isoflavone 7-O-glucoside-6″-O-malonyltransferase (E.C. 2.3.1.115), molecular weight 112 000, pI 5.3 and optimum pH 8.0, acts on 7-glucosides of biochanin A, genistein, pratensein, orobol, formononetin, apigenin, luteolin, kaempferol, quercetin and quercetagetin, maackiain 3-glucoside, 2′,4,4′-trihydroxychalcone-4′-glucoside and indoxyl-β-D-glucoside, and slowly on a number of other glucosides, including many non-flavonoid compounds [D445].

Glycine max enzyme, molecular weight 48 000 acts on pentachlorophenyl-β-D-glucoside and malonyl CoA to form the 6-O-malonylglucoside [G247]. Another substrate is *p*-nitrophenyl-β-D-glucoside [H660]. Daucus carota acts on β-glucosides of *p*-nitrophenol and 3,4-dichloroaniline [H118]. A similar reaction is found in wheat [J709].

Rosmarinic acid synthetase (E.C. 2.3.1.140)

Coleus blumei enzyme, optimum pH 7–7.5, acts on caffeoyl CoA and (*R*)-3,4-dihydroxyphenyllactate to form rosmarinic acid by esterification of the alcoholic hydroxyl of 3,4-dihydroxyphenyllactate with caffeate; it is specific for the (*R*)-isomer, and the reaction is reversible. Analogues can be formed by using combinations of substrates, which include *p*-coumaroyl CoA and *p*-hydroxyphenyllactate [G420].

Glycerol ester formation

Human hepatocytes incorporate the substituted benzoic acid lifibrol into triglycerides, with palmitic, stearic, oleic, linoleic, linolenic and arachidonic acid as other components of the triglyceride [H533].

Rat liver monoacylglycerol acyltransferase acts on the CoA derivatives of benzoate, 3-phenoxybenzoate and 1-naphthylacetate to incorporate the acyl moieties into 2-hexadecylglycerol. They are also incorporated into 1,2-dipalmitoylglycerol by the action of diacylglycerol acyltransferase (E.C. 2.3.1.20) [F749]. Rat hepatocytes form triglycerides in which ibuprofen and 3-phenoxybenzoate are incorporated. The product structures are uncertain. Incorporation is not observed with more polar acids, such as 3-phenylbutyrate [F745].

Adipocytes form fenbufenoylglycerol from fenbufen, which then condenses with palmitoyl CoA to form a diester with liver monoacylglycerol acyltransferase as catalyst [H795].

Chlorogenic acid: chlorogenate caffeoyl transferase

2 Chlorogenate (3-O-caffeoylquinate) → isochlorogenate (3, 5-di-O-caffeoyllquinate) + quinate

Ipomoea batatas (sweet potato) tuber enzyme, molecular weight 25 000, pI 4.6 and optimum pH 5.0 is strictly specific; it requires no cofactors [F179].

Chlorogenate-glucarate O-hydroxycinnamoyltransferase (E.C. 2.3.1.98)

Tomato cotyledon enzyme, optimum pH 5.7, pI 5.75 and molecular weight 40 000 is monomeric; the reaction forms quinic acid and 2-O-caffeoylglucarate from chlorogenate and glucarate; galactarate is also an acceptor. The activation energy is 57 kj/mol [K721, K723].

Quinate O-hydroxycinnamoyltransferase (E.C. 2.3.1.99)

Feruloyl CoA + quinate →
O-feruloylquinate + CoA

This enzyme is found in Secale cereale, with CoA esters of ferulate, caffeate, sinapate and *p*-coumarate as substrates [K722]. It is also found in tomato [K723].

Potato tuber enzyme consists of three isozymes, molecular weight about 41 500, two of which are specific for quinate, and the third additionally shows slight activity towards shikimate. The substrates are CoA derivatives of *p*-coumarate, ferulate and caffeate, with chlorogenate as the product from caffeate; the free acids are inhibitors [A3755]. Another study found significant activity with shikimate. In the presence of CoA, the reverse reaction is found with chlorogenate and 5′-(*p*-coumaroyl)quinate. The activity in tubers is modulated by the temperature conditions of storage [A3145].

Ipomoea batatas enzyme, molecular weight 25 000, pI 8.6 and optimum pH 6.0, acts on quinate, and only poorly on shikimate. Substrates are D-glucosides of cinnamate, *p*-coumarate and caffeate [F143].

Studies with tomato have shown that conjugation is strictly restricted to the 5′-position in quinate [A3149].

The activity is found in all of 30 Angiosperms studied, suggesting that it is found in most if not all Angiosperms. However no activity was found in Pinus pinea (Gymnosperm) or Ceratopteris thalictroides (Pteridophyta) [A3758].

Galactarate O-hydroxycinnamoyltransferase (E.C. 2.3.1.130)

Feruloyl CoA + galatarate →
O-feruloylgalactarate + CoA

This enzyme is found in Secale cereale, with CoA esters of ferulate, caffeate, sinapate and *p*-coumarate as substrates [K722].

Shikimate O-hydroxycinnamoyltransferase (E.C. 2.3.1.133)

Feruloyl CoA + shikimate →
O-feruloylshikimate + CoA

This enzyme is found in Secale cereale, with CoA esters of ferulate, caffeate, sinapate and *p*-coumarate as substrates [K722].

***p*-Hydroxycinnamoyl CoA: shikimate *p*-hydroxycinnamoyl transferase**

Cichorium endiva enzyme, molecular weight 58 000 and optimum pH 6.5, carries out this reaction reversibly, with the formation of *p*-coumaroylshikimate and CoA. With the exception of Ceratopteris, this activity was found in every plant genus examined: Agrostemma, Betula, Capsicum, Caragana, Catalpa, Catharanthus, Coffea, Coleus, Datura, Drosophyllum, Forsythia, Galium, Geum, Juglans, Linum, Lonicera, Lycopersicon, Malus, Nicotiana, Padus, Petroselinum, Phaseolus, Pimpinella, Pinus, Rheum, Rauwolfia, Rubia, Salix, Sedum, Solanum and Stevia [B202].

Glucarate O-hydroxycinnamoyltransferase

Feruloyl CoA + glucarate →
O-feruloylglucarate + CoA

This enzyme is found in Secale cereale, with CoA esters of ferulate, caffeate, sinapate and *p*-coumarate as substrates [K722].

Glucarolactone O-hydroxycinnamoyltransferase

Feruloyl CoA + glucaralactone → O-feruloylglucaralactone + CoA

This enzyme is found in Secale cereale, with CoA esters of ferulate, caffeate, sinapate and *p*-coumarate as substrates [K722].

Alcohol O-cinnamoyltransferase (E.C. 2.3.1.152)

The existence of this enzyme is based on the presence of 1-O-*trans*-cinnamoyl-β-D-glucopyranosyl(1→6)-β-glucopyranose and analogues in Physalis peruvianis, Pisidium guajava and Vaccinium vitis-idaea [K789].

β-Glucogallin O-galloyltransferase (E.C. 2.3.1.90)

Quercus robur leaf enzyme, optimum pH 6.0–6.5, catalyzes dismutation of 1-galloyl-β-D-glucose, with the formation of glucose and digalloylglucose as products [K894].

Rhus typhina leaf enzyme specifically acts on 1,6-di-O-galloyl-β-D-glucose and 1-galloyl-β-D-glucose to form 1,2,6-tri-O-galloyl-β-D-glucose [K888].

Glucogallin-tetrakisgalloylglucose O-galloyltransferase (E.C. 2.3.1.143)

Quercus robur enzyme, molecular weight 260 000 and optimum pH 6.3 is found in young leaves, and is stable between pH 5.0 and 6.5. It forms 1,2,3,5,6-pentagalloylglucose from 1,2,3,6-tetragalloylglucose with 1-galloyl-β-D-glucose as acyl donor [K726].

Sinapoylglucose-choline O-sinapoyltransferase (E.C. 2.3.1.91)

Sinapis alba and Raphanus enzymes, molecular weights 60 000 and optimum pH 7.2 (Raphanus) and 7.6 (Sinapis) act on choline and 1-O-sinapoyl-β-D-glucose to form sinapine; 1-feruloyl- and 1-(*p*-coumaroyl)glucose are also substrates. There is no requirement for cations or thiols; the activation energy is 53 kj/mol [K720].

Phosphatidylcholine conjugation

Adipocytes form fenbufenoyl phosphatidylcholine from fenbufen [H795].

Phenylacetylcarnitine formation

This compound is formed in rat; it is also found in patients with phenylketonuria, where phenylacetic acid levels are raised [K521].

Benzoylmalate formation

Glycine max forms this compound from benzoate; the time course of the reaction indicates that benzoylglucose is an intermediate [A3679].

Benzyl alcohol forms O-benzoyl-L-malate in barley, presumably via benzoate [A1726].

SAM: benzoic acid carboxyl methyltransferase

Antirrhinum majus enzyme, optimum pH 7.5 and molecular weight 100 000 is dimeric. It is activated by K^+ or NH_4^+, and is highly specific for the formation of methyl benzoate [K650].

SAM: salicylic acid carboxyl methyltransferase

Clarkia breweri enzyme is a dimer, molecular weight 40 300; the amino acid sequence has been determined from the corresponding DNA sequence. The product is methyl salicylate [J521, K239].

B. Sulphate esters

Phenolsulphotransferases (E.C. 2.8.2.1)

$$ArOH + PAPS \rightarrow ArOSO_3H + PAP$$

Studies in the period covered by this review detected two forms of this enzyme, one of which acts on simple phenols (PST-P), and the other on catecholamines (PST-M). This section is in consequence divided into three parts.

a. General studies.

The enzyme requires sulphate and sulphate-activating enzymes [A2065] or added phosphoadenosine phosphosulphate (PAPS) [B72, D979].

Human enzymes acting on dopamine and *p*-nitrophenol are found in many brain areas; one is thermolabile and the other thermostable [D233]. Placental enzyme acts on catecholamines and simple phenols [C322]. Human enzyme from different tissues shows different ratios of activity toward phenol and dopamine. Using these substrates differences in thermal stabilities and inhibition properties were detected, and this has been interpreted to indicate the presence of PST-P and PST-M [B834]. A study with the three isozymes SULT1A1, SULT1A3 and SULT1B2, prepared by recombinant techniques (PSTP-M and thyroid hormone sulphotransfeases respectively), found that bisphenol A, 4-nonylphenol, stilboestrol and 17α-ethynyloestradiol are primarily substrates for PSTP. Dopamine is sulphated mainly by PSTM, although it is a significant substrate for PSTP. 4-Octylphenol and *p*-nitrophenol are good substrates for both these isozymes. None of the above compounds are good substrates for SULT1B2, although most of them show some activity [K344].

Human erythrocyte enzyme with HMPG as substrate has an optimum pH of 7.5 and uses PAPS as co-substrate. Endogenous inhibitors have been detected [B72]. It is cytosolic, and also acts on *p*-acetamidophenol, serotonin, phenol, noradrenaline, tyramine and dopamine, with increasing activity [A3814].

Human lung enzyme, molecular weight 35 000–38 000, which appears not to be PST-P or M, requires PAPS, with a broad specificity for simple phenols and catecholamines; dopamine is the best substrate [D979].

Rat brain enzyme acts on HMPG, DHPG, HMPE and pyrogallol, the latter yielding three products; neither serotonin nor normetanephrine are substrates [A1240]. Another study found an optimum pH in the range 6.8–8.6; other substrates are HVA, VMA, dopac, dopamine and noradrenaline. Neither Mg^{2+} nor mercaptoethanol activate, but ATP is inhibitory [A153]. A further study found a molecular weight of 69 000 and an optimum pH 5.5–6.4. Substrate studies found that simple phenols, VMA, HMPG, HVA, dopamine, adrenaline, noradrenaline and dopamine are substrates, whereas DOPAC, DOMA, HVA, DHPG, metadrenaline, normetadrenaline, serotonin, vanillyl alcohol and *p*-hydroxybenzaldehyde are not [C441]. Rat cerebral enzyme, which acts on hydroxyl groups in tyrosyl peptides, requires PAPS and is found primarily in microsomes [E341].

Rat liver cytosolic enzyme has been separated chromatographically into five fractions, all with subunit molecular weights in the range 28 000–36 000. Three of the fractions show high activity towards *p*-nitrophenol, and the remaining two are much less active [D933]. Two isozymes of a dimeric rat liver enzyme, molecular weights about 65 000, act on simple phenols and catecholamines, optimum pH 5.5 and 6.2 for β-naphthol and 8 for tyrosine methyl ester. They were found to have almost identical amino acid compositions [B61, B941]. Protocatechuate is sulphated in the 3- and 4- positions in the ratio 1:4.8, with an optimum pH 7.4 [B724]. N-Hydroxy-2-acetamidofluorene is a poor substrate [G317].

A rat stomach enzyme, molecular weight 32 000, has a double optimum at pH 5.4 and 6.6 and acts on *p*-nitrophenol, α- and β-naphthols and salicylamide as well as HMPE and HMPG [D807].

Rat platelet enzyme acts on *p*-nitrophenol, and the activity parallels that found in liver [F631].

This activity has been detected liver from rat, rabbit, mouse, cat and guinea pig, mouse kidney, rabbit adrenal and rabbit brain, but not in human liver, rat kidney and intestine or mouse brain [A2067].

Using isoprenaline as substrate, activity has been found in liver from monkey, dog, mouse, rat, rabbit and guinea pig. Activity was also found in kidney, small intestine and lung from only some of these species [B665].

Rat and rabbit enzymes show optimal activity at pH 7.8 [A2065].

Chick embryo enzyme that acts on 4-methylumbelliferone is detectable at five days incubation, with an increase until 20 days. Based on specific activity, a small peak in activity at seven days is followed by a larger, broader peak at 15 days [A3328].

Channel catfish (Ictalurus) enzyme acts on benzpyrene phenols and other phenols. One isozyme, molecular weight 41 000,which is found in liver and gut is immunologically similar to human enzyme, but a liver isozyme, molecular weight 31 000 is not [K497].

b. PST-M.

Human hepatoma enzyme requires Mn^{2+}. Dopamine is a good substrate, and dopa, tyrosine and *m*-tyrosine are lesser substrates; the D-isomers are better substrates than L-[H888]. Small intestine enzyme is a dimer, molecular weight 69 000, and is thermolabile. Dopamine and *p*-nitrophenol are substrates at high concentration [F116].

Human liver enzyme appears to act on L-T_3, but only poorly [E672].

Human ileum enzyme, molecular weight 69 000, which acts on dopamine is thermolabile. It appears that phenol is also a substrate, but only at high concentration [F770].

Human platelet enzyme acts on *m*-tyramine, noradrenaline, adrenaline, serotonin, *p*-hydroxyamphetamine, isoprenaline, salbutamol, α-naphthol, paracetamol, and at high concentration (1 mM) salicylamide [C523]. Dopamine is sulphated primarily (88 per cent) in the 3-position [E186]. The enzyme activity is not altered in either phaeochromocytoma or uraemic patients [E195].

Human brain enzyme, molecular weight 250 000 and optimum pH 7.0, acts on a large number of phenolic analogues of dopamine and noradrenaline, as well as on serotonin. It is inhibited by sodium chloride, but this is slight at physiological concentrations. The kinetics are apparently complex [D583]. It is inhibited by about 45 per cent by 0.3 M NaCl [E198]. Another study on brain cortex enzyme found a molecular weight of 62 000 and an optimum pH 7.8–8.0. Catecholamine analogues are much better substrates than serotonin [D741].

Human and rat liver enzymes act on 4-hydroxypropranolol with high (3 μM) affinity. Although the K_m is the same for both isomers of 4-hydroxypropranolol the V_{max} is different, which leads to stereospecificity [F735].

Rat brain enzyme, which requires PAPS as co-substrate, acts on N-acetyldopamine with optimum pH 9.0. It was not determined which sulphotransferase is responsible for another optimum found at pH 6.6 [E493]. PST-M appears to be absent from rat kidney [E100].

The enzyme is absent from dog platelets [E186].

In marmoset the enzyme acts on tyramine. It is found in lung, liver, small intestine, with small amounts in stomach and kidney, and only traces in brain [F226].

Adrenaline is sulphated in dog, monkey, rat, guinea pig and rabbit, with activity in liver and small intestine, but not in brain or heart [A3444].

Tyramine is sulphated in macaque liver with optimum pH 9.2–9.4. Activity is found (in decreasing order) in macaque, rat, mouse and guinea pig. In macaque the enzyme is more active in intestine than in liver, but in the other species studied the intestinal activity is very low [A2066].

c. PST-P.

Human lung enzyme is a 'mixed' type that acts on adrenaline and noradrenaline as well as simple phenols [D977]. Small intestine enzyme acts on *p*-acetamidophenol [F116]. In liver the sulphation of L-T_3 correlates with PST-P activity [E672].

Human platelet enzyme acts on paracetamol, salicylamide and phenol at low (5 μM) concentration [C523]. Enzyme designated SULT1A1, which acts on 2-naphthol, is assayed by the reverse reaction; with PAP and *p*-nitrophenyl sulphate as substrates; *p*-nitrophenol is released [K46].

Human liver enzyme, which exists as two isozymes that act on *p*-nitrophenol, is thermostable. It also acts on dopamine for which it has a low affinity, optimum pH 7.15 [E211]. Purified enzyme is dimeric, molecular weight 68 000, and acts on phenol and *p*-nitrophenol. Antibody studies suggest that it is closely related to PST-M [F692].

Human brain enzyme has been separated into two fractions; P_1, which acts on phenol, optimum pH 8.5, is inhibited 80 per cent by 0.3 M sodium chloride, whereas the P_{11} form is much less affected by ions. P_1 is inhibited by phosphoadenosine phosphate competitively relative to PAPS, and by ATP non-competitively relative to phenol; both enzymes are inactivated by 2,6-dichloro-4-nitrophenol [E198].

Human ileum enzyme, molecular weight 69 000, is thermostable [F770].

Two alleles of the human enzyme are found. In one ^{213}Arg is replaced by His, resulting in an enzyme with low activity [K257].

Human and rat liver enzymes show a low affinity (500 μM) for 4-hydroxypropranolol, and unlike PST-M they exhibit no stereospecificity [F735].

Rat liver cytosol contains two isozymes, one of which is thermolabile, optimum pH 9, and the other isozyme, optimum pH 6.4, is more stable; they both act on paracetamol [D460]. The former must be considered to be PST-M despite the recorded specificity. Kidney enzyme acts on *p*-nitrophenol, α- and β-naphthols and salicylamide, but not on catecholamines or catecholamine metabolites [D807].

Dog liver enzyme, molecular weight 32 000–34 000, reacts to antibodies like a PST-P. It acts on α-naphthol, vanillin, *p*-nitrophenol, tyramine, serotonin and dopamine. The V_{max} for dopamine is low although the K_m is similar to that for α-naphthol. The activity towards serotonin and tyramine is low with a low V_{max} and K_m greater than 100 μM (1 μM for α-naphthol) [J292].

Beef adrenal medulla enzyme acts on HMPG, but there appears to be little activity towards catecholamines [D187].

Marmoset enzyme, which is found in lung, liver, small intestine, with small amounts in stomach and kidney, acts on phenol. It is almost absent from brain [F226].

Thyroid hormone sulphotransferases

Human PST-P and PST-M (designated SULT1A1 and SULT1A3 respectively) both require PAPS as co-substrate and conjugate 3,3′-T_2, rT_3, T_3 and T_4 with decreasing activity; these substrates are mutually inhibitory. 3,5-T_2, 3-T_1 and T_0 are not substrates. Inhibition studies suggest that there are other similar sulphating enzymes in liver and kidney [K90]. Human liver T_3-conjugating activity is thermostable and correlates well with PST-P, the main liver sulphoconjugase, but not with PST-M activity. However, purified PST-M does conjugate T_3 [E672].

Rat liver iodothyronine sulphotransferase, optimum pH 8.0, conjugates 3,3′-T_2 and T_3 [J495]. Arylsulphotransferases I and IV from rat liver and monkey hepatoma conjugate 3,3′-T_2, rT_3, T_3, 3-T_1 3′-T_1 and T_0, 3,3′,5-triiodothyropropionate, 3,3′,5-triiodothyroacetate and tetraiodothyroacetate (only sulphotransferase I), but not T_4, 3,5-T_2 or tetraiodothyropropionate [B770].

Rat uterus iodothyronine sulphotransferase, optimum pH 6.0, conjugates 3,3′-T_2, T_3 and T_4 [K649].

Eubacterium trans-sulphatase (see below) sulphates T_3 [E432, G602].

Tyrosine-O-sulphate formation

Studies with tyrosine have usually failed to detect sulphate conjugation. However, studies with Caco-2 human gut epithelial cells, human Chang

liver cells and canine Madin-Derly liver cells have detected this reaction [H371]. Human sulphotransferase M acts on D-tyrosine [J644].

Tyrosine ester sulphotransferase (E.C. 2.8.2.9)

In male rat liver this activity appears to be identical with sulphotransferase IV (E.C. 2.8.2.1) [K735], optimum pH 8 [B941].

Tyrosylpeptide sulphotransferase (E.C. 2.8.2.20)

Human liver enzyme is microsomal, optimum pH 6.4, and requires Mn^{2+} [F752]. Human tyrosylprotein sulphotransferase, molecular weight about 50 000–54 000, which is found in the Golgi network of practically every tissue, especially liver, requires PAPS [J724].

Rat cerebral enzyme, which acts on the hydroxyl groups in tyrosyl peptides, requires PAPS and is found primarily in microsomes [E341]. Rat liver microsomal enzyme also requires PAPS [J614], molecular weight 50 000–54 000 and optimum pH 5.5 [J532].

Oestrogen sulphotransferases (E.C. 2.8.2.4)

In human liver both oestrone and 17β-oestradiol are sulphated at the 3 position. Both PST-P and dehydroepiandrosterone sulphotransferase catalyse the reaction, but not PST-M [G87].

A study on beef adrenal enzyme, optimum pH 7–8, demonstrated that it acts on a large range of oestrones and analogues. At least some of them are sulphated at the 3-position, but not at the 2- or 4-position. Some simple phenols are very poorly sulphated, but many hydroxylated polynuclear hydrocarbons are substrates. For optimal reaction a lipophilic group *para* to the hydroxyl group and an oxygen atom on the D ring for hydrogen bonding to the enzyme less than 0.372 nm above the ring are required [A1211].

In beef placenta oestrone and oestrone-3-sulphate are interconverted, but each reaction occurs in separate parts of the placenta [D520].

In guinea pig oestrone is sulphated, and both oestrone-3-sulphate and 17β-oestradiol-3-sulphate are converted into17β-oestradiol disulphate without exchange of sulphate [A1936].

Rat liver cytosol enzyme, optimum pH 5.5–6.0, acts on oestradiol and oestrone [D500].

Oestrone is sulphated in sheep [A472].

Activity in gilt uterus appears at day three of the oestrus cycle, rising sharply at day six to a maximum at day nine [A1450].

In hen oestrone, 16-epioestriol, 16-oxo-17β-oestradiol, 17α-oestradiol and 17β-oestradiol are sulphated at the 3-position, and both oestradiols are disulphated [A3652].

Flavonoid sulphotransferases

Three sulphotransferases, molecular weight 35 000, have been isolated from Flaveria chloraefolia shoot tips. A transferase specific for the 3 position (E.C. 2.8.2.25), pI 5.4, shows optima at pH 6.5 and 8.5, and acts (in decreasing order) on rhamnetin, isorhamnetin, quercetin, patuletin and kaempferol, but not on quercetagetin, gossypetin or myricetin. The 3′-specific enzyme (E.C. 2.8.2.26), pI 6.0 and optimum pH 7.5, acts (in decreasing order) on 3-sulphate esters of quercetin, patuletin and tamarixetin but not kaempferol or isorhamnetin, nor on aglycones. The 4′-specific enzyme (E.C. 2.8.2.27), pI 5.1 and optimum pH 7.5, acts (in decreasing order) on 3-sulphates of quercetin, kaempferol, isorhamnetin and patuletin, but not tamarixetin, nor on aglycones [F243, G769]. A 7-specific enzyme acts on isorhamnetin-3-sulphate, the 3,3′- and 3,4′-disulphates of quercetin, but not on quercetin-3- or 3′-sulphate, nor on aglycones (E.C. 2.8.2.28) [F210].

N-Hydroxyarylamine sulphotransferase

Human adrenal and liver enzymes act on 4-hydroxylaminobiphenyl [H304, H434];

presumably substitution occurs on the hydroxyl group.

N-Hydroxylaminofluorene is O-sulphated in mouse [D756].

N-Hydroxy-2-acetamidofluorene is sulphated in man, monkey, mouse, and rat liver [A1840, A2086, A2206, D756, K34]. This compound is a poor although significant substrate for rat liver cytosolic phenolsulphotransferase; two N-hydroxyarylamine sulphotransferase isozymes have been found for which N-hydroxy-2-acetamidofluorene and *p*-nitrophenol are both good substrates [G317]. Although in many cases the group conjugated has not been determined, the amido nitrogen is improbable. This reaction is part of the carcinogenic activation process of N-hydroxy-2-acetamidofluorene [G675].

Alcohol sulphotransferase (E.C. 2.8.2.2)

The benz[*a*]anthracene metabolites 12-hydroxymethyl-7-methylbenz[*a*]anthracene, 7-hydroxymethyl-12-methylbenz[*a*]anthracene and 7,12-dihydroxymethylbenz[*a*]anthracene are sulphated by dehydroepiandrosterone-steroid sulphotransferase in human liver, which differs from PST-P and M [J683].

Sulphatoglucoside formation

Brassica forms *o*-nitrobenzyl-β-D-sulphatoglucopyranoside and *E*- and *Z*-*o*-nitrobenzaldoxime-β-D-(6-sulphato)glucopyranoside as well as *o*-nitrophenylglucosinolate from *o*-nitrobenzaldoxime. Other substrates are benzaldoxime, nitro and halogen-substituted benzaldoximes, as well as some aliphatic analogues. It would appear that hydrolysis and reductive steps precede conjugation [F657].

Renilla-luciferin sulphotransferase (E.C. 2.8.2.10)

Renilla reniformis enzyme is specific for Renilla-luciferin [K831].

Trans-sulphatase (arylsulphate sulphotransferase, E.C. 2.8.2.22)

These enzymes transfer the sulphate group from, for instance, *p*-nitrophenol to another phenolic group.

Human gut flora (Eubacterium) enzyme uses 4-methylumbelliferyl and *p*-nitrophenyl sulphates as sulphate donors, and tyramine, rutin, quercetin, esculetin (at position 6), baicalin and, by far the best, baicalein as sulphate receivers [H354]. It is a homotetramer, pI 3.9, molecular weight 315 000 and optimum pH 8–9 using tyramine as substrate. Another sulphate donor is *p*-acetylphenyl sulphate. Acceptors include α- and β-naphthol, oestradiol, phenol, tyrosine methyl ester, tyrosine-containing peptides, tyramine, triiodothyronine, ethyl *p*-hydroxybenzoate, 4-methylumbelliferone, salicylamide, *p*-acetamidophenol and the catecholamines adrenaline and dopamine, and dopa, specifically at the 4-position [E191, E432]. In another study with this species quercetin formed the 3,3′-disulphate and the 3,3′,7-trisulphate, but a monosulphate was not detected [F513].

Haemophilus enzyme is a tetramer, molecular weight 290 000, with *p*-nitrophenyl sulphate, 4-methylumbelliferyl sulphate, α- and β-naphthyl sulphates as sulphate donors. Sulphate acceptors include phenol, resorcinol and α-naphthol [H756].

Klebsiella enzyme, which sulphates phenol and requires Mg^{2+}, is a dimer, molecular weight 160 000. The pIs for the subunits are 5.3 and 10–10.5 [G756].

5.2 *Sulphamate formation*

Amine sulphotransferase (E.C. 2.8.2.3)

$$R.NH_2 + PAPS \rightarrow R.NH.SO_2.OH + PAP$$

Guinea pig amine N-sulphotransferase requires PAPS as co-substrate. The substrate requires an unprotonated amino group for activity. Substrates include aniline, *p*-chloroaniline,

β-naphthylamine, DMI, tetrahydroquinoline, tetrahydroisoquinoline, and some aliphatic amines. The optimum pH is specific for each substrate, and lies in the range 6–10. Many phenols are also substrates, including oestrone and tyrosine [E456].

Human liver cytosolic hydroxysteroid sulphotransferase (E.C. 2.8.2.15) N-sulphates aniline, MPTP and and 1-((5-chloro-2-oxo-3(2*H*)-benzothiazolyl)acetyl)piperazine, and differs from the enzyme that sulphates phenols [J571].

Rabbit liver cytosol contains two enzymes, one of which acts on DMI and male steroid hormones, but not on phenols. The other, molecular weight 34 000, is almost inactive towards phenols and alcohols, but sulphates aniline, DMI, MPTP and 1-((5-chloro-2-oxo-3(2*H*)-benzothiazolyl)acetyl)piperazine [J914].

In rat and mouse liver the enzyme that sulphates 1-((5-chloro-2-oxo-3(2*H*)-benzothiazolyl)acetyl)piperazine (dealkyltiaramide) is different from the one that sulphates the primary alcohol group of tiaramide. The pH optima are modified by buffers, but the values for dealkyltiaramide is about 9–10, and for tiaramide 8–9. Rat enzyme is markedly inhibited by 0.5 M NaCl and KCl, whereas mouse enzyme is only slightly affected by these salts. Activity is much lower in female rat than in male [C571].

Pig liver enzyme acts on many amines with PAPS as co-substrate; the optimum pH varies from 6 to 10, depending on substrate. Aniline, *p*-chloroaniline, demethylimipramine, β-naphthylamine, tetrahydro-4-phenylpyridine, tetrahydroisoquinoline and tetrahydroquinoline are substrates [K923].

5.3 *Glycoside formation*

Flavone apiosyltransferase (E.C. 2.4.2.25)

Parsley enzyme, optimum pH 7.0, requires UDPapiose, but no coenzymes. It acts on flavone-7-O-β-D-glucosides; for instance 7-O-β-D-glucosylapigenin yields apiin [K827].

Arabinoside formation

Silene dioica enzyme, optimum pH 7.2–7.5 acts on isovitexin and UDParabinose to form isovitexin-2″-O-arabinoside. Isovitexin-7-O-xyloside is also a substrate, but isovitexin-7-O-glucoside is not, nor can UDPglucose or UDPrhamnose substitute for the co-substrate. The reaction is stimulated by Mg^{2+} or by Mn^{2+} [A3759].

Zea mays indolylacetylinositol arabinosyltransferase (E.C. 2.4.2.34) activity is found in immature kernels, to form indol-3-ylacetyl-*myo*-inositol arabinoside [K734].

Fructoside formation

Claviceps purpurea β-D-fructofuranoside, optimum pH 5.7 or 6.5, depending on substrate, forms elymoclavine-O-β-D-fructofuranoside and elymoclavine-1-O-β-D-fructofuranosyl(2→1)-O-β-D-fructofuranoside from elymoclavine. Other substrates are chanoclavine, lysergol and dihydrolysergol [F516].

Galactoside formation

Zea indolylacetyl-*myo*-inositol galactosyltransferase (E.C. 2.4.1.156) requires UDPgalactose to form indolylacetyl-*myo*-inositol galactoside, a major Zea indole. Activity is found in immature kernels [K811].

Aspergillus oryzae β-galactosidase transfers the galactoside moiety of *p*-nitrophenyl-β-D-galactoside to elymoclavine, chanoclavine, lysergol, 9,10-dihydrolysergol and ergometrine [H11].

E. coli β-D-galactosidase acts on 4-methylumbelliferyl-β-D-xyloside and *p*-nitrophenyl-β-D-galactoside to form galactosyl(β1→4)xylyl(β)-4-methylumbelliferone and a small proportion of the (β1→3) analogue [J399].

α-Glucoside formation

Bacillus subtilis enzyme, molecular weight 54 000 or 65 000 (different methods), with an optimum pH for starch as co-substrate of 6–7; it acts on quinol [H296].

Leuconostoc mesenterioides sucrose phosphorylase (E.C. 2.4.1.7) transfers α-D-glucose units from sucrose to the 4′- and 4″- positions of (-)-epigallocatechin gallate, forming 4′-mono- and 4′,4″-diglucosides [J5].

Formation of ester β-D-glucosides

Although it is generally assumed that these plant natural products contain a β-linked glucopyranose moiety, these data have often not been demonstrated.

Chenopodium rubrum enzyme requires UDPglucose and acts on ferulate, sinapate, *p*-coumarate and cinnamate [G255].

In Glycine max, benzoate is converted into benzoylglucose transiently. Other substrates are α-naphthylacetate, α-naphthoate and probably phenylacetate [A3679].

Sweet potato (Ipomoea batatas) tuber enzyme, molecular weight of 45 000, is specific for carboxyl-containing compounds. Substrates include cinnamate, *o*- and *p*-coumarate, caffeate, ferulate, benzoate and vanillate (E.C. 2.4.1.177) [D70, F145].

Quercus robur leaf gallate 1-β-D-glucosyltransferase (E.C. 2.4.1.136), optimum pH 6.5–7.0 and molecular weight 68 000, forms 1-galloyl-β-D-glucoside; it is specific for UDPglucose. A number of benzoic acids are substrates (except salicylic acid); cinnamic acids are less good [K736, K737].

Raphanus sativus enzyme, optimum pH 5.8–6.0 or about 7, is found in dry seed and during germination. Co-substrate is UDP- or TDPglucose; other analogues are inactive. The reaction is enhanced by thiols and is reversibly inactivated by thiol-binding compounds. A reversible reaction is found with sinapate (best), benzoate, vanillate, anthranilate, *p*-hydroxybenzoate, cinnamate, ferulate, caffeate, 3,5-dimethoxycinnamate and coumarate(s), but 3,5-dihydroxybenzoate is a poor substrate [B440, B599].

This reaction is found widely, including Coleus, Pilea, Cistus, Cestrum, Glycyrrhiza echinata, Prunus serotina, Glycine max, mung bean and ripe tomato [A3475, A3585, B493, C756, F445]. Benzoate forms benzoylgentiobioside as well as benzoylglucose in Aconitum japonicum, Coffea arabica, Dioscoreophyllum cumminsii and Nicotiana tabacum; it is unclear whether this involves a stepwise glycoside addition [F445].

Cucumis sativus forms glucose esters with a series of mono- and dihydroxybenzoates [A611].

Brassica napus and UDPglucose: sinapic acid glucosyltransferase (E.C. 2.4.1.120), molecular weight 42 000 and pI 5, conjugates sinapate reversibly [J712]. Raphanus sativus enzyme also forms 1-O-sinapoyl-β-glucose reversibly [K787].

Ester glucoside at C-6

Glycyrrhiza echinata, Dioscoreophyllum cumminsii and Aconitum japonicum conjugate phenylacetate with the 6-hydroxyl of glucose [F445].

Formation of ether D-glucosides

A. Animals

In man, both 3,6-dihydroxy-3,4-benzpyrene and 1-naphthol form glucosides with added UDPglucose, the former yielding the 6-glucoside. With added UDPgalacturonate the corresponding galacturonides are formed [H575].

Pig liver, riboflavin-conjugating enzyme, pI 3.7, optimum pH 6.0, transfers the α-glucosyl group from phenyl-α-maltoside or other maltosides to form riboflavin glucoside. The enzyme is stable at pH 3.5–9, and at 55°. Other substrates are esculetin and rutin [C847].

Coho salmon forms a glucoside from 1-naphthol [A3879].

Housefly microsomal enzyme, optimum pH 8.5, requires UDPglucose as well as Mg^{2+}; other divalent cations are not so good. It conjugates 1-naphthol [A2238].

Enzymes in Melanoplus sanguanipes (grasshopper), Periplaneta americana, Manduca sexta, Agrotis ipsilon (cutworm), Tenebrio molitor and Trilobium confusum act on a range of phenols (E.C. 2.4.1.35). Guaiacol is a substrate in all these species, but phenol, vanillin, salicylaldehyde, umbelliferone and a number of other phenols are substrates in only a few of these species, except that M. sexta has a broad specificity for simple phenols and natural products. UDPglucose or (less good) GTPglucose and TDPglucose are co-substrates [G816, G897].

p-Nitrophenol forms a glucoside in cockroach, stick insect, cricket, mealworm, Porina and wax moth larvae, housefly, blowfly and earwig [C494].

Drosophila xanthurenic acid: UDPglucosyltransferase, optimum pH 7.1, which conjugates the 8-hydroxyl group is both microsomal and cytosolic and requires Mg^{2+} or Mn^{2+} [F636].

B. Plants and microorganisms

a. Broad specificity; xenobiotic substrates.

Many studies on plants do not differentiate between α- and β-glycosides. Most glycosides are, in fact, β-glycosides, and where the stereospecificity of synthesis is not stated, β- can be assumed.

Soyabean (Glycine max) enzyme, molecular weight 47 000 and pI 4.8, acts on pentachlorophenol [G247]. Other substrates are quercetin and 2,2-bis(*p*-chlorophenyl)acetate. It appears to be a monomer, molecular weight about 50 000 and pI 4.9 [H402]. G. max, Triticum aestivum (wheat) Avena fatua and Agrostemma githago form *p*-nitrophenyl-β-D-glucoside [H660, J709].

Daucus carota (carrot) enzyme acts on *p*-nitrophenol [H118].

Gardenia jasminoides forms β-D-glucosides from phenol, catechol, resorcinol, quinol, *o*-, *m*- and *p*-nitrophenol [E338].

b. Flavonoid 3-glucosyltransferases
(UDPglucose: flavonol 3-O-D-glucosyltransferase, E.C. 2.4.1.91; UDPglucose: cyanidin 3-O-D-glucosyltransferase, E.C. 2.4.1.115).

Daucus carota UDPG: cyanidin 3-O-glucosyltransferase, optimum pH 8.0, requires ascorbate. Other substrates include delphinidin, pelargonidin, quercetin and kaempferol, but not naringenin, eriodictyol or dihydroquercetin [E280].

Hippeastrum petal enzyme is a homodimer, molecular weight 49 000, pI 5.6 and optimum pH 5, and requires UDPglucose as co-substrate. Good substrates include kaempferol, dihydrokaempferol and quercetin, whereas naringenin, isosakuranetin, pelargonidin cyanidin and malvidin are poor substrates [E636]. UDPG: anthocyanidin 3-O-glucosyltransferase in Hippeastrum and Tulipa petal and leaf is cytosolic [A2523].

Norway spruce needle flavonol 3-O-β-D-glycosyltransferase, molecular weight 40 000, optimum pH 8.4 and pI 5.0, acts on kaempferol reversibly. Other substrates are isorhamnetin, quercetin, rhamnetin and myricetin [G215].

Petunia hybrida enzyme, optimum pH about 8.2, acts on cyanidin and delphinidin. Substrates are mutually inhibitory [A3191].

Pisum sativum enzyme, optimum pH about 8, acts on kaempferol, quercetin and myricetin [C90].

Red cabbage seedling UDPG: cyanidin 3-O-glucosyltransferase, optimum pH about 8, acts additionally on pelargonidin, paeonidin, malvidin, kaempferol, quercetin, isorhamnetin, myricetin and fisetin [A1733].

Senecio hybridus UDPglucose: cyanidin 3-O-glucosyltransferase, exhibits molecular weight 52 000 and optimum pH 7.5 [J722].

Silene dioica UDPG: cyanidin 3-O-glucosyltransferase, optimum pH 7.5, appears to have a molecular weight of 60 000 and can exist as a dimer. It also acts on pelargonidin and delphinidin, but not on flavonols nor on the 5-position of anthocyanins [B407].

Pollen from Alnus, Quercus, Narcissus, Tulipa and Secale contains flavonol 3-O-

glycosyltransferase, possibly associated with the pollen wall. Substrates are quercetin and kaempferol [B680].

The reaction has also been observed in Crocus sativum, Ipomoea batatas, Vitis and Zea mays [E120, G124, G137].

A. niger enzyme, molecular weight about 370 000 and pI 4 may act on the 3 position of cyanidin [C900].

c. Flavonoid 4′- glucosyltransferase

An Allium cepa enzyme, molecular weight 48 000, optimum pH 7.7–8.0 and pI 6.0 is specific for the 4′-position of catechol flavonoids including quercetin, myricetin, rhamnetin, kaempferol, luteolin and apigenin (in decreasing order). It does not require Mn^{2+}, Mg^{2+} or Ca^{2+}, and it is unaffected by EDTA, but Cu^{2+} is inhibitory. It is inhibited by *p*-chloromercuribenzoate, reversible by mercaptoethanol; it requires thiols for stability [G248].

d. Flavonoid 2′- and 5′- glucosyltransferase

Chrysosplenium americanum enzyme, molecular weight 42 000, pI 5.1 and optimum pH 7.5–8 requires UDPglucose. It acts on a range of polyhydroxylated polymethoxyflavonols, and substrates with both 2′- and 5′- hydroxyls yield both monoglucosides [C755].

e. Anthocyanin 5-O-glucosyltransferase

Petunia hybrida pollen enzyme, optimum pH 8.3, acts on the 3-(*p*-coumaroyl)rutinosides of delphinidin and petunidin, but not on the corresponding rutinosides. The enzyme does not have a cation requirement [D198].

f. UDPglucose: anthocyanidin-3-rhamnosyl-glucoside 5-O-glucosyltransferase
(E.C. 2.4.1.116)

Silene dioica enzyme, molecular weight 55 000 and optimum pH 7.4 for anthocyanidin-3-rhamnosylglucoside, has an optimum at pH 6.5 with anthocyanidin-3-glucoside as substrate [B410]; it requires Ca^{2+}, and EDTA is inhibitory. Pelargonidin-3-rhamnosylglucoside is also a substrate, but cyanidin-3-glucoside is only marginally active at pH 6.5 [B408].

g (1). Flavonoid 7- glucosyltransferase
(E.C. 2.4.1.81)

Chrysanthemum segetum UDPG: 3′,4′,5,7-tetrahydroxyflavone 7-O-glucosyltransferase has an optimum pH of 6.85–8.25, depending on substrate; substrates include gossypetin, quercetin, kaempferol, myricetin, naringenin, eriodictyol, apigenin and luteolin [J320].

Petroselinum crispum (hortense) UDPG: luteolin β-D-glucosyltransferase (E.C. 2.4.1.81), molecular weight 50 000, optimum pH 7.5 and stability range pH 6.5–9.5 acts on a range of flavonoids, with luteolin as the best substrate. TDPglucose is an alternative co-substrate [K739].

Petunia hybrida leaf contains three isozymes, molecular weight about 54 000 and optimum pH 7.5. Substrates include naringenin, hesperetin, kaempferol, quercetin, apigenin and luteolin [K303].

g (2). UDPG: isoflavone 7-O-β-D-glucosyl-transferase (E.C. 2.4.1.170)

Cicer orietinum enzyme, molecular weight 50 000, optimum pH 8.5–9.0 and pI 5.4 acts on biochanin and formononetin; many other flavonoids are not substrates [K738].

g (3). Flavanone 7-O-β-D-glucosyltransferase
(E.C. 2.4.1.185)

Citrus paradisi (grapefruit) enzyme, optimum pH 6.5–7.5 and activation energy 7.8 kcal/mol is found in leaves. Different substrates demonstrate the presence of several isozymes; hesperetin isozymes pI 4.0, 4.4 and 4.5; naringenin pI 4.4 and 3.9. It differs from the enzyme that acts on naringenin chalcone [K891]. Another study, with naringenin and hesperetin as substrates reported molecular weight 55 000, optimum pH 7.5–8.0 and pI 4.3, with no action on other flavones or flavanones [K810].

h. UDPglucose: salicyl alcohol glucosyltransferases.

The reaction is catalysed by almond β-glucosidase with D-glucose as co-substrate. 1-Phenylethanol is another substrate [H558].

In Datura innoxa only a small proportion of salicyl alcohol is converted into salicin, whereas most is converted into *o*-hydroxybenzyl-β-D-glucose [A1725].

Gardenia jasminoides enzyme, molecular weight 51 000 and optimum pH 9.0–9.5, is specific for salicyl alcohol, yielding only salicin [D71, D715].

Trilobium confusum phenol β-glucosyltransferase acts on salicyl alcohol, but similar enzymes from other insect species studied are apparently inactive towards this substrate. UDPG is co-substrate, and GDPG and TDGP are somewhat less active [G816].

i. UDPglucose: p-hydroxybenzoate glucosyltransferase (E.C. 2.4.1.194)

Lithospermum erythrorhizon, molecular weight 47 500, pI 5.0 and optimum pH 7.8, conjugates the phenolic group. It is highly specific, with *p*-nitrophenol only marginally active. This reaction is an early step in the formation of shikonin [G341]. Another publication claims that the molecular weight is 51 000 [J365].

Pinus densiflora pollen enzyme, molecular weight 33 000 and optimum pH 7.5, requires UDPG and is activated by Ca^{2+} and EDTA. It acts on the phenolic group of *p*-hydroxybenzoate [F108].

j. Quinol

Datura innoxa, D. meteloides, Antennaria microphylla and Gardenia jasminoides catalyze this reaction [A1725, E338, F873, H300].

Juglans regia leaf and J. major callus enzymes, optimum pH 7–7.5, convert quinol into arbutin. It is specific for UDPglucose, and requires mercaptoethanol [A3472].

Rauwolfia serpentina forms arbutin and, apparently, quinol diglucoside [G726]. The enzyme molecular weight is 52 000 [K346].

Bacillus subtilis enzyme, molecular weight 67 000, pI 5.1 and optimum pH 6, is stable between pH 5 and 8. It is not activated by Ca^{2+}. Malto-oligosaccharides are much better glucose donors that maltose. As well as quinol many other phenols are substrates [H234].

k. Vanillin

Coffea arabica, Prunus amygdalus, Gardenia jasminoides and Nicotiana tabacum enzymes act on vanillin [G930].

l. Coniferyl alcohol (E.C. 2.4.1.111)

Forsythia ovata enzyme(s) convert coniferyl alcohol into coniferin (4-glucoside) and isoconiferin (side-chain glucoside). The optimum pH is buffer-dependent, in the range 7.5–8.0. It requires a thiol and is inactivated by thiol-binding reagents, but divalent cations are not required. It also acts on sinapyl alcohol, ferulate, scopoletin, hydrangetin and isorhamnetin, but not on several other analogues. A study carried out on a large range of species found this activity in all of them, including bryophytes, pteridophytes, gymnosperms, dicotyledons and monocotyledons. Highest activity was found in Ginkgo biloba, Pinus pinea, Picea glauca and Forsythia ovata [A3365].

Paul's scarlet rose enzyme, molecular weight 52 000 and optimum pH 7.5, requires UDPglucose and a thiol. It is specific for coniferyl and sinapyl alcohols, with lesser activity on cinnamic acids and some flavonoids. The crude enzyme is unstable, even frozen; stability is improved by mercaptoethanol and ethylene glycol [K809].

m. UDPG: o-dihydroxycoumarin 7-O-glucosyltransferase (E.C. 2.4.1.104)

Nicotiana tabacum culture enzyme, molecular weight 49 000, pI 5.0 and optimum pH 7.5, acts on esculetin, scopoletin, daphnetin, hydrangetin and umbelliferone to form cichoriin, scopolin, daphnin, hydrangin and skimmin respectively; there is no cation requirement, but divalent

cations and thiol-binding reagents are inhibitors. Caffeate (yields 4-glucoside), protocatechuate, vanillate and syringate are also substrates, whereas ferulate, 5-hydroxyferulate, sinapate and pyrocatechuate are poor substrates [B442, B819, K556].

n. Alizarin 2-β-glucosyltransferase (E.C. 2.4.1.103)

Streptomyces aureofaciens enzyme, optimum pH 7.1, requires UDPglucose and acts on alizarin, 2-hydroxy-, 1,3-dihydroxy-, 2,6-dihydroxy- and 3-hydroxy-1-methoxyanthraquinones [B462, B463].

o. Hydroxyanthracenequinone glucosyltransferase (E.C. 2.4.1.181)

Cinchona succirubra enzyme, molecular weight 50 000 and optimum pH 7, is composed of five isozymes pI 4.1, 4.3, 4.5, 4.8 and 5.3. A number of hydroxyanthraquinones including alizarin, chrysophanol and emodin are substrates, as well as hydroxycinnamates and flavones [K889].

p. Mandelonitriles (E.C. 2.4.1.85 and 2.4.1.178)

Prunus serotina (black cherry) enzyme, optimum pH 7–8, requires UDPglucose, and acts on the side-chain hydroxyl group of mandelonitrile to form prunasin. Benzyl alcohol, mandelate and benzoate are also conjugated, but prunasin is not a substrate [C756].

Sorghum bicolor conjugates the (*S*)-isomer of *p*-hydroxymandelonitrile to form dhurrin. The amino acid composition has been determined. Other substrates are mandelonitrile and (poor) benzyl alcohol and benzoate [K313].

Triglochin maritima forms side-chain glucosides from *p*-hydroxymandelonitrile and 3,4-dihydroxymandelonitrile [D58].

q. Oligoglycosides

Petunia pollen flavonol 3-O-glycosyltransferase is composed of two isozymes, which act on kaempferol and quercetin specifically at the 3 position. Other substrates include myricetin, the 3-galactoside, 3-glucoside and 7-rhamnoglucoside of kaempferol, 4′-O-methylkaempferol, 7-O-methyl- and 3′,7-di-O-methylquercetin. The products are the corresponding 3-O-(2″-O-β-D-glucopyranosyl)-β-D-galactopyranosides and, apparently, where appropriate the corresponding 3-diglucoside [H658].

An enzyme in Pisum sativum converts kaempferol-, quercetin- and myricetin-3-glucosides into (2→1)β-diglucosides. A second enzyme acts on these diglucosides to form the corresponding (2→1)β-triglucosides. Both have optimum pH about 8 [C90].

Triticum aestivum, Glycine max, Avena fatua and Agrostemma githago form β-D-glucoside and β-D-gentiobioside conjugates from *p*-nitrophenol; the former may be an intermediate in formation of the latter conjugate [J709].

r. UDPglucose: 2-coumarate O-β-D-glucosyltransferase (E.C. 2.4.1.114)

Melilotus alba enzyme is cytosolic [B369].

s. UDPglucose: cis-p-coumaric acid β-D-glucosyltransferase

Sphagnum fallax enzyme, molecular weight 56 000 and optimum pH 9.3 acts on *cis*- but not *trans*-*p*-coumarate, and only poorly on *cis*-caffeate. Conjugation occurs at the *para* position [J384].

t. UDPglucose: betanidin β-D-glucosyltransferases

Dorotheanthus bellidiformis enzymes, molecular weight 55 000 and optimum pH 7.5 act on the 5- position to form betanin, and the 6- position to form gomophrenin I. The first enzyme is composed of three isozymes, whereas the second is a single form [J185].

u. Vitexin and isovitexin (E.C. 2.4.1.105 and 2.4.1.106 respectively)

In Silene alba, 2″-O-glucosylating enzymes require Mg^{2+}, Mn^{2+}, Co^{2+} or Ca^{2+}. One acts on vitexin, optimum pH 7.5, and the other on isovitexin, optimum pH 8.5 [B203]. The latter enzyme requires UDPglucose, and also acts on isoorientin [B385].

v. Tyrosine β-glucosyltransferase

Manduca sexta larval fat body enzyme, optimum pH 7.5–9, is specific for tyrosine and requires UDPglucose; TPDglucose is not as good. It is activated by Mg^{2+} [J40].

w. Indoxyl: UDPglucose glucosyltransferase

This reaction is of historical interest, since it forms indoxyl glucoside (indican) which is stored in Isatis tinctoria (woad), and on hydrolysis the released indoxyl is spontaneously oxidized to indigo.

Baphicacanthus cusia enzyme, molecular weight 60 000, optimum pH 8.5 and pI 6.5, forms indican from indoxyl. The substrates include 4-, 5-, 6- and 7-hydroxyindole, but not oxindole [K347].

Polyganum tinctorium indican synthase is composed of two isozymes, one of which has a molecular weight of 53 000 or 48 000 (different methods) and optimum pH about 10 [K375].

x. UDPG: scopoletin β-D-glucosyltransferase (E.C. 2.4.1.128)

Nicotiana enzyme, which is stimulated by 2,4-D, forms scopolin [K741].

y. 2,4-Dihydroxy-7-methoxy-2H-1,4--3(4H)-one 2-D-glucosyltransferase (E.C. 2.4.1.202)

Zea mays enzyme, molecular weight 50 000 and optimum pH 8.5, is composed of two isozymes, activated by Ca^{2+} or Mg^{2+} and stabilized by reducing agents [K892].

N-Glucoside formation

5-Aminosalicylate forms an N-β-D-glucoside that is unstable at acid pH. It can also be formed spontaneously at neutral pH [F456].

In Daucus carota 3,4-dichloroaniline forms the β-D-glucoside [H118]. The corresponding reaction in Glycine max is catalyzed by an enzyme, molecular weight 48 000 [G247].

Glucosinolate formation

Brassica converts *o*-nitrobenzaldoxime into *o*-nitrophenylglucosinolate [F657].

Glucuronides (E.C. 2.4.1.17)

All glucuronyl transferases are at present classified under this E.C. number.

A number of glucuronyl transferases have been classified in one publication, although this classification is undoubtedly incomplete. For instance, an enzyme designated as UGT 1A1 acts on bilirubin and phenols, UGT 1A3 conjugates primary, secondary and tertiary amines, UGT 1A4 acts on tertiary amines and alcohols, UGT 1A6 on planar phenols and UGT 1A9 on bulky phenols [J416].

Ester glucuronide synthesis

Many carboxylic acids are conjugated with glucuronic acid, but the enzymology is not as well understood as the formation of ether glucuronides. The following studies are illustrative.

In ferret, benzoate, *p*-nitrobenzoate, diphenylacetate, α-naphthylacetate and (less effective) β-naphthylacetate and hydratropate are substrates, whereas phenylacetate, *p*-chlorophenylacetate, *p*-nitrophenylacetate and indole-3-acetate are not substrates [A394, A3046].

Benzoate and phenylacetate are conjugated in fruit bat [A884, A1451].

A guinea pig liver enzyme acts on anthranilate, with UDPglucuronate as co-substrate [A865].

In human patients with an inborn metabolic error that eliminates bilirubin glucuronidation the conjugation of the acyl group of diflunisal was unimpaired [J183].

In rabbit, all substituted benzoates studied were conjugated. Substituents included nitro, halogens, methyl, amino and hydroxyl in all the possible positions on the aromatic nucleus [H519].

The rat liver enzyme that conjugates (*R*)- and (*S*)-naproxen is composed of at least two active fractions, pI 7.8 and 8.7. One of the fractions preferentially acts on the (*R*)-isomer, and the other on the (*S*)-isomer [F726].

Benzoate and *p*-aminobenzoate are conjugated in rat, mouse, hamster, dog and marmoset [A651, A3771, B201, C381, D914].

Benzoate is conjugated in rat, bandicoot, Tasmanian devil, potoroos, padmelon, brushtail possum, sugar glider and echidna [D914].

In pigeon diphenylacetate is well conjugated, whereas substituted phenylacetates and indole-3-acetate are at best poorly conjugated. Hen did not conjugate any of the phenylacetates studied [A395]. Diphenylacetate is conjugated in a range of mammalian species [A2527].

Ether β-D-glucuronides

The co-substrate for this reaction is UDPglucuronate.

a. Phenolic and bilirubin conjugation

Clinically, bilirubin conjugation is important in human neonatal jaundice because high concentrations of unconjugated bilirubin cause kernicterus and brain damage.

In patients with an inborn metabolic error that eliminates bilirubin glucuronidation the conjugation of phenolic substrates was unimpaired [J183].

Purified rat liver enzyme, molecular weight 57 000, is induced by phenobarbital and acts on phenols, but not on bilirubin [A3827].

In different strains of rat the activity towards chloramphenicol does not correlate with activity towards bilirubin [A2511]. Bilirubin conjugating enzyme shows different properties from that which acts on 1-naphthol; for instance, galactosamine causes a reduction in 1-naphthol conjugation, whereas bilirubin is unaffected [A372].

b. Phenolic and alicyclic glucuronides

A number of studies have shown that, with or without induction with phenobarbital or 3-methylcholanthrene, solubilized enzyme can be crudely separated into two fractions with different properties [e.g. A1919, A1961, B983].

Human brain isozyme UGT1A6 acts on serotonin [K108]. Gut and lymphocyte enzymes have a broad specificity, with a large number of substrates [B800, J783].

Solubilized mouse liver microsomal enzyme has been fractionated into two types, pI 6.7 and 8.5. The first is induced by 3-methylcholanthrene and acts on the 'type 2' substrates, 4-hydroxybiphenyl, morphine, naphthol, 2-, 6-, 8- and 9-hydroxy-3,4-benzpyrene. The second is induced by 3-methylcholanthrene and phenobarbital, and acts on the 'type 1' substrates, 3-, 10-, 11- and 12-hydroxy-3,4-benzpyrene, phenolphthalein and oestrone. Both fractions act on the 'type 3' substrates *p*-nitrophenol, 4-methylumbelliferone, 1-, 4-, 5- and 7-hydroxy-3,4-benzpyrene, and 2-hydroxybiphenyl. All the 'pI 8.5' activities are induced by 3-methylcholanthrene [C459, D315].

Mouse brain activity is less than 1 per cent of that found in liver. It acts on *o*- and *p*-nitrophenol, and 4-hydroxybiphenyl [C266].

The activity of rat liver enzyme that acts on morphine increases 20-fold between days one and 20 post partum; the increase in gut enzyme activity is much less [C221]. The crude enzyme has a broad specificity [B962]; its molecular weight is 57 000 [A3827].

Rat liver glucuronidation of *p*-nitrophenol and 4-methylumbelliferone is inhibited by 5-(*p*-hydroxyphenyl)-5-phenylhydantoin [A1668].

Rat liver microsomal enzyme acts on a range of nitrocatechols, but compounds in which the aromatic moiety is conjugated with unsaturated groups react much less effectively [J546].

In rat *p*-hydroxyamphetamine is conjugated in liver, but not in lung, brain, heart, kidney, intestine and spleen [A4].

Rat liver nuclei contain some conjugating enzyme; most of this is associated with the nuclear envelope [A2002].

Rat conjugates 2-phenyl-1,3-propanediol monocarbamate. The claim that the product is an α-glucuronide is presumably a misprint; the claim goes without comment [K56].

Purified rabbit liver microsomal enzyme, solubilized with the non-ionic detergent Emulgen 911, conjugates *p*-nitrophenol, but not oestrone; an oestrone-conjugating enzyme is also found (see below) [B983].

Guinea pig liver microsomal enzyme, optimum pH 7.5, conjugates 7-hydroxychlorpromazine. This and rat enzyme also conjugate several hydroxylated metabolites of chlorpromazine, promazine and imipramine; the guinea pig enzyme also acts on oestrone and oestradiol [A2092]. Studies on the kinetics showed an atypical pattern at low co-substrate concentration, and it is claimed that this cannot be explained by multiple enzyme forms [A865].

HMPE is conjugated in rat, rabbit, guinea pig and human liver, but not in mouse and cat liver, rat kidney or gut [A2067]

Dog liver microsomal enzyme, molecular weight 50 000, acts on phenol and on the 3-position of morphine [H786].

Rainbow trout liver microsomal enzyme acts on T_3 and T_4, with optimum pH greater than 8.5 and 6.8–7.8 respectively [J319].

c. Oestrogens

1. 17β-Oestradiol

In rat liver microsomes both 3- and 17-glucuronidation occurs [J498] in the ratio 1:2.5, apparently by three different enzymes, each with different activities at the two sites; in rabbit the ratio is 1:20, apparently catalyzed by a single enzyme [C603]. In rhesus monkey 17-glucuronidation is preponderant [A2897].

3-Glucuronidation is found in guinea pig, man and pig, and rabbit blastocyte [A1273, A1936, F272, K33].

3- And 17-glucuronidation is found in man [A1196]; 17-glucuronidation is found in human kidney [A250], but in gut mucosa 3-glucuronidation is the sole reaction [K134].

2. Oestriol-3-glucuronide

This reaction has been observed in dog [A1302, A2628], man [D133], pig liver, kidney and gut [A1273] rabbit [A987], rat [A3102] and sheep [A398].

3. Oestriol-16α-glucuronide

In baboon oestriol is conjugated at the 16 position in liver and kidney, whereas 3-conjugation occurs elsewhere in the body, but not in kidney [A1111].

The reaction is observed in rat, where liver is one site of reaction [A3102, C242], rhesus monkey liver [A2897], dog [A1302, A2628] and man, where kidney is one site of reaction [A156, A822, D133].

4. Oestriol-17-glucuronide

The reaction has been observed in rat [A3102].

5. Oestrone-3-glucuronide

The reaction has been observed in cat, dog, guinea pig, hen, human gut, mouse liver microsomes, pig liver, kidney and gut, quail, rabbit, rat, rhesus monkey and trout [A242, A401, A951, A1040, A1273, A1936, A2897, C562, C603, D315, F272, J498, J783]. Rat liver enzyme is induced by 3-methylcholanthrene (but not by phenobarbital), with a change in kinetic properties, which suggests that the induced enzyme is different from non-induced enzyme [A1368].

Rabbit liver oestrone glucuronyltransferase also conjugates (less effectively) 17β-oestradiol,

oestriol, some phenols and (ring) substituted anilines [F309]. Another study found that the purified microsomal enzyme, solubilized with the non-ionic detergent Emulgen 911, does not conjugate *p*-nitrophenol [B983].

d. Miscellaneous reactions

UDPglucuronate: baicalein 7-O-glucuronosyltransferase

Scutellaria baicalensis enzyme is dimeric, molecular weight 110 000, monomeric molecular weight 52 000 and pI 4.8. It is specific for baicalein and flavones with a substituent *ortho* to the 7-hydroxyl group [K402].

Luteolin glucuronosyltransferases

Rye primary leaves contain the enzymesf luteolin 7-O-glucuronosyltransferase (E.C. 2.4.1.189), molecular weight 34 000, pI 4.80, optimum pH 6.5 and 8.5 and activation energy 23 kj/mol which forms luteolin-7-O-β-D-glucuronide, luteolin-7-O-β-D-glucuronide 7-O-glucuronosyltransferase (E.C. 2.4.1.190), molecular weight 37 000, pI 4.75, optimum pH 6.5 and activation energy 50 kj/mol which forms luteolin-7-O-β-D-diglucuronide, and luteolin-7-O-β-D-diglucuronide 4′-O-glucuronosyltransferase (E.C. 2.4.1.191), molecular weight 29 000, pI 4.75, optimum pH 7 and activation energy 38 kj/mol which forms luteolin-7-O-(β-D-glucuronosyl(1→2)-β-D-glucuronide)-4′-O-β-D-glucuronide [K890].

Sugar glucuronides

Chenopodium rubrum enzyme acts on feruloylglucose and *p*-coumaroylglucose, the latter forming feruloylglucuronosyglucose, with UDPglucuronate as co-substrate [G255].

Hydroxylamine glucuronides

Human and rat liver act on N-hydroxy-2-acetamidofluorene [E219, H92]; rabbit liver conjugates N-hydroxyphenacetin and N-hydroxyacetanilide [C588]. In rat, the reaction is found in liver and mammary microsomes [D273]. *p*-Chloro-*N*-hydroxyacetanilide is another substrate for rat liver enzyme [A1840].

N-Glucuronide formation

Human embryo kidney UDPglucuronyltransferase UGT 1A3 and UGT 1A4 glucuronidate primary amines including 2-, 3- and 4-aminobiphenyl, benzidine, *p*-phenetidine, aniline, dapsone, 7-amino-4-methylcoumarin, α- and β-naphthylamine and 2-aminofluorene, but not 2- and 4-aminophenol or secondary amines including diphenylamine and demethylclozapine. Demethylimipramine, nortriptyline, tertiary amines, including amitriptyline, trifluoperazine, diphenhydramine, pyrilamine, triflupromazine, loxapine, meperidine, imipramine, and clozapine (both the secondary and tertiary amino groups) are not substrates [H541, J416].

In man (where studied, liver microsomes contain the enzyme activity) quaternary glucuronides are formed by tertiary amine: UDPglucuronosytransferase with amitriptyline, chlorpheniramine, chlorpromazine, clomipramine, clozapine, cyproheptadine, diphenhydramine, doxepin, doxylamine, imipramine, lamotrigine, loxapine, pheniramine, pyrilamine, trazodone, trimipramine, and tripelennamine as substrates [C614, E932, F718, F769, G18, G492, H162, J137]. Antibody studies show that it differs from phenol UDPglucuronosytransferase [G509].

Rabbit liver oestrone UDPglucuronyltransferase acts on aniline, 4-aminobiphenyl, α- and β-naphthylamine [D288, F309]. A human liver enzyme, pI 6.2 acts on 4-aminobiphenyl and α-naphthylamine, but another, pI 7.4 acts on α-naphthylamine but not on 4-aminobiphenyl [F309]. In rat the reaction on α- and β-naphthylamine has been found in hepatocytes [G743].

Although it has been suggested that quaternary glucuronides are formed only in primates, guinea

pig glucuronidates lamotrigine on a heterocyclic nitrogen [F763], and rat liver glucuronidates amitriptyline, imipramine and chlorpromazine [C614, G492].

Lactoside formation

Cow (milk) forms the N^4-lactoside of sulphamethazine from the parent compound [G373].

Rhamnoside formation (E.C. 2.4.1.159)

Silene dioica (red campion) petal enzyme, molecular weight 45 000 and optimum pH 8.1, acts on cyanidin-3-glucoside with UDP-L-rhamnose as co-substrate to form cyanidin-3-(6″-rhamnosyl)glucoside. It is stimulated by Mg^{2+}, Mn^{2+} and Co^{2+}. Other substrates are the 3-O-glucosides of pelargonidin and delphinidin; cyanidin-3,5-diglucoside is a poorer substrate [B405, B409].

Xyloside formation

Euonymus alatus leaf UDP-D-xylose: flavonol 3-O-xylosyltransferase (E.C. 2.4.2.35), molecular weight 48 000, pI 6.1 and optimum pH 7.0, acts on kaempferol, quercetin and fisetin, but not on dihydroflavonols [G444].

Penicillium acts on catechol and xylan to form β-xylosylcatechol and xylobiosylcatechol [J487].

Sinapoylglucose-sinapoylglucose O-sinapyltransferase (E.C. 2.3.1.103)

Raphanus sativus, molecular weight 55 000 and optimum pH 8.0 does not require cations or thiols. It catalyzes dismutation of the substrate with activation energy 62 kj/mol to form 1,2-di-O-sinapoyl-β-D-glucose; substrates are 1-sinapoylglucose and 1-feruloylglucose [K724].

Galloyl exchange of glucosides

A Quercus robur enzyme, optimum pH 6.0–6.5, catalyzes a rapid exchange between glucose and 1-galloyl-β-D-glucose [K894].

5.4 *Conjugation of thiols*

CoA conjugation

$$\mathrm{RCOOH + CoA + ATP \rightarrow AcylCoA + AMP + pyrophosphate}$$

Beef liver mitochondrial enzyme, molecular weight 66 000, acts on a series of substituted benzoates, but not on those substituted in the *o*-position, nor on naphthylacetates. This is the first step in the formation of hippurates [H740].

Human liver contains two isozymes, both of which conjugate benzoate, *p*-hydroxybenzoate and phenylacetate, one conjugates salicylate, but only poorly, and the other conjugates a naphthylacetate [K220].

Rat liver microsomal (*R*)-ibuprofenoyl CoA synthetase is identical with long chain acyl CoA synthetase (E.C. 6.2.1.3), molecular weight 72 000, which requires ATP and Mg^{2+}; (*S*)-ibuprofen is inhibitory. The CoA ester is involved in chiral inversion of the substrate [J234].

Cactus (Cephalocereus senilis) (hydroxy)cinnamate: CoA ligase acts on cinnamate, *p*-coumarate, caffeate, *p*-methoxycinnamate and ferulate, but not on sinapate [H633].

Forsythia ferulate: CoA ligase requires ATP and CoA; Mg^{2+} and a thiol are also required for maximal activity. It is an enzyme in the sequence that converts ferulate into coniferyl alcohol [A848].

In Glycine max two *p*-coumarate: CoA ligase isozymes (E.C. 6.2.1.12) have been detected [A2271], optimum pH 7.8 and 8.5. Both act on cinnamate, *o*-, *m*- and *p*-coumarate, caffeate, ferulate and isoferulate, whereas the pH 7.8 enzyme acts on sinapate,

3,4-dimethoxycinnamate and 3,4,5-trimethoxycinnamate. *Cis*-*p*-coumarate is only 1 per cent as effective as the *trans*-isomer. The reaction requires ATP and a divalent cation (Mg^{2+}, Mn^{2+}, Co^{2+}, or Ni^{2+}; Ca^{2+} and Zn^{2+} are relatively ineffective). Both are susceptible to substrate inhibition, and it is activated by tris buffer (at less than 100 mM for the 'pH 7.8' isozyme and 300–400 mM for the 'pH 8.5' isozyme) [A2148].

Pea seedling contains one major isozyme, molecular weight 75 000, and two minor isozymes, molecular weight less than 20 000. There is some evidence for the interconversion of these forms. Substrates include *p*-coumarate, ferulate, caffeate, isoferulate and cinnamate, but sinapate, 3,4-dimethoxycinnamate and *p*-methoxycinnamate are not substrates. A minor isozyme acts on all these compounds except cinnamate. Studies with runner bean, Glycine max shoot, aged cucumber, aged marrow, aubergine, red and green pepper and leek show that each species has its own specificity. *p*-Coumarate and isoferulate are substrates in all these species, ferulate in all but green pepper, caffeate in all but aubergine and red pepper, whereas sinapate is a substrate in runner bean, G. max and leek, *p*-methoxycinnamate in runner bean and leek, but cinnamate is substrate only in G. max and marginally in cucumber [A2514].

Three isozymes are found in Petunia, all with optimum pH 7.5–7.8. One acts on *p*-coumarate and caffeate, a second on *p*-coumarate and sinapate, whereas the third acts on cinnamate, *p*-coumarate, ferulate and (poorly) caffeate [A2845].

Poplar stem hydroxycinnamoyl: CoA ligase, which is composed of three isozymes, pI 4.4, 5 and 6.35, acts on *p*-coumarate, with different distribution in xylem sclerenchyma and parenchyma; there is a correlation between the different forms and the monomeric composition of the lignins in these tissues [C740].

In potato *p*-coumarate: CoA ligase (E.C. 6.2.1.12) is found only on ageing after slicing the tuber, presumably as a response to injury. Substrates are *p*-coumarate, ferulate, caffeate, *m*- and *p*-methoxycinnamate [A204].

In swede *p*-coumarate: CoA ligase is only found in aged slices, and only one form is found. It is one of the enzymes in the sequence that converts ferulate into coniferyl alcohol [A216].

Tomato *p*-coumarate: CoA ligase acts on *o*-, *m*- and *p*-coumarate, caffeate, ferulate and isoferulate, and poorly on *m*- and *p*-methoxycinnamates; other cinnamates without a hydroxyl group are not substrates. This enzyme is part of the sequence that forms chlorogenate and 5′-(*p*-coumaroyl)quinate [A3149].

Willow stem enzyme, molecular weight 57 000 and optimum pH 7, acts on *p*-coumarate, ferulate and (best) caffeate; cinnamate and sinapate are not substrates [D466].

Desulfitomaculum enzyme acts on several benzoates [K210].

Mycobacterium phlei *o*-succinylbenzoate-CoA ligase (E.C. 6.2.1.26) requires ATP and CoA, with the formation of AMP. It is stable at pH 1 [K744].

An enzyme in Penicilliun chrysogenum, optimum pH 6.8, acts on phenylacetate, phenoxyacetate, *o*- and *p*-methylphenoxyacetate, but not phenylpropionate. This enzyme is in the sequence that leads to the formation of penicillins [A2291, C483].

In Pseudomonas *p*-chlorobenzoate: CoA ligase (E.C. 6.2.1.33) is a homodimer, subunit molecular weight 57 000, pI 5.3 and optimum pH 8.4. It requires CoA, ATP and a divalent cation (Mg^{2+}, Co^{2+} or Mn^{2+}). Substrates include benzoate, *p*-halobenzoates, with lower activity on some other *para*-disubstituted benzoates. This is the first reaction in the sequence that converts *p*-chlorobenzoate into *p*-hydroxybenzoate [G729, H645, K191], forming *p*-chlorobenzoyl CoA [H216]. A Pseudomonas aromatic acid: CoA ligase contains three isozymes. One is a dimer, molecular weight 120 000 and optimum pH 8.5–9.2, another is a monomer, molecular weight 60 000 and optimum pH 9.3, and the third, molecular weight 65 000 and optimum pH 8.5. They act on benzoate, anthranilate, monofluorobenzoates, and the two monomeric isozymes also act on *o*-toluate [G342].

A study in Pseudomonas with phenylacetate as substrate (phenylacetate: CoA ligase, E.C. 6.2.1.30) found a molecular weight of 52 000 and optimum pH 8.5 for the enzyme which is insensitive to oxygen, confirmed the requirement for Mg^{2+} or Mn^{2+}, and found that ATP is degraded to AMP and pyrophosphate. The enzyme is unstable, and is stabilized by glycerol and/or phenylacetate. Analysis of the N-terminal sequence showed little congruence with similar ligases. It is found in cells grown anaerobically in the presence of phenylacetate; analogues are ineffective. Aerobic growth produces low enzyme activity [G890]. Another study in P. putida found a molecular weight of 48 000 (denatured) and pI 5.4–4.9, with a requirement for ATP, CoA and Mg^{2+} or Mn^{2+}. Other acids are not substrates [K743].

Pseudomonas putida cinnamoyl: CoA ligase has an optimum pH of 6.5 and molecular weight of 53 000. Good substrates include *p*-coumarate, ferulate and caffeate, whereas *m*-coumarate, 3,4-methylenedioxycinnamate, *p*-methoxycinnamate and 3,4,5-trihydroxycinnamate are poor substrates. A series of other cinnamates are not substrates [B298].

Two isozymes are found in a denitrifying Pseudomonas. Both act on anthranilate and *o*-fluorobenzoate; only one isozyme acts on *o*-toluate, *m*- and *p*-hydroxybenzoates. Phenylacetate is substrate for at least one isozyme [F65]. A study on Pseudomonas has detected anthranilate: CoA ligase (E.C. 6.2.1.32) [K742].

Rhodopseudomonas palustris benzoate: CoA ligase (E.C. 6.2.1.25) requires Mg^{2+} and ATP, with benzoate, *o*- and *p*-fluorobenzoates and *o*-chlorobenzoate as substrates, but other analogues are inactive [E605]. *p*-Hydroxybenzoate: CoA ligase (E.C. 6.2.1.27) requires Mg^{2+} and ATP; acetyl CoA is not an acetyl donor [F48].

An anerobic syntrophic benzoate-degrading culture benzoyl: CoA ligase, molecular weight about 420 000, subunit molecular weight 58 000 and optimum pH 8, requires acetyl CoA and Mg^{2+}. It acts on benzoate, monofluorobenzoates and some heterocyclic acids [H500].

Succinyl CoA: benzylsuccinate CoA transferase

Thauera aromatica acts reversibly on (*R*)-(+)-benzylsuccinate, with succinyl CoA (a common CoA donor) as co-substrate, forming (*R*)-(+)-benzylsuccinyl CoA and succinate. This is an early step in the reaction sequence that leads from toluene to benzoyl CoA [K302].

Cinnamoyl CoA: phenyllactate CoA transferase

Clostridium sporogenes enzyme, molecular weight 46 000 forms cinnamate and (*R*)-phenyllactyl CoA from cinnamoyl CoA and (*R*)-phenyllactate [K534].

Glutathione S-aryltransferase (E.C. 2.5.1.18)

$$ArR + GSH \rightarrow GSAr + RH;$$

R is usually a halide or nitro group.

Human platelet cytosolic enzyme, molecular weight 60 000 and pI 4.65, acts on 1-chloro-2,4-dinitrobenzene. It is present in chorial villi, and a little is found in amnion [A3953].

Japanese and rhesus monkey enzymes act on nitro compounds with the release of nitrite. Substrates (in decreasing order) include *o*-dinitrobenzene, 4-nitroquinoline-N-oxide, 3,4-dinitrobenzoate and *p*-dinitrobenzene, with slight or no activity towards other compounds. Results suggest non-reactivity when the nitro group is *o*- or *p*- to a carboxyl, hydroxyl or ether group, or *m*- to a second nitro group [F139].

In female mouse, enzyme acting on 1-chloro-2,4-dinitrobenzene is found in liver, lung and intestine (in reducing order). Activity is low one month after birth and rises to a peak at nine months and then falls rapidly to a stable level at 12–13 months, similar to the one month level [B875].

Pig brain enzyme is composed of four isozymes that act on a number of nitrobenzenes. The main one is dimeric, molecular weight 43 000 and optimum pH 6.5–7.5; its amino acid composition has been determined. Substrates include *o*- and *p*-dinitrobenzene, 1-chloro-2,4-dinitrobenzene,

1,2-dichloro-4-nitrobenzene, 2,4-, 2,5- and 3,4-dinitrobenzoate, *p*-nitrobenzyl chloride, 2,5-dinitrophenol and *p*-nitrophenethyl bromide [C901].

Rabbit enzyme is found in liver, gut and lung. Activity is low at birth and increases slowly to the adult level by four months. In lung the corresponding activity increase is twofold. In kidney the activity falls 50 per cent at birth, and then increases threefold to the adult level at weaning [A2132].

Rat liver cytosol contains five isozymes that act on 1-chloro-2,4-dinitrobenzene [D303]; based on fractionation and induction studies, activity on this compound and on 1,2-dichloro-4-nitrobenzene appears to be due to different enzymes. Activity is found in microsomes, mitochondria and cytosol. Phenobarbital induces microsomal and cytosolic enzymes, but 3-methylchloanthrene and 2,3,7,8-tetrachlorodibenzo-*p*-dioxin induce only cytosolic enzyme [B702]. Another study detected about eight isozymes [A3509]. Rat liver enzyme is inhibited by 10^{-6} M trialkyl- and triaryltin and triethyllead, but less effectively by dialkyl analogues or by triethylgermanium [A1664].

Enzyme acting on 1-chloro-2,4-dinitrobenzene is found in rabbit, guinea pig, hamster, rat, dog and human bladder [C685].

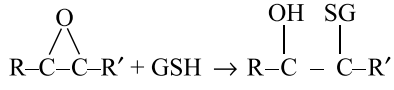
Enzyme that acts on 1-chloro-2,4-dinitrobenzene and/or 1,2-dichloro-4-nitrobenzene is found in liver and kidney from sheepshead, pinfish, jack crevalle, southern flounder, winter flounder, Atlantic stingray, bluntnose ray, small skate, nurse shark, spiny lobster and blue crab [B69].

Callinectus sapidus (blue crab) hepatopancreas contains two isozymes, pI 5.7 and 5.9. Substrates include 1-chloro-2,4-dinitrobenzene, *p*-nitrophenyl acetate, *p*-nitrobenzyl chloride, bromosulphophthalein and benzpyrene-4,5-oxide. The amino acid composition of both isozymes has been determined [E434].

Three enzymes from Melanogaster act on 1-chloro-2,4-dinitrobenzene, but not on styrene oxide or on 2-(*p*-nitrophenoxy)propene oxide [D303].

Ascaris suum and Moniezia expansa enzymes, molecular weight 37 000 with a broad optimum at about pH 8.3, act on 1-chloro-2,4-dinitrobenzene. Activity is stimulated slightly by Co^{2+}, and inhibited by Cu^{2+}, Fe^{3+} and Hg^{2+}. The product is S-(2,4- (not 2,3- as stated) dinitrophenyl)glutathione [A3038].

Glutathione S-epoxidetransferases



Human enzyme has been fractionated into isozymes designated π (acidic, pI < 5.5, in placenta), α–ε (basic, pI > 7.5, in liver) and μ (neutral, in liver). Substrates studied were benzpyrene-4,5-oxide, styrene oxide and pyrene-4,5-oxide. They are distinguished by their activity on styrene oxide. π-Enzyme substitutes the substrate with glutathione proximal to the aromatic nucleus, α–ε distal to the nucleus and μ forms both products [E928].

Human placental enzyme (cytosolic) acts on styrene oxide with a broad optimum (pH 8.5–9). The activity decreases between 25 weeks gestation and term [C21].

In rat liver two isozymes, designated A_2 and C_2, have been separated. The C_2 enzyme is specific for oxides with (*R*)-configuration, and is high-affinity. (5*S*, 6*R*)- and (5*R*, 6*S*)-benzanthracene-5,6-oxides, and (4*S*, 5*R*)- and (4*R*, 5*S*)-benzpyrene-4,5-oxides, phenanthrene-9,10-oxide and pyrene-4,5-oxide all form products solely with the (*S*, *S*)-configuration. Analogues with at least one aryl-heterocyclic (aza) ring form a lower proportion of the (*S*, *S*) product. The A_2 enzyme forms a lower proportion of the (*S*, *S*) product for all substrates, and is low-affinity. A further isozyme designated B has a stereospecificity similar to that of A [C472, D235]. Another study found that isozymes A and E act on epoxides [J583]. This activity is optimal at pH 10 [D313].

In rat lung six isozymes are found, with pI 4.8, 5.3, 6.0, 6.8, 7.2 and 8.8. They are all dimers, with common monomers [D912].

Rat cytosolic enzyme has been found in liver, lung, testis and heart. These (unfractionated) act preferentially on (*R*)-configured oxides (benzanthracene-5,6-oxide, benzpyrene-4,5-oxide, styrene oxide and pyrene-4,5-oxide); in particular, the heart enzyme shows a 93 per cent selectivity. With (*R*,*S*)- substrates there is little stereoselectivity for the products [D842]. Liver and kidney activity is about 5 per cent of the adult level at birth, and increases linearly to the adult level by 40–45 days [A3043].

Besides liver and kidney, most rat tissues show some activity, including ovary and adrenal. Two major and two or three minor components have been separated, with pI in the range 6.5–7.5 [A143, A1964, A3440, A3678].

Rat ovary activity increases threefold from birth to near the adult level at 30 days post partum. In adrenal, activity remains nearly constant for the first 60 days, then declines by about 70 per cent to the adult level. These development patterns differ somewhat depending on whether benzpyrene-4,5-oxide or styrene oxide are used as substrate, suggesting the presence of more than one enzyme [A3461].

Rabbit enzyme (cytosolic) acts on styrene oxide with highest activity in liver (optimum pH 7), and with lesser activity in kidney, lung (optimum pH 7.5) and intestine [A2509]. In liver there is little activity at birth; it increases to the adult level at weaning. In kidney it increases twofold to the adult level between birth and weaning. Intestinal activity falls at birth, then increases twofold to the adult level at weaning. In lung, the increase to the adult level is only small [A2132].

Mouse enzymes are separable into three α-class isozymes, one π-class isozyme and one μ-class isozyme (based on differing specificities), all of which conjugate (−)-*anti*- and (+)-*syn*-11,12-dihydro-11,12-dihydroxybenzo[*g*]chrysene-13,14-oxide, especially an α-class isozyme designated GSTA1-1 [K270].

Sheep liver enzyme, molecular weight about 40 000, requires no cofactors [A143]. It has a broad specificity for arene and alkene oxides, and also acts on styrene sulphide [A2282].

Activity is much less in rabbit and man than in guinea pig [A3678].

Callinectus sapidus hepatopancreas glutathione S-aryltransferase isozymes also act on benzpyrene-4,5-oxide [E434].

Enzyme that acts on styrene oxide and benzpyrene-4,5-oxide is found in liver and kidney from Atlantic stingray, black drum, bluntnose ray, croaker, dogfish, eel, jack crevalle, king of Norway, large skate, lobster, mangrove snapper, mullet, nurse shark, pigfish, redfish, sea bass, sheepshead, small skate, southern flounder, thorny skate and winter flounder [B69]. Activity in liver from teleost species is similar to that in rat liver, and usually higher than in elasmobranch species [A1694].

Oxyhaemoglobin as glutathionyltransferase

In man, 4-dimethylaminophenol forms a series of products, triply substituted with glutathione or thiol groups, apparently at positions 2, 3 and 5, with up to three of either group in any one product [F138]. Presumably, the thiol products are formed by breakdown of glutathione derivatives.

Glutathione S-aralkyltransferase (E.C. 2.5.1.18)

In rat, (1-bromoethyl)benzene is converted into N-acetyl-S-(1-phenylethyl)-L-cysteine and (2-bromoethyl)benzene into N-acetyl-S-(2-phenylethyl)-L-cysteine, which are final products from glutathione conjugates. The pattern of mercapturate formation is different from that with styrene, suggesting that styrene formation is not involved [A3708].

Glutathione conjugation with peroxidase

A glutathione thiyl radical formed by the action of peroxidase has been detected, which is believed to conjugate with the terminal carbon of styrene, followed by oxidation adjacent to the aromatic

nucleus, to yield the corresponding dihydrohydroxy compound. In the absence of oxygen several conjugates are formed, including (*R*)- and (*S*)-S-((2-hydroxy-1- and 2-phenyl)ethyl)glutathione [E80, E205]. N-Acetylbenzidine is a substrate, forming N-acetyl-N′-(glutathion-S-yl)benzidine-S-oxide [K412].

Glutathione S-aralkylsulphate transferase?

A cytosolic preparation from in rat liver converts 7-hydroxymethyl-12-methylbenzanthracene sulphate into S-((12-methylbenzanthracenyl)-7-methyl)glutathione [B965].

Glutathione conjugation, with esters as substrates

Five out of eight rat liver enzymes that act on 1-chloro-2,4-dinitrobenzene also de-esterify methylparathion with glutathione as acceptor, forming S-(*p*-nitrophenyl)glutathione [A3509]. Other products are O-methyl-O-(*p*-nitrophenyl)phosphorothioate, O-(*p*-nitrophenyl)phosphorothioate and S-methylglutathione [E225]. Similar reactions have been detected in human placenta [E64].

Chicken liver enzyme demethylates tetrachlorvinphos with glutathione as methyl acceptor [A2532].

Glutathione conjugation, with ethers as substrates

Pea seedling cytosolic enzyme, optimum pH 9.3–9.5, acts on 2,4′-dinitro-4-trifluoromethyldiphenyl ether and glutathione to form *p*-nitrophenol and, probably, S-(2-nitro-4-trifluoromethyl)glutathione, but several other diphenyl ethers are not substrates. It is inhibited by several substituted ureas, aniline derivatives, sulphobromophthalein and by substituted diphenyl ethers [A1148].

Glutathione conjugation, with cysteine conjugates as substrates

Mouse acts on the cysteine conjugate of paracetamol to form the corresponding glutathione conjugate in place of cysteine [D341].

Glutathione conjugation, with glucuronide as substrates

Rat liver glutathione S-transferases act on 1-O-clofibrylglucuronide to form S-(*p*-chlorophenoxy-2-methylpropanoyl)glutathione. The reaction also occurs spontaneously [H141].

Glutathione conjugation with tertiary amine elimination

Cynomolgus monkey acts on melphalan (*p*-(bis(2-chloroethyl)amino)phenylalanine) to form *p*-(S-glutathionyl)phenylalanine. It is proposed that the reaction involves the formation of a cyclic aziridinium (a quaternary) ion. The authors, in support of this mechanism, quote that N,N-dimethyl-*p*-toluidine is not a substrate, but trimethyl-*p*-toluidinium does yield the corresponding glutathione adduct [E874].

Cysteine conjugation with thiophenol

E. coli enzyme acts on thiophenol, pyridoxal phosphate, ammonium ion and serine to form S-phenyl-L-cysteine [J485].

Thiol S-methyltransferases (e.g. E.C. 2.1.1.9)

Human kidney thiopurine methyltransferase (E.C. 2.1.1.67) acts on thiophenol as well as on amino-, carboxyl-, methoxy-, methyl-, halogen-, nitro- and acetamido-substituted thiophenols [C917, D926].

Rat liver enzyme acts on thiophenols with S-adenosylmethionine as co-substrate [C121].

Brassica oleracea thiol methyltransferase is composed of five isozymes, molecular weights 26 000–31 000 with optima at pH 5, 6 and 8. Substrates include 4,4′-thiobisbenzenethiol, thiosalicylic acid and thiophenol; thiobenzoic acid is a poor substrate, but phenols are not substrates [K594].

Tetrahymena thermophila enzyme is cytoplasmic, molecular weight 41 000 and optimum pH 7.5. Substrates are thiophenols substituted with nitro or chloro groups, as well as thiosalicylate and thiobenzoate, but phenols and anilines are not substrates; S-adenosylmethionine is the co-substrate [E96].

S-Adenosylmethionine: thioether S-methyltransferase

Mouse lung enzyme, molecular weight 28 000, pI 5.3 and optimum pH 6.3, is mostly cytosolic, with highest activity in lung, but with some in liver. It acts mainly on aliphatics, including selenium and tellurium analogues, as well as on thioethers. Benzyl methyl thioether is a substrate, but the product has not been identified; by analogy with dimethylselenide, which forms trimethylselenonium ion, it would appear to be benzyl dimethyl sulphide. The reaction is inhibited by sinefungin and by S-adenosylhomocysteine [E677].

5.5 *Formation of amides and substituted amides*

Amide formation

In Streptomyces violaceoniger benzoic acid and a series of substituted benzoates form the corresponding benzamides [E279].

Coprinus L-tryptophan oxidase forms indole-3-acetamide as a subsidiary reaction [K563].

Formylation of arylamines

$$RNH_2 + \text{N-formyl-L-kynurenine} \rightarrow RNHCHO + \text{L-kynurenine}$$

2-Aminoanthraquinone is formylated in rat [A3818].

4-Aminobiphenyl, α- and β-naphthylamine, 2-aminofluorene and 1-aminopyrene are formylated in rabbit, guinea pig and rat, with N-formyl-L-kynurenine as formyl donor. In rabbit liver the rate of formylation is greater than acetylation. Rat also formylates *p*-aminophenol, *p*-chloroaniline, *p*-toluidine and *p*-anisidine [F109]; hepatocytes are active towards *p*-aminophenol [K60].

2-Aminofluorene is formylated by Pacific oyster [F890].

1-Aminopyrene is formylated both by gut flora [F841] and in goldfish [H877].

5-Aminosalicylate is formylated in man and pig. Studies with rat liver have shown a requirement for N-formyl-L-kynurenine [F924].

2-Formamido-4,6-dinitrotoluene and 4-formamido-2,6-dinitrotoluene are formed from TNT by Phanerochaete chrysosporium [K202].

Formylation of alkylamines

A number of studies in man, rabbit, guinea pig and rat have demonstrated that 4-formamidoantipyrine is formed as a major product from aminopyrine [A1941, A1942, A2362, A2372, B10, H167]. Some authors have claimed that it is not clear whether the formyl group arises by formylation of 4-aminoantipyrine or by oxidation of a methyl group [A1939]; others claim that methyl oxidation is definitely involved [A1941]. Presumably 4-methylaminoantipyrine, which some studies have detected as a metabolite, is the proximal substrate for this putative oxidase.

Formate dihydrofolate ligase (E.C. 6.3.4.17)

Human breast cancer and Lactobacillus casei enzymes, optimum pH 8.5, require ATP, formate and Mg^{2+} to form 10-formyldihydrofolate; it is slightly activated by K^+ [K745].

Formyltetrahydrofolate synthetase (formate tetrahydrofolate ligase, E.C. 6.3.4.3)

$$\text{THF} + \text{ATP} + \text{formate} \rightarrow \text{10-formylTHF} + \text{ADP} + \text{P}_\text{i}$$

Pig liver enzyme is part of a complex composed of methylenetetrahydrofolate dehydrogenase (E.C. 1.5.1.5), 10-formyltetrahydrofolate synthetase (E.C. 6.3.4.3) and methenyltetrahydrofolate cyclohydrolase (E.C. 3.5.4.9). The molecular weight is 150 000 (gel filtration) or 100 000 (gel electrophoresis) [A2844].

In immature chick, 10-formyltetrahydrofolate synthetase activity is decreased by about 40 per cent by folate or oestradiol; these effects are additive [A1680].

In Clostridium cylindrosporum, an enzyme that requires Mg^{2+} acts on tetrahydrofolate reversibly, with ADP and formyl phosphate as co-substrates, to yield N^{10}-formyltetrahydrofolate and ATP [E360].

Arylamine acetyltransferase (E.C. 2.3.1.5)

$$\text{Ar.NH}_2 + \text{acetyl CoA} \rightarrow \text{Ar.NHCOCH}_3$$

Procainamide and sulphadimidine are acetylated in man; about 50 per cent of subjects are fast acetylators, and the remainder are slow [A2562].

Rat and rabbit liver parenchymal cell enzyme acetylates sulphamethazine, sulphanilamide and *p*-aminobenzoate; in addition sulphadiazine is acetylated in rabbit cells. Non-parenchymal cells show no activity [B110].

2,4-Toluenediamine forms 4-acetamido-2-aminotoluene and a trace of 2-acetamido-4-aminotoluene in liver from hamster, guinea pig, rabbit, mouse and rat, with only marginal activity in man and none in dog. In hamster, guinea pig, rabbit and mouse the diacetyl derivative is also formed. The enzyme is cytosolic and requires acetyl CoA as co-substrate. Mouse enzyme shows a broad optimum at pH 7.5; in rat the activity decreases steadily from pH 6 to 9, and in rabbit there is a broad optimum at pH 6–7.5. In hamster and rabbit the activity is also found in kidney, intestinal mucosa and lung, but in some cases these tissues form diacetyl derivatives only poorly [A311].

In rabbit at least two enzymes are found. One, 'hepatic', found mainly in liver and intestine acts on sulphamethazine, optimum pH 5.5–7, and an 'extrahepatic' enzyme, optimum pH 6–7 which acts on *p*-aminobenzoate, is found in all tissues studied especially liver and gut. 'Hepatic' enzyme is stable at 4°. The study was carried out on both fast and slow sulphamethazine acetylators, based on liver activity. The enzyme in spleen and kidney does not correlate with the liver activity and may represent another enzyme; gut enzyme appears to be a mixture of both enzymes. 'Extrahepatic' enzyme is unstable at 4° [A869]. Liver enzyme has a molecular weight of 33 500, pI 5.2 and a broad optimum pH 5.9–8.6. A large number of anilines are substrates including some substituted in the *ortho* position [E399].

Acetylation of sulphonamides and other amines in rabbits appears to be controlled by an autosomal gene, with heterozygotes acetylating rapidly, and affected homozygotes (about 25 per cent of the population) acetylating slowly. There are virtually no animals that acetylate at an intermediate rate. Sulphamethazine forms N^4-acetylsulphamethazine [A1037].

Mouse enzyme, molecular weight 31 000, with a broad optimum near neutrality, acts on *p*-aminobenzoate; it is identical with arylhydroxamic acid: N,O-acetyltransferase (E.C. 2.3.1.118) [F174]. The same identity has been demonstrated with a rat liver cytosolic enzyme, molecular weight 32 000 [H566].

Hamster liver cytosol contains two isozymes, with *p*-aminobenzoate, 2-aminofluorene and 4-aminobiphenyl as substrates [F114].

Rat and sheep pineal enzymes, which act on aniline and *p*-phenetidine, require acetyl CoA as co-substrate. Two isozymes appear to be present, one of which acts predominantly on arylamines and the other on aralkylamines. The activity of the former is unaffected by pre-treatment with isoproterenol or cycloheximide [D282].

In sheep, acetylation of aniline is observed in rumen, duodenum, jejunum, ileum and colon. Other substrates include *p*-aminophenol,

p-aminobenzoate, *p*-anisidine and *p*-nitroaniline [A2788].

Chick pineal enzyme acts on aniline, *p*-phenetidine and 2-aminofluorene, but with much lower activity towards phenethylamine and 5-methyoxytryptamine. Activity is also found in kidney [F694]. Liver enzyme, molecular weight about 34 000 and optimum pH about 8.6, acts on *p*-nitroaniline. Its activity is lower than in pigeon liver, but higher than in rabbit liver [E384].

Aniline acetylating enzyme requiring acetyl CoA is found in Bacillus cereus and Cordyceps militaris, whereas Arthrobacter, Nocardia, Pseudomonas, Serratia and a range of other Bacillus species are poor sources of the activity. The optimum pH of B. cereus enzyme is 7.0; it is not stable above 30°. Other substrates include *p*-nitroaniline, 3,5-dimethyl-4-nitroaniline, *p*-nitrobenzalhydrazone, 4-amino-4′-nitroazobenzene, but not a range of other nitroanilines and phenylhydrazones. All 41 strains tested in this study showed some activity [E276].

Pseudomonas aeruginosa enzyme, which acts on 2-aminofluorene, has an optimum pH of 8.5 [J652].

Both Enterobacter aerogenes and Aeromonas hydrophila enzymes, molecular weights 44 900 and optimum pH 7.5 and 7.0 respectively, act on 2-aminofluorene [J677, J816].

Lactobacillus acidophilus enzyme, molecular weight 44 900 and optimum pH 7.0, acts on 2-aminofluorene. It is inhibited by Zn^{2+}, Ca^{2+}, Mg^{2+}, Fe^{2+} and Cu^{2+}. Pre-incubation with acetyl CoA protects the enzyme against inactivation by iodoacetamide [K208].

Enterobius vermicularis (nematode) enzyme, molecular weight 44 900 and optimum pH 7.5, acts on 2-aminofluorene and is inhibited by Zn^{2+}, Ca^{2+} and Fe^{2+} [K174].

Acetyl derivatives of primary alkylamines

$$R.NH_2 + \text{acetyl CoA} \rightarrow R.NHCOCH_3$$

Rat brain enzyme, which acts on phenethylamine and tryptamine, requires acetyl CoA. Activity is evenly distributed throughout all the brain areas examined, with the highest activity in cerebellum [A807].

Rat pineal enzyme, which is involved in melatonin synthesis, is so unstable that it has proved extremely difficult to isolate [H758]. It exists in two forms, with molecular weights 10 000 and 95 000, and acts on serotonin [E497].

Rat liver enzyme, which acts on tryptamine and serotonin, is inhibited competitively by melatonin at 10^{-6} M, whereas the pineal enzyme is not inhibited [A1350].

Rat and sheep pineal enzyme, which acts on tryptamine, serotonin, 6-fluorotryptamine and 5-methoxytryptamine (forming melatonin), requires acetyl CoA. Two enzymes appear to be present, one of which acts predominantly on arylamines and the other on aralkylamines. The latter is induced 100-fold by treatment with isoproterenol in rat, and cycloheximide treatment of sheep reduces nocturnal activity by 90 per cent [D282].

Chick pineal acetylates serotonin. At 16–20 days age the enzyme shows a diurnal rhythm in the presence of diurnal lighting. This rhythm is much decreased in constant dark, and is eliminated in constant light. Its activity increases before hatching and then remains fairly constant, irrespective of lighting conditions. In contrast, cerebral and cerebellar activity increases only marginally between 11 days incubation and adult [A1626].

Quail duodenum enzyme, optimum pH 5.8, acts on tryptamine, serotonin and 5,6-dihydroxytryptamine [H685].

Macrobrachium rosenberghii (prawn) optic lobe enzyme, optimum pH 6.5, acts on tryptamine, 5-methoxytryptamine and phenethylamine, but it has no action on aniline or *p*-phenetidine [G824].

Shrimp acetyl CoA: arylamine N-acetyltransferase acts on 2-aminofluorene and *p*-aminobenzoate [K485].

Drosophila melanogaster nervous system enzyme, molecular weight 29 500, acts on tyramine, serotonin and dopamine. Activity is much greater than for monoamine oxidase or catecholamine O-methyltransferase. This, in conjunction with high dopa decarboxylase activity, directs dopa to the formation of N-acetyldopamine [A643, H758].

Periplaneta americana indoleamine N-acetyltransferase, optimum pH 6.0 and 9–9.5, is found only in accessory female reproductive glands and in head ganglia. It acts on tryptamine and serotonin, with acetyl CoA as co-substrate [J632, J633].

Musca domestica enzyme, which acts on tyramine, is a monomer, molecular weight 27 600, optimum pH 7.2 and pI 5.8 [G914].

Cockroach testicular enzyme, molecular weight 28 000–30 000 (depending on method) and optimum pH 6.0, requires acetyl CoA. Substrates are tryptamine, serotonin, dopamine, octopamine, noradrenaline, tyramine and 5(?)-methoxytryptamine [H835].

An enzyme in Boophilus microplus acts on octopamine [G780].

D-Tryptophan N-acetyltransferase (E.C. 2.3.1.34)

Saccharomyces cerevisiae enzyme is specific for the D-isomer, and probably requires acetyl CoA [K893].

L-Aminoacid acetyltransferase (E.C. 2.3.1.1)

$$R.CHNH_2.COOH + \text{acetyl CoA} \rightarrow R.CHNHCOCH_3.COOH + CoA$$

Xanthomonas campestris acetylates L-tryptophan, but the reaction is not found in Pseudomonas syringae [E435].

In Claviceps purpurea L-tryptophan and probably L-tyrosine are acetylated [A3655].

Two strains of Cordyceps militaris acetylate L-tryptophan [A993].

Mercapturates (acetyl CoA: S-substituted cysteine N-acetyltransferase, E.C. 2.3.1.80)

Many xenobiotics undergo conjugation with glutathione, and these conjugates can be hydrolyzed to the corresponding S-(L-cysteine) conjugates. They are further metabolized by acetylation to mercapturate (N-acetyl-L-cysteine) conjugates. Few studies on the acetylation step have been carried out at an enzyme level.

Activity is found towards S-benzyl-L-cysteine in rat liver and kidney microsomes. In males the activity at five days after birth is 1–2 per cent of the adult level, but it is somewhat higher in females. The activity then increases slowly, followed by an exponential phase to reach the adult level in liver at 40 days, whereas in kidney it exceeds the adult level at 40 days [A3043].

6-Aminopenicillanic acid – phenylacetyl CoA transferase

The pure enzyme from Penicillium chrysogenum is identical with 6-aminopenicillanic acid phenoxyacetyl CoA transferase. Its optimum pH is 7.0, it requires Mg^{2+}, is stimulated by thiols and is inhibited by thiol-binding reagents. Both aromatic substrates are equally good, but *p*-methylphenoxyacetyl Co A is a less effective substrate [D12]. The reaction is an essential step in the formation of penicillins. The enzyme is also found in Aspergillus nidulans [F646].

Puromycin N-acetyltransferase

Streptomyces alboniger enzyme, molecular weight 23 000, acetylates the tyrosyl residue of puromycin. It also acts on O-demethylpuromycin and its analogue chryscandin [D879].

Conjugation of carboxylic acids

a. Alanine

Alanine is conjugated with indole-3-acetate in crown gall [A2843] and with 2,4-dichlorophenoxyacetate in Glycine and Zea [A3200].

b. Arginine

Rat brain synaptosome tyrosine-arginine ligase (E.C. 6.3.2.24), molecular weight 240 000–245 000, optimum pH 7.5–9.0 and pI 6.1–6.2, requires ATP and Mg^{2+} to form L-tyrosyl-L-

arginine [K857].

c. Aspartate

N-Benzoylaspartate is formed in barley from benzyl alcohol, presumably with benzoate as intermediate [A1726].

Oxindole-3-acetylaspartate and indole-3-acetylaspartate are formed from indole-3-acetate in a Populus hybrid [H349]. Indole-3-acetylaspartate is formed in Dalbergia dolichopetala seeds [E729], pea, Teucrium canadense, sycamore, crown gall and Arabidopsis [A635, A2843, A3220, E307, J713]. This reaction in Vicia faba is the first step of a reaction sequence in which the indole nucleus is oxidized [E437].

Glycine max conjugates α-naphthylacetate and phenylacetate with aspartate. The corresponding acylglucosides appear to be transitory intermediates [A3679].

Aspartate is conjugated with 2,4-dichlorophenoxyacetate in Glycine max and corn [A3200].

d. Benzoyladenylate formation

This is formed from benzoate in N. crassa [A750].

e. Benzoylhydroxylamate formation

This is formed from benzoate and hydroxylamine in N. crassa [A750].

f. Glutamate

In cow and quail, *m*-phenoxybenzoate is conjugated with glutamate [A3194, F838].

Indole 3-acetate is conjugated with glutamate in Teucrium canadense, Arabidopsis and crown gall [A2843, E307, J713]. This conjugate is formed with 2,4-dichlorophenoxyacetate in Glycine max and corn [A3200].

Dihydrofolate synthase (E.C. 6.3.2.12) acts on dihydropteroate with glutamate and ATP as co-substrates, to form dihydrofolate and ADP. Serratia indica enzyme requires a univalent cation (K^+, NH_4^+, Rb^+) and a divalent cation (Mg^{2+}, Mn^{2+}, Fe^{2+}) [A2836]. Pea enzyme is mainly mitochondrial, from which it is easily released. Activity is maximal six to eight days after gemination. Spinach leaf enzyme is also mitochondrial [A2473]. Pea seedling enzyme, molecular weight 56 000 and optimum pH 8.8, also requires a univalent cation (K^+, NH_4^+, Rb^+) and a divalent cation (Mg^{2+}, Mn^{2+}) and is specific for dihydropteroate; pteroate and tetrahydropteroate are not substrates. It is inhibited by ADP and Ag^+; *p*-chloromercuribenzoate inhibition is reversed by 2-mercaptoethanol [A1363, A2240]. E. coli enzyme acts on dihydropteroate and requires a univalent cation (K^+, NH_4^+, Rb^+) and a divalent cation (Mg^{2+}, Mn^{2+}). It is specific for dihydropteroate; pteroate, tetrahydropteroate and polyglutamates are not substrates, and dihydrofolate is inhibitory [A1360, A1362].

g. Glutamine

In man, phenylacetylglutamine is formed from phenylacetate, and this conjugate is essentially the only one formed in man with this acid [A128, A132, H550]; it is a major urinary component.

In addition to man, phenylacetylglutamine is formed from phenylacetate in rhesus, cynomolgus, green, red bellied, mona and squirrel monkeys, mangabey, drill, baboon, capuchin and marmoset [A196].

Indole 3-acetate is conjugated with glutamine in man, Macaca, Cercopithecus, Papio, Saimiri Aotus and Cebus, but not in a range of other mammals [A274].

Diphenylacetate is conjugated in rat [C313].

h. Glycine and hippurate conjugates; relationship with other conjugation reactions

Many acids are conjugated with glycine, in particular benzoates; only a small proportion of those studied are listed here.

The first step in the formation of hippurates is formation of CoA conjugates, an ATP-driven reaction [H740]. Both these reactions occur in the soluble fraction of liver mitochondria [A1369].

Lipoate reduces the formation of hippurate; it appears to deplete hepatic CoA [H722].

The formation of hippurates is just one of several possible conjugation routes. A study on conjugation of phenylacetate in different animal species found that in man and both old and new world monkeys there is a little (none in man) conjugation with glycine, most conjugation is with glutamine and a little with taurine. In all other mammals and birds studied, conjugation was observed with glycine, but none with glutamine, and in most cases, some conjugation with taurine. In dog, ferret and mouse, some acyl glucuronide is formed [A196]. Other studies in rat found a small proportion diverted to the glutamine and glucuronide pathways [C308, C381]. Glycine conjugation is found in elephant and hyaena [A2387].

In rat, a linear relationship has been demonstrated between the polarity of *p*-substituted benzoates and the proportion converted into hippurates [F693].

Glycine conjugates are formed in ferret from benzoate, *p*-nitrobenzoate, phenylacetate, *p*-chlorophenylacetate, *p*-nitrophenylacetate, 1- and 2-naphthylacetate and indole-3-acetate, whereas taurine conjugates are formed from phenylacetate, *p*-chlorophenylacetate, *p*-nitrophenylacetate, 1- and 2-naphthylacetate and indole-3-acetate. Glucuronides are formed from benzoate, *p*-nitrobenzoate, 1- and 2-naphthylacetate and diphenylacetate, but not from indole-3-acetate [A394].

m-Phenoxybenzoate is conjugated with glycine in a range of mammals and in mallard, and all of them in addition form the glucuronide, and several conjugate it with taurine [B638].

In rabbit, both hippurates and glucuronides are formed from benzoate, monochlorobenzoates, monofluorobenzoates, 3- and 4-methylbenzoates, *p*-hydroxy-, *p*-cyano- and *p*-methoxybenzoates, whereas only glycine conjugates are formed with nitrobenzoates, aminobenzoates, *o*-methyl-, *o*- and *m*-hydroxy-, and 4-acetamidobenzoates [H519].

Indole-3-acetate is conjugated with glycine in a range of mammals including new world monkeys, but not by old world monkeys or man. In man it is mainly conjugated as acyl glucuronide (but not in any of the other species studied) and with glutamine. Taurine conjugates are found in monkeys, Mustela and Columbia [A274].

In man and rat, kidney and liver are sites of glycine conjugate formation [G834, J908].

In rat brain, both benzoate and *m*-trifluoromethylbenzoate form hippurates [A3730].

In rat and a number of marsupials benzoylglucuronide is formed as well as hippurate [D914].

Salicylic acid is conjugated with glycine in rat [B56], and is an important metabolite of aspirin [B201]; this is also a finding in many species including man.

In marmoset the proportion of benzoate conjugated with glycine decreases with increasing dose [B201].

Benzoate is mainly converted by horse into hippurate, with a trace as glucuronide. Salicylate is similarly conjugated. 2-Naphthylacetate is primarily conjugated with glycine, with lesser amounts of glucuronide and taurine conjugate [B801].

Lion, civet and genet form hippurate from benzoate, and in the same species 1-naphthylacetate is conjugated with glycine, whereas taurine and glucuronide conjugates are formed only in civet and genet [A1312].

In pipistrelle bat both benzoate and phenylacetate are conjugated with glycine [A3356].

i. Glycylvaline

m-Phenoxybenzoate forms this conjugate in mallard, but a large number of mammalian species do not exhibit this reaction [B622, B638]. It has also been observed in quail [F838].

j. Leucine

This conjugate is formed with 2,4-dichlorophenoxyacetate in Glycine max and Zea mays [A3200].

k. Lysine

Benzoate and *p*-chlorobenzoate form N^2-benzoyl-N^6-*p*-chlorobenzoyl- and N^6-benzoyl-N^2-*p*-chlorobenzoyllysines in chicken [A2253].

Pseudomonas syringae, subspecies savastanoi, forms indoleacetyl-lysine synthetase (E.C. 6.3.2.20) [K921].

l. Ornithurate and analogues

Ornithurate is formed from benzoate in chicken, pheasant and Coturnix [A1156], quail [E516] and Tuatara [B449].

Symmetrical ornithine conjugates are formed from phenylacetate, *p*-nitrophenylacetate, *p*-chlorophenylacetate and 1-naphthylacetate in hen, but not in pigeon [A131, A395]. A similar conjugate is formed with *p*-chlorobenzoate in chicken [A2253].

m. Mixed ornithine conjugates

In quail and chicken, *m*-phenoxybenzoate is conjugated with N^2-acetylornithine at the 5 position [C40, F838]. Additionally, in chicken benzoate, *m*-hydroxybenzoate and *m*-phenoxybenzoate form small amounts of other ornithine conjugates; N^2-benzoyl-N^5-*m*-phenoxybenzoyl, N^5-benzoyl-N^2-*m*-phenoxybenzoyl, N^2-benzoyl-N^5-*m*-hydroxybenzoyl and N^5-benzoyl-N^2-*m*-hydroxybenzoyl (main conjugate) [E941].

N^2-Benzoyl-N^5-*p*-chlorobenzoyl-, N^5-benzoyl-N^2-*p*-chlorobenzoyl-, N^2-benzoyl-N^5-*p*-hydroxybenzoyl- and N^5-benzoyl-N^2-*p*-hydroxybenzoylornithine conjugates are formed with a mixture of *p*-chlorobenzoate, benzoate and *p*-hydroxybenzoate in chicken [A2253].

n. Phenylalanine

This conjugate is formed with 2,4-dichlorophenoxyacetate in Glycine max and Zea mays [A3200].

E. coli phenylalanine N-acetyltransferase (E.C. 2.3.1.53), optimum pH 8, requires acetyl CoA and acts on L-phenylalanine, L-phenylalanyl-L-tyrosine and some aliphatic amino acids [K924]. A similar reaction is involved in human phenylketonuria, where N-acetyl-L-phenylalanine is a major metabolite.

o. Pteroylpolyglutamates

Pig liver folylpoly-γ-glutamate synthetase (E.C. 6.3.2.17) is composed of two isozymes, both with monomeric molecular weight 62 000 and optimum pH 9.5. The reaction requires a reducing agent, Mg^{2+} and a monovalent cation; K^+ is best, with folate, dihydrofolate and tetrahydrofolate as substrates. The reaction sequence is, for instance:

$$\mathrm{THF} + \mathrm{ATP} \rightarrow \mathrm{ADP} + \mathrm{P_i} + \text{tetrahydrofolylglutamates}$$

Depending on substrate, the products contain two to seven glutamyl residues, and it appears that the glutamate residues are added sequentially [E277].

In E. coli, dihydropteroate is conjugated with glutamate to yield dihydrofolate; pteroate and tetrahydropteroate are not substrates, nor are oligoglutamyl analogues. It requires ATP, Mg^{2+} or Mn^{2+}, and NH_4^+, K^+ or Rb^{2+}. Tetrahydrofolate yields its mono- and then the diglutamyl analogue [A1362].

Folylpolyglutamate synthetase (E.C. 6.3.2.17) from pig liver acts on pteroates, dihydropteroates and tetrahydropteroates with up to seven glutamate residues, building up the chain one unit at a time. The reaction rate decreases sharply with increasing chain length [K455].

p. Serine

E. coli 2,3-dihydroxybenzoate-serine ligase (E.C. 6.3.2.14) acts on L-serine and pyrocatechuate. Its appearance is prevented by the presence of Fe^{2+} [K855].

q. Taurine

In rainbow trout, both benzoate and *m*-phenoxybenzoate form taurine conjugates; benzoate also undergoes this reaction in bluegill, perch and minnow [E582, E911], channel catfish [F554] and in southern flounder [E900].

m-Phenoxybenzoate is conjugated with taurine in mouse and quail [A3250, C127, C133, F838]. A large study found that marmoset, hamster, ferret,

cat, gerbil and mouse form the taurine conjugate, but this conjugate was not detected in rat, guinea pig, rabbit, sheep or mallard [B638].

An extensive study with phenylacetate found taurine conjugates in man, old and new world monkeys, bushbaby, slow loris, dog, cat, ferret, rabbit, mouse, rat, hamster and pigeon, although in most cases this was a minor conjugation route. The reaction was not detected in guinea pig, vampire bat or chicken [A196].

Taurine conjugates are formed in ferret from phenylacetate, *p*-chlorophenylacetate, *p*-nitrophenylacetate, 1- and 2-naphthylacetate and indole-3-acetate [A394].

A study with indole-3-acetate found conjugation with taurine in old and new world monkeys (Macaca, Cercopithecus, Papio, Saimiri, Aotus and Cebus), Mustela and Columbia, but not in a range of other mammals [A274].

In pigeon and hen, taurine conjugates are formed with phenylacetate, *p*-chlorophenylacetate, *p*-nitrophenylacetate and 1-naphthylacetate; indole-3-acetate is conjugated in pigeon [A395].

r. L-Tryptophan

This conjugate is formed with 2,4-dichlorophenoxyacetate in Glycine max and Zea mays [A3200].

s. Tyramine

Nicotiana tabacum, infected with TMV, contains cytosolic feruloyl CoA: tyramine N-feruloyl CoA transferase (E.C. 2.3.1.110), molecular weight 45 000. It has a broad specificity, with octopamine, dopamine, noradrenaline, 3-methoxytyramine, tyramine, phenethylamine and (poor) *p*-sympatol as acyl receptors, and the CoA conjugates of ferulate, cinnamate, *p*-coumarate, sinapate, dephosphoferuloyl CoA and feruloyl-4′-phosphopantetheine as donors [D558, F72].

t. Valine

Indole-3-acetate is conjugated with valine in crown gall [A2843].

N-Malonyltransferases

Arachis seedling contains D-tryptophan N-malonyltransferase (E.C. 2.3.1.112), anthranilate N-malonyltransferase (E.C. 2.3.1.113) and 3,4-dichloroaniline N-malonyltransferase (E.C. 2.3.1.114), molecular weights 38 000, 50 000 and 45 000 respectively [K727].

Daucus carota catalyzes this reaction with 3,4-dichloroaniline to form N-malonyl-3,4-dichloroaniline [H118].

Peptide formation with heterocyclic amines

A calf enzyme acts on phenothiazine to form N-conjugated short chain peptides of phenothiazine and 3-hydroxyphenothiazine; the peptide chains appear to have little similarity in structure [D410].

Amidation by transacetylation and transformylation

Liver from several mammalian species transfers the formyl group from 4-formamidobiphenyl to α- and β-naphthylamine, from α-formamidonaphthalene to 4-aminobiphenyl, 2-aminofluorene and β-naphthylamine, from β-formamidonaphthalene to 4-aminobiphenyl, 2-aminofluorene and α-naphthylamine, and from 1-formamidopyrine to 4-aminobiphenyl [F109].

5-Aminosalicylate is formylated in rat and human liver. In rat the reaction proceeds when the reactants are fortified with N-formyl-L-kynurenine, which suggests that the reaction is a transformylation [F924].

E. coli amino acid transacetylase transfers an acetyl group from a range of N-acetyl-L-amino acids to L-phenylalanine [K924].

N-Carbamoylation

Dog metabolizes methylphenidate to form the corresponding carbamide [C14].

5.6 *Phosphorylation reactions*

Phosphate ester formation

Although O-phosphorylation by protein kinases is a well-established mechanism for activation of enzymes, few studies have detected the formation of phosphate esters in phase 2 metabolism of xenobiotics; this may be a consequence of technical problems in handling phosphate ester metabolites.

Man, monkey and rat form phosphate esters from N-hydroxy-2-acetamidofluorene [A2086].

In sheep, phenol is converted into phenol and quinol phosphates [A3717]. In cat phenol is phosphorylated, but not naphthols [A2].

In housefly, and probably in grass grub and blowfly, both 1-naphthol and *p*-nitrophenol yield phosphate and glucoside-6-phosphate esters [A1604]. These reactions have also been detected with *p*-nitrophenol in cockroach, stick insect, mealworm, Porina and wax moth larvae, housefly, blowfly and earwig, except that the glucoside ester has not been detected with mealworm and Porina [C494].

Phenylalanine adenylyltransferase (E.C. 2.7.7.54)

Penicillium cyclopium acts on ATP and phenylalanine to form N-adenylylphenylalanine and pyrophosphate; it appears to be an intermediate in the formation of cyclo-(anthaniloyl-phenylalanyl) [K906].

Anthranilate adenylyltransferase (E.C. 2.7.7.55)

Penicillium cyclopium acts on ATP and anthranilate to form N-adenylylanthranilate and pyrophosphate; it appears to be an intermediate in the formation of cyclo-(anthaniloyl-phenylalanyl) [K906].

Flavokinase (E.C. 2.7.2.26)

$$\text{Riboflavin} \rightarrow \text{FMN}$$

This reaction has been detected in rat [A919, C145, E406].

FMN adenylyltransferase (E.C. 2.7.7.2)

$$\text{FMN} + \text{ATP} \rightarrow \text{FAD} + \text{pyrophosphate}$$

This activity is found in rat and mouse [A919, A3780]. In plants it is activated by Mg^{2+} and slightly by Zn^{2+}; it is found in Arachis hypogea, Cajanus indicus, Cannavalia gladiata, Cicer arietinum, Dolichos lablab, D. biflorus, Ipomoea batatas, Papaver sativum, Phaseolus radiatus, Ricinus communis, R. mungo, Sesamum indicum and Solanum tuberosum [K828].

(2,3-Dihydroxybenzoyl)adenylate synthase (E.C. 2.7.7.58)

E. coli enzyme, molecular weight 59 000 requires ATP, releasing pyrophosphate. It also acts on several *o*-hydroxybenzoates, but not on other analogues [K830].

Actinomycin synthetase I

Streptomyces antibioticus enzyme acts on ATP and 3-hydroxy-4-methylanthranilate to form 3-hydroxy-4-methylanthraniloyladenylate, with the release of pyrophosphate. This reaction is in the sequence that leads to the formation of actinomycin D [G791].

Protein-tyrosine kinase (E.C. 2.7.1.112)

This enzyme is found in chicken and man; it is enhanced by infection with Rous sarcoma virus [K918]. Rat membrane vesicle enzyme requires ATP as phosphorylating agent, and is enhanced by low Zn^{2+} concentrations; it phosphorylates the tyrosine residues of several proteins [K918, K919].

Phenylalanine tRNA ligase (E.C. 6.1.1.20)

This activity has been detected in rat liver and Saccharomyces cerevisiae [K941].

Tyrosine tRNA ligase (E.C. 6.1.1.1)

Pea root contains two isozymes, molecular weights about 50 000 and 70 000, which require ATP and Mg^{2+}. It acts on tRNA from plants and beef, but not E. coli [K825].

Tryptophan tRNA ligase (E.C. 6.1.1.2)

Beef pancreas enzyme, molecular weight 110 000 appears to be a tetramer composed of 2 pairs of similar chains [K854].

5.7 *Ether formation*

Catechol O-methyltransferase (COMT, E.C. 2.1.1.6)

$$Ar.(OH)_2 + SAM \rightarrow Ar.OH.OMe$$

a. Animals

This reaction is one of the major pathways by which the catecholamine hormones are inactivated. It is of particular importance in Parkinson's disease, in which the synthesis of dopamine is seriously compromised by destruction of dopaminergic neurones. Inhibition of COMT would potentially reduce the losses of dopamine, with possible alleviation of symptoms; some nitrocatechol substrate analogues are strongly inhibitory.

Human brain enzyme, which is 55–80 per cent microsomal, acts on noradrenaline and dopamine [B118]. Its activity is scarcely altered in parkinsonism [A381].

Human erythrocyte enzyme is inhibited by S-adenosylhomocysteine [A2956].

Human liver and placental enzymes act on noradrenaline, adrenaline, dopamine and isoproterenol in the *meta* position. The K_m for the placental enzyme is lower than for the liver enzyme [A3831]. Placental enzyme, which is activated by cysteine, is monomeric, molecular weight 23 000 [G171]. Another study found the molecular weight to be 25 000, with pI 5.3 [F795]. A further study on placenta isolated an enzyme, molecular weight 49 000 and pI 5.0 [A2905].

Human liver, brain and placental enzymes are composed of two isozymes, similar to the corresponding rat enzyme (molecular weights 24 000 and 47 500, with pI 4.9 and 4.8, and Stokes radii 2.01 and 2.87 nm respectively). These forms are not inter-converted, and are considered to be genetically different [A3793].

In man and rat, the small intestinal enzyme is found in mucous membrane and muscle layers, in fractions, both particulate and soluble [E693].

In pig liver, methylation of dopac is inhibited competitively by 2,3-dihydroxypyridine, which is not a substrate [C211]. Substrates include D-adrenaline, benserazide, carbidopa, 5-S-(L-cysteinyl)-L-dopa, α-difluoromethyldopa, D- and L-dopa, dopac, α-fluoromethyldopa and α-methyldopa [B813]. In liver and brain, the enzyme is cytosolic only, and is evenly distributed throughout brain [A2977]. Antibody and other studies suggest that the brain and liver enzymes are identical [A3550].

In pig kidney, the activity rises steadily from 10 days before birth to 70 days post partum. In heart, maximal activity is found around birth, after which it declines slightly. In spleen it peaks 15 days post partum, and then declines by 40 per cent. In brain the activity fluctuates around birth, and then remains steady from two weeks post partum. In adrenal, activity doubles at birth and then slowly declines [A1569].

In mouse liver, 70 per cent of the activity is associated with the plasma membrane [A345].

Rat cerebral microvessels show activity, considered to be extraneuronal [A3619]; it is both soluble and membrane-bound [C477]. Two forms of liver enzyme are found, molecular weight 25 000 and pI 5.1; they differ in internal disulphide bonding [F795, F797]. The ratio of activity in liver, brain and eythrocytes is 100:10:1, with optimum pH 9, 8.2 and 9 respectively. The ratio of *meta* to *para* methylation is similar in brain and erythrocyte, and different from that in liver. A number of substituted catechols are substrates [A2817].

Rat liver enzyme, optimum pH 7.3–8.2, requires Mg^{2+} and is inhibited by Ca^{2+}. Protocatechuate is both *meta* and *para*-methylated [A56, C169]; this is also observed with caffeate [A187]. After purification by affinity chromatography, its molecular weight is 23 000, and the pure enzyme is very unstable [A340]. A minor isozyme has molecular weight 47 500. The major and minor isozymes have pI 4.9 and 4.8, and Stokes radii 2.01 and 2.87 nm respectively [A3793]. Another study found two isozymes, pI 4.66 (main) and 4.54, both optimum pH 7.8–8.2 [A1408]. An insoluble isozyme with optimum pH 8.5, molecular weight 21 000 and a requirement for Mg^{2+}, is similar to cytosolic enzyme after solubilization [A2586]. It is inhibited by a series of 3-nitrocatechols with IC_{50} about 10–500 nM and, less effectively, by 4-nitrocatechols and 3-cyanocatechols with an electron-withdrawing group *meta* to the nitro group or other substituent. For 3-nitrocatechols, best inhibition occurs when the substituent is *n*-pentoyl or conjugated heterocyclic groups of ester and amide types. Many of these compounds are relatively non-toxic, which makes them potentially useful as drugs for sparing dopamine in the treatment of parkinsonism [E923]. A particularly good inhibitor is RO-4-4602, which is effective at 10^{-5} M [A2585].

Rat lung, kidney, liver and brain enzymes are both membrane-bound and cytosolic. Using dopamine and protocatechuate as substrates the *meta*/*para* ratio for methylation is four to six with cytosolic enzyme, but higher with membrane enzyme (8–60). Dopamine shows higher ratio values than other substrates. The ratio increases as substrate concentration is reduced, particularly for dopamine [D297].

Rat erythrocyte enzyme is both particulate and cytosolic, optimum pH about 8.1 [A457]. Two cytosolic isozymes are found, with pI 4.70 for the particulate enzyme [A1408], they exhibit a similar specificity, requirement for Mg^{2+} and optimum pH, but they differ in thermal stability and K_m [A1382].

A major study with liver enzymes examined *meta* and *para* methylation. For neutral and acidic substrates, the *m*/*p* ratio is independent of pH, but for amine substrates the ratio decreases with increasing pH. In this study the ratio was independent of enzyme source (three rat strains, guinea pig, rabbit, mouse and monkey), and was the same for particulate and cytosolic enzymes (in contrast with above results), but it depended on the concentration of divalent ions. Polar side-chain substituents inhibit *p*-substitution [A486]. Resorcinols are not substrates [A724].

Rabbit, rat and guinea pig lung enzymes, which require Mg^{2+}, act on *l*-proterenol, optima pH 7.2 for microsomal enzyme and broad (7.5–9) for soluble enzyme [A115].

Tetrahymena pyriformis enzyme is cytosolic [A3131].

A theoretical analysis of the action of COMT has been undertaken [B545].

b. Plants.

Alfalfa root nodule enzyme, molecular weight about 103 000, acts on caffeate and 5-hydroxyferulate [B487].

Apple fruit enzyme, molecular weight 78 000, pI 5.25 and optimum pH 6.8, acts on a range of catechols, including cinnamates and flavonoids. The report implied that Mg^{2+} is not required for activity [D258].

Aspen xylem enzyme, molecular weight 40 000, acts on caffeate and 5-hydroxyferulate [G624].

Bambusa contains caffeate O-methyltransferase (E.C. 2.1.1.68), pI 4.61 [A169].

Brassica oleracea enzyme contains two isozymes, both with molecular weight 42 000 and optimum pH 7.6, but with different pI. They are not activated by cations. Substrates include caffeate, 5-hydroxyferulate, quercetin, 3,4,5-trihydroxycinnamate and esculetin, but not chlorogenate or protocatechuate [F367].

Chrysosplenium americanum enzyme, molecular weight 65 000, pI 5.4 and optimum pH 7.5–8.5, requires Mg^{2+} and methylates the 3′ position of 3,7-di-O-methylquercetagetin [B832, C579].

Cortaderia selloana (pampas grass) enzyme acts on caffeate to yield only ferulate. Protocatechuate is methylated in both positions; *meta*-methylation activity is largely destroyed by

heating the enzyme preparation at 45°, whereas *para*-methylation is retained [A187].

Daucus carota S-adenosylmethionine: caffeoyl CoA 3-O-methyltransferase (E.C. 2.1.1.104) requires Mg^{2+}; other catechols are inactive, but caffeoyl-3′-dephosphoCoA is a substrate. It is inhibited by S-adenosyl-L-homocysteine [F94, K731].

Glycine max culture yields two isozymes of caffeate O-methyltransferase (E.C. 2.1.1.68); one is unstable at 4°. The stable one, which acts on caffeate (forming ferulate) and 5-hydroxyferulate, is considered to be involved in lignin formation, and the other, which acts on luteolin and quercetin, to be involved in flavonoid synthesis [A2434, K728].

Lotus corniculatus flower bud enzyme, pI 5.1 and optimum pH 7.7, acts on position 3′ of flavonols [C905].

Nicotiana leaf contains three isozymes, molecular weights 90 000, 93 000 and 100 000, with pI 4.80, 5.21 and 4.74 respectively, is stable at 0°. Most substrates are methylated at the *meta* position, but with some *p*-substitution for protocatechualdehyde, esculetin and protocatechuate; in the latter case *p*-substitution predominates with the 'pI 5.21' enzyme [B490]. Many catechols are substrates [A3778]. Cell cultures also have a broad specificity; isozymes, molecular weights 70 000 and 74 000, and optimum pH 8.3 and 7.3, respectively, have been detected. In this study caffeate was methylated primarily in the *m*-position, for esculetin the ratio was near unity, and for quercetin *p*-substitution predominated. In each case the 'pH 8.3' enzyme *p*-methylated to a greater extent than the 'pH 7.3' enzyme [A3437, A3757].

Parsley S-adenosyl-L-methionyl: caffeoyl CoA 3-O-methyltransferase (E.C. 2.1.1.104), molecular weight 48 000, pI 5.7 and optimum pH 7.5, requires Mg^{2+}, and is activated by fairly high concentrations of phosphate or by tris and sodium chloride; EDTA, Mn^{2+} and Ca^{2+} are inhibitory. Methyl caffeate, chlorogenate, rosmarinate and *trans*-5-O-caffeoylshikimate are also substrates, but not caffeate [F160].

Parsley luteolin O-methyltransferase (E.C. 2.1.1.42), molecular weight about 48 000 and optimum pH about 9.7 requires Mg^{2+}. Luteolin and its 7-glucoside are the best substrates; other catechols have a much lower affinity [K805].

Petunia hybrida petal anthocyanin methyltransferase is cytosolic, converting cyanidin into paeonidin [C743].

A poplar hybrid (tremula/alba) caffeoyl CoA O-methyltransferase is found in all lignifying cells [K625]. Populus trichocarpa enzyme is composed of two isozymes [K516].

Spinach beet caffeate O-methyltransferase (E.C. 2.1.1.68), optimum pH 6.5 does not require Mg^{2+}; it has a broad specificity [A2315].

Trillium apetalon leaf enzyme is dimeric, molecular weight 78 000, optimum pH 7 and pI 5.3. It is stimulated by EDTA and dithiothreitol, and is inhibited by *p*-chloromercuribenzoate, iodoacetate and by several divalent heavy metal ions [K250].

Vitis vinifera S-adenosylmethionine: cyanidin-3-glucoside 3′-O-methyltransferase, optimum pH 7.7–9.8, requires Mg^{2+}. It is less active towards cyanidin than its glucoside [H886].

Zea mays S-adenosylmethionine: quercetin-3′-O-methyltransferase, optimum pH 8.5, requires dithioerythritol, and Mg^{2+} or Mn^{2+}. Eriodictyol, quercetin and luteolin are substrates [F173, G223].

c. Microorganism

Streptomyces griseus enzyme, molecular weight 36 000, pI 4.4 and optimum pH 7.5 requires Mg^{2+}. Substrates include simple catechols and esculetin [K652].

Phenol O-methyltransferases (E.C. 2.1.1.25)

a. Animals

Human erythrocyte stroma activity (with *p*-acetamidophenol as substrate) correlates highly with aliphatic S-methyltransferase (E.C. 2.1.1.9), suggesting that they are the same enzyme. The optimum pH is 9.0, and it is stable at room temperature. It does not require Mg^{2+}, and is not inhibited by Ca^{2+}, but tropolone and

S-adenosylhomocysteine are inhibitory [A2956, C741].

Rabbit, rat and guinea pig lung enzymes act on phenol and phenols substituted with one or two methyl groups (all possible structures were tested), or with ethyl and bromo groups [A115].

Rat liver mitochondrial 5-demethylubiquinone-9 methyltransferase which requires S-adenosylmethionine is found on the inner membrane [A3084].

b. Plants

Alfalfa (Medicago) and licorice (Glycyrrhiza) chalcone 2′-O-methyltransferases require S-adenosylmethionine and act on isoliquiritigenin and licodione respectively (H908).

Alternaria alternata alternariol O-methyltransferase, molecular weight 43 000, requires S-adenosylmethionine [G473]. A. tenuis enzyme, molecular weight 110 000 and optimum pH 8.0 requires Mg^{2+} [E301].

Apple fruit enzyme (quercetin O-methyltransferase), which has a requirement for Mg^{2+}, acts on the 3 position of quercetin, and the 7 position of 3-O-methylquercetin. It has a structural requirement for 3′,4′-dihydroxy groups for substrate activity. The molecular weight is 47 000, shows a double optimum pH at 7.3 and 8.3 and pI 4.9 [D258].

Argemone platyceras S-adenosylmethionine: (*R*)- and (*S*)-norlaudanosoline 6-O-methyltransferase (E.C. 2.1.1.128), molecular weight 47 000 and optimum pH 7.5, acts on the 6- and to a small extent, the 7-position of norlaudanosoline. It does not act on other classes of phenols. This activity is also found in Adlumia fungosa, Argemone intermedia, Berberis henryana, B. wilsoniae, B. stolonifera, Chelidonium majus, Cissampelos mucronata, Corydalis sempervirens, C. pallida, Eschscholtzia tenuifolia, Fumaria officinalis, Glaucium flavum, Papaver somniferum, Thalictrum tuberosum and T. sparsiflorum [D77]. A. platyceras S-adenosylmethionine: 6-O-methylnorlaudanosoline 5′-O-methyltransferase (E.C. 2.1.1.121; it should be called 3′-methyltransferase) forms nororientaline, with methylation on the benzyl moiety. It is highly specific; it does not act on (*R*)- or (*S*)-norlaudanosoline, laudanosoline, simple phenols, flavanoids or coumarins, amongst others [D76].

Berberis koetineana S-adenosyl: 3′-hydroxy-N-methyl-(*S*)-coclaurine-4′-O-methyltransferase (E.C. 2.1.1.116), molecular weight 40 000 and optimum pH 8.5, is highly specific for the (*S*)-isomer. It acts on other analogues, such as norlaudanosoline and (*S*)-3′-hydroxycoclaurine. The enzyme is not separable from 6-O-methyltransferase activity [F854].

Berberis wilsoniae and B. aggregata S-adenosyl-L-methionine: columbamine O-methyltransferase (E.C. 2.1.1.89), molecular weight 52 000 and optimum pH 8.9 are vesicle-bound enzymes that methylate columbamine at the 2 position to form palmatine, but they are inactive towards tetrahydrocolumbamine [E268]. This activity is highly specific [E256].

Berberis (*S*)-scoulerine 9-O-methyltransferase (E.C. 2.1.1.117), molecular weight 63 000 and optimum pH 8.9, requires S-adenosylmethionine to form (*S*)-tetrahydrocolumbamine [D581].

Calamondin orange (Citrus mitis) has been demonstrated to contain, besides catechol O-methyltransferase, enzymes that O-methylate a range of flavones and isoflavones at the 4′, 5, 6, 7 and 8 positions, and possibly at the 3′ position, including substrates with methoxy substituents [A3987].

Catharanthus roseus 11-O-demethyl-17-O-deacetylvindoline O-methyltransferase (E.C. 2.1.1.94) is highly specific, and is involved in the formation of vindoline [K729].

Chrysosplenium americanum flavonol 3-O-methyltransferase (E.C. 2.1.1.76), molecular weight 65 000, pI 4.8 and optimum pH 7.5–8.5, requires S-adenosylmethionine and Mg^{2+}. It acts only on the 3-position of quercetin. The activity is also found in Calamondin orange and Nicotiana [B830, B832, C579].

Chrysosplenium americanum flavonol 6-O-methyltransferase, molecular weight 65 000, pI 5.7 and optimum pH 7.5–8.5, requires S-adenosylmethionine and Mg^{2+}. It acts on 3,7-di-O-methyl- and 3,3′,7-tri-O-

methylquercetagetin. Similar activity on quercetin is also found in orange and tobacco [B830, B832, C579].

Cicer arietinum culture isoflavone 4′-methyltransferase (E.C. 2.1.1.46), molecular weight 110 000 and optimum pH 9, is specific for 4′-hydroxyisoflavones such as daidzein. It is inhibited by heavy metals, *p*-chloromercuribenzoate and S-adenosylhomocysteine. It is considered to be an ordered bi bi reaction with S-adenosylmethionine and S-adenosylhomocysteine as leading reaction partners [A1493].

Citrus aurantium S-adenosylmethionine: eriodictyol 4′-O-methyltransferase, molecular weight 52 000 and optimum pH about 7.5 is activated by Mg^{2+} or by EDTA [H591].

Coptis japonica S-adenosylmethionine: 3′-hydroxy-N-methylcoclaurine-4′-O-methyltransferase, molecular weight 80 000 and optimum pH 8.0 is dimeric and forms reticuline by an ordered bi bi reaction. It also acts on (*R*,*S*)-laudanosoline and (*R*,*S*)-norlaudanosoline, and is inhibited by several divalent cations [K572]. (*R*,*S*)-Norcoclaurine 6-O-methyltransferase (E.C. 2.1.1.128), molecular weight 95 000 and pI 4.7 is dimeric, and requires S-adenosylmethionine to form coclaurine by a bi-bi ping-pong mechanism. It is inhibited by divalent cations [D77, K785].

Daucus carota root 6-hydroxymellein O-methyltransferase (E.C. 2.1.1.107), molecular weight 76 000, pI 5.7 and optimum pH 7.5–8.0, requires S-adenosylmethionine for methylation at the 6-position, and is inhibited by both reaction products. It is not found in fresh root, but is induced by the action of, for instance, 2-chloroethylphosphonic acid [J13, K730].

Eschscholtzia californica 10-hydroxydihydrosanguinarine 10-O-methyltransferase (E.C. 2.1.1.119), molecular weight 49 000 and optimum pH 8.5 is highly specific, forming dihydrochelirubine [K777].

Glycyrrhiza echinata licodione 2′-O-methyltransferase (E.C. 2.1.1.65) is specific for the *o*-hydroxyl group; another substrate is isoliquiritigenin, but other compounds are poor substrates [K886].

Lentinus lepideus enzyme O-methylates the methyl esters of *p*-coumaric and sinapic acids, but is inactive towards the acids themselves and the corresponding methyl benzoates [A214].

Lotus corniculatus flower bud enzyme, pI 5.5 and optimum pH 7.9 or 8.1, acts on the 8-position of 8-hydroxykaempferol and 8-hydroxyquercetin (E.C. 2.1.1.88). The enzyme contains a labile thiol group and requires S-adenosylmethionine, Mg^{2+}; EDTA is inhibitory [C905, D904].

Yellow lupin root isoflavone 5-O-methyltransferase, molecular weight 55 000, pI 5.2 and optimum pH 7, requires S-adenosylmethionine, but not Mg^{2+}. Substrates include genistein, derrone, 2′-hydroxygenistein, the 8-prenyl analogues 2,3-dehydrokievitone (best), lupiwighteone, and exhibit some activity towards caffeate and 2′-hydroxy-3′-prenylgenistein [F182].

Medicago sativa isoflavone 7-O-methyltransferase acts on daidzein, genistein and other analogues [G322].

Ocimum basilicum (basil) SAM: chavicol O-methyltransferase (SAM: allylphenyl O-methyltransferase), optimum pH 7.5, acts on chavicol but not eugenol, with high activity almost exclusively in young leaves. Another cultivar shows activity towards both chavicol and eugenol [K692].

Parsley culture S-adenosymethionine: xanthotoxol and bergaptol methyltransferases (E.C. 2.1.1.70 and 2.1.1.69 respectively) form xanthotoxin and bergapten respectively [D983].

Pimpinella anisum S-adenosylmethionine: anol O-methyltransferase acts on anol, an obligatory intermediate in the formation of epoxypseudoisoeugenol 2-methylbutyrate. Other substrates include eugenol, chavicol, dihydroanol and vanillin, but *p*-methoxycinnamyl alcohol, *p*-coumarate and *p*-coumaryl alcohol are not substrates [J188].

Pisum S-adenosylmethionine: 6a-hydroxymaackiain 3-O-methyltransferase is composed of two isozymes, molecular weights 43 000 and 66 000 and pI 4.9 and 5.2, respectively, with optimum pH 7.9 [F396].

Prunus flavonoid 7-O-methyltransferase, molecular weight 36 000, pI 4.1 and optimum pH

7.5, acts on sophoricoside, genistein and quercetin [G982].

Rice (Oryza sativa) flavone 7-O-methyltransferase acts on naringenin, apigenin, luteolin and kaempferol as well as caffeate; isoflavones are not substrates. The enzyme is only found in UV-irradiated plants [J190].

Robinia pseudoacacia seedlings and other plant parts contain apigenin 4′-O-methyltransferase (E.C. 2.1.1.75), optimum pH 9.0; it forms acacetin [C100].

Ruta graveolens enzyme, molecular weight 85 000–110 000 (more than one enzyme?) is specific for the 5 and 8 positions of bergaptol and analogues. The substrates studied were bergaptol, xanthotoxol, 5-hydroxyxanthotoxin (optimum pH 7.3–8) and 8-hydroxybergapten (optimum pH 8.5–9) [A3572].

Silene pratensis isoorientin 3′-O-methyltransferase (E.C. 2.1.1.78) forms isoscoparin [C351].

Thalictrum bulgaricum 12-hydroxydihydrochelirubine 12-methyltransferase (E.C. 2.1.1.120) is specific, forming dihydromacarpine; it is probably cytosolic. A 10-methyltransferase is also found [K776].

Thalictrum minus S-adenosylmethionine: norcoclaurine 6-O-methyltransferase is a dimer, molecular weight 72 000, pI 4.3 and optimum pH 9.0, and is inhibited by S-adenosylhomocysteine [H578].

Tinospora cordifolia and a number of other plant genuses contain (*R*,*S*)-norcoclaurine 6-O-methyltransferase (E.C. 2.1.1.128) [H629].

c. Microorganisms

Aspergillus parasiticus demethylsterigmatocystin O-methylase (E.C. 2.1.1.109), molecular weight 150 000, monomeric molecular weight 43 000, pI 4.4 and a broad optimum pH 6.5–9, appears to methylate dihydrodemethylsterigmatocystin as a second substrate [J511]. The enzyme is composed of two types of subunit and requires S-adenosylmethionine [E964] to catalyze a key reaction in the formation of aflatoxins. It is inhibited by thiol-binding reagents and heavy metals [K266]. Sterigmatocystin 6-O-methylase (E.C. 2.1.1.110) is also found [K732].

Aspergillus terreus emodin O-methyltransferase is probably a hexamer, molecular weight 332 000, pI 4.4 and optimum pH 7–8 that requires S-adenosylmethionine to form questin. It is highly specific [G633], but the close analogues, catenarin, ω-hydroxyemodin and 2-chloroemodin are also substrates, all with S-adenosylmethionine as co-substrate [C334].

Mycobacterium O-methylates pentachlorophenol, tetrachloroquinol and tetrachlorocatechol [A3330, D137].

A Phanerochaete chrysosporium O-methyltransferase, a homodimer, molecular weight 71 000, requires S-adenosylmethionine. It acts on isovanillate, protocatechuate, *m*-hydroxybenzoate, gallate and several other hydroxybenzoates, specifically methylating at the *meta* position [J339].

A Phanerochaete chrysosporium enzyme is monomeric, molecular weight 53 000 with optimum pH 7–9. A series of potential simple phenolic substrates has demonstrated a structural requirement for an *ortho* or *para* substituent for significant activity, but not all compounds with this structure are substrates [G782].

Rhodococcus chlorophenolicus O-methylates several halogenated quinols [E761].

Saccharomyces cerevisiae hexaprenyl dihydroxybenzoate methyltransferase (E.C. 2.1.1.114) acts on 3-hexaprenyl-4,5-dihydroxybenzoate and S-adenosylmethionine; the nucleotide sequence has been determined [K781].

Iodophenol O-methyltransferase (E.C. 2.1.1.26)

The reference provided supporting this E.C. numbered reaction is incorrect; it has not been possible to find alternative bibliography.

Hydroxyindole O-methyltransferase (E.C. 2.1.1.4)

This enzyme catalyzes an essential step in the formation of the pineal hormone melatonin from N-acetylserotonin, which, among other activities, is involved in controlling the biological clock in vertebrates.

Both beef and chicken pineal enzymes are dimeric, monomeric molecular weight 39 000. They differ in specificity, electrophoretic properties and antibody reactions. Serotonin and bufotonin are poor substrates; the enzyme is subject to substrate inhibition by N-acetylserotonin (mM range) [C522]. Another study with beef enzyme indicated that the native enzyme is a mixture of polymeric forms, optimum pH 8.1 [A3834].

Beef and rat pineal enzymes are inhibited by pyridoxal phosphate, apparently by forming an inactive Schiff base with L-S-adenosylmethionine that interacts with the enzyme. The inhibition is competitive with S-adenosylmethionine and non-competitive with N-acetylserotonin. Inhibition by pyridoxal phosphate is abolished by 10^{-4} M noradrenaline [A803, A2493]. The enzyme also methylates 17β-oestradiol at position 3 [A3339].

Chick pineal enzyme at 15 days age showed an activity rise with age faster in illuminated animals than in those kept under dark conditions, but those exposed to normal diurnal lighting showed an intermediate rate of increase, but without a diurnal rhythm in enzyme activity [A249].

Trout retina enzyme has optima at pH 7.6 and 8.4 [D30]. In steelhead trout the activity increased during the dark period (pre-midnight – 4 a.m.), and then declined steadily by 50 per cent during the day [A1485].

Tocopherol O-methyltransferase (E.C. 2.1.1.95)

Capsicum chromoplast membranes convert γ-tocopherol into α-tocopherol; the reaction requires S-adenosylmethionine [D580].

O-Demethylpuromycin O-methyltransferase (E.C. 2.1.1.38)

Streptomycin alboniger enzyme, optimum pH 8, is highly specific and requires S-adenosylmethionine [K846].

Tetrahydrocolumbamine 2-O-methyltransferase (E.C. 2.1.1.89)

Berberis aggregata enzyme requires S-adenosylmethionine to form tetrahydropalmatine; it is highly specific [K947].

(*S*)-Scoulerine 9-O-methyltransferase (E.C. 2.1.1.117)

Berberis enzyme, molecular weight 63 000 and optimum pH 8.9, acts on (*S*)-scoulerine to form (*S*)-tetrahydrocolumbamine, by methylation at position 9 [D581].

Methylation of tertiary alcohol

Dog, monkey, baboon and man O-methylate 1,1-dimethyl-2-(4-(α,α,β,β-tetrafluoroethyl) phenyl)ethanol. This is claimed to be the first report of tertiary alcohol methylation [A3021].

Methylation of *gem*-diol

Rat forms 9-hydroxy-9-methoxycicloprofen from cicloprofen [A2353].

Methylation with methyl chloride

Phanerochaete chrysosporium acts on isovanillate to form veratryl alcohol, probably with veratrate as the intermediate. S-Adenosylmethionine is not the methyl donor; the best donor is methyl chloride, which may be formed from methionine [J237].

Phellinus pomaceus O-methylates phenol, with chloromethane as co-substrate [G208].

Formation of polyphenoxyphenols

Rhizoctonia praticola extracellular laccase catalyzes a series of complex reactions between syringate and pentachlorophenol or any of a

number of polychlorinated phenols, as substrates. Although the structures of the products were not fully characterized, some were *para*-linked polyphenoxyphenols and others appeared to be *o*-quinones, although the mass spectral data were equivocal for some quinones. The products with syringate and pentachlorophenol were 2,6-dimethoxy-4-pentachlorophenoxyphenol and 4-pentachlorophenoxypoly(2,6-dimethoxyphenoxy)-2,6-dimethoxyphenol, where 'poly' is one, two or three units, depending on the substrate mixture. Syringate and 2,4,5-trichlorophenol form 5-(2,4,5-trichlorophenoxy)-3-methoxy-*o*-quinol [D690].

5.8 *N-Alkylation*

N-Methyltransferases

a. Phenylethanolamine N-methyltransferase (PNMT; E.C. 2.1.1.28)

This enzyme is essential for the formation of the catecholamine hormone adrenaline.

Human and monkey enzymes are found in most brain areas. In monkey brain there was a range of one order of magnitude in activity between different areas, with little in the frontal cortex and cerebellum. In human brain the activity was similar to that in monkey brain areas, with little in the frontal cortex or mamillary bodies [A2823]. Human and rabbit adrenal enzymes act on noradrenaline, normetanephrine, phenylethanolamine, 3,4-dichlorophenylethanolamine and 3,4-dichlorophenylethylenediamine. They are inhibited by α-methylphenethylamines with a range of small substituents on the aromatic nucleus. The affinity is almost identical for enzymes from both species [A498].

Beef adrenal medulla enzyme, molecular weight 30 000, is composed of four isozymes, pI 5.1, 5.2, 5.3 and 5.4 [E397]. In contrast to rat adrenal, beef adrenal enzyme is strongly activated by inorganic phosphate and, to a lesser extent by chloride and sulphate at 200 mM [D294]; in contrast another study claimed that it is inhibited 60 per cent by 75 mM NaCl [A1685], as well as by a series of substrate analogues, especially phenylethanolamines, but not competitively [A1643]. It is present in only some cells [A1409].

Beef brain isozymes, molecular weights 32 000 and 65 000, are possibly a monomer and dimer, with optimum pH 8–9, depending on substrate. Substrates include normetanephrine, octopamine, metanephrine, *p*-sympatol, noradrenaline and adrenaline, with the reaction rate reduced by about 80 per cent for the monomethyl substrates. In some cases there is substrate inhibition [A1463].

A dog liver enzyme, not found in monkey or rat liver, requires S-adenosylmethionine as co-substrate, but not 5-methyltetrahydrofolate. It acts on 7,8-dichlorotetrahydroisoquinoline (best), with optimum pH 8.0. Other substrates include epinine, dopamine, adrenaline and (poor) noradrenaline, phenethylamine and phenylethanolamine, but not indolamines [C657].

Rabbit adrenal enzyme has many properties in common with human enzyme (see above) [A498]. It is inhibited by 2-aminotetralins, and by 2,3,4,5-tetrahydro-1*H*-2-benzazepines substituted with one or more chloro groups on the aromatic moiety [A1851, A3443].

Rat brain activity is low at birth, and then starts to increase at three days until at two weeks post partum it reaches 10 times the adult level [A2665]. It is found primarily in the medulla oblongata with lesser amounts in locus ceruleus, basal hypothalamus and some other areas, but not in cerebellar cortex, hippocampus or olfactory bulb [A2823]. Brain and adrenal enzymes are inhibited by 1,2,3,4-tetrahydroquinoline-7-sulphonamide at 10^{-6} M [A3439].

Rat stomach exhibits this activity [H620], as do rat retinal neurones [E253]. Adrenal enzyme forms a transient ternary complex with S-adenosylmethionine during the methylation step [A623]. Adrenal enzyme is composed of two isozymes, molecular weight 37 000; they are not interconvertible [A144].

b. Arylamine/2-substituted ethylamine N-methyltransferases

Human brain cytosolic enzyme, optimum pH 8.25, methylates 1,2,3,4-tetrahydroisoquinoline

with S-adenosylmethionine as co-substrate [F228].

Rabbit liver isozymes (E.C. 2.1.1.49), molecular weight 30 000, pI 4.9 and 5.1 show slightly different kinetics towards a wide range of substrates, including tryptamine and substituted tryptamines, phenethylamine and amphetamine, anilines, benzylamine, heterocyclic amines, including tetrahydroquinoline and tetrahydroisoquinoline, and DMI [A1311, C156, E6]. Another study found the enzyme to be monomeric, molecular weight 27 000, pI 4.8 and optimum pH 7.5. Its amino acid composition has been determined. It acts on a range of anilines and tryptamines with S-adenosylmethionine as co-substrate, but tyramine, indole and benzylamine are not substrates. The mechanism appears to be rapid equilibrium random bi-bi [C333].

Rabbit lung indoleamine N-methyltransferase is monomeric, molecular weight 31 500 and optimum pH 7.9, with tryptamine as substrate. It is activated by dithiothreitol [C111].

Rabbit and human lung indoleamine N-methyltransferases (E.C. 2.1.1.4) act on N-methyltryptamine. Rabbit enzyme in particular is strongly inhibited by 2,3,4,6,7,8-hexahydropyrrolo[1,2-*a*]pyrimidine [A1662]. Rabbit lung enzyme, which acts on tryptamines and N-methyltryptamines, is inhibited by several N,N-dimethyltryptamines and by S-adenosylhomocysteine [A106]. This lung enzyme is not found in guinea pig or rat [A115].

Rabbit lung and rat lung enzymes N-methylate tryptamine, N-methyltryptamine, serotonin and N-methylserotonin, with S-adenosylmethionine or 5-methyltetrahydrofolate as co-substrate [A111].

Rat brain enzyme requires N-methyltetrahydrofolate as co-substrate. Indoleamines, phenethylamines, octopamine and other phenylethanolamines are substrates; one product is N,N-dimethyltryptamine [A1307, A1311]. The optimum pH is about 6.4, and may be modified by metabisulphite. The reaction rate is highest for primary amines and least for tertiary amines, if they react at all. The molecular weight is much higher than for COMT; catechols are not substrates [A80, A1310].

Rat liver benzyltetrahydroisoquinoline methyltransferase, molecular weight 27 500 and optimum pH 7.7–8.0, acts on tetrahydropapaveroline and requires S-adenosylmethionine as co-substrate. The context suggests that it is an 'ordinary' N-methyltransferase. Inhibition is brought about by pyrogallol, N-ethylmaleimide and *p*-chloromercuribenzoate [A53].

Rat skin enzyme, which methylates dopamine and noradrenaline, is different from PNMT although noradrenaline is a substrate [F622]. It also occurs in some organs after denervation, which should eliminate PNMT [E867].

Tinospora cordifolia enzyme, a monomer, molecular weight 85 000 and optimum pH 8.6, N-methylates (*S*)-norcoclaurine and (*S*)-coclaurine, but not the (*R*)- isomers. Dicentra spectabilis enzyme shows the same stereospecificity, but Fumaria capreolata, Chonodendron tomentosum, Argemone platyceras, Papaver somniferum, Berberis stolonifera and B. juliana act on both (*R*)- and (*S*)-isomers [H629].

Tyramine N-methyltransferase (E.C. 2.1.1.27)

This activity is found in Opuntia [A3977]. The formation of hordenine in barley implies that the same reaction occur in that species.

β-Carboline 2-N-methyltransferase

Beef brain cytosolic enzyme, optimum pH 8.5–9, is activated by Fe or Mn salts. The substrates are 9-methylnorharman and S-adenosylmethionine [H949].

N-(1(*R*)-(carboxyl)ethyl)-(*S*)-norvaline: NAD^+ oxidoreductase (L-norvaline forming)

Arthrobacter enzyme forms secondary amines with pyruvate as amine acceptor. As well as phenylalanine and phenylalaninol a range of aliphatic amino acids are substrates to form the corresponding N-(1-(*R*)-(carboxyl)ethyl)-(*S*)-

amino acids. Primary amines and amino acid esters are not substrates [J212].

Methyleneimine formation

Rat brain converts phenethylamine into methylene-β-phenylethylimine, with 5-methyltetrahydrofolate as methylene donor; the reaction is considered to be enzymatic [A2285], although the product is the Schiff base that is spontaneously formed with formaldehyde.

Formimino transfer

An enzyme found in a range of mammalia and organs acts on tetrahydrofolate and formimino-L-glutamic acid to form 5-formiminotetrahydrofolate [K937]

Quaternary amine formation

Rabbit liver S-adenosylmethionine N-methyltransferase acts on a range of pyridines, including 2-, 3- and 4-phenylpyridines, 3-benzylpyridine, 7-azaindole, quinoline, isoquinoline and quinoxaline [E824].

S-Adenosylmethionine: (*S*)-tetrahydroberberine N-methyltransferase is found in Corydalis vaginans, Berberis stenophylla, Dicentra spectabilis, Fumaria officinalis and Papaver somniferum. C. vaginans enzyme, molecular weight 72 000 and optimum pH 8, acts on (*S*)-stylopine and canadine; it is specific for (*S*)-isomers [E299].

Tetrahydropteroylglutamate methyltransferase

Rat liver enzyme, optimum pH 6.7, acts on 5-methyltetrahydropteroylglutamate and 5-methyltetrahydropteroylpentaglutamate with L-homocysteine as co-substrate to form methionine and the demethylated glutamates [A2502].

Phaseolus vulgaris enzyme, molecular weight 40 000 and optimum pH 6.5, catalyzes the reaction anaerobically [A3085].

N,N-Dimethyladrenaline formation?

A study on retinal catecholamines tentatively identified the presence of N-methyladrenaline [A8]; further tests showed that the chromatographic standard used was in fact N,N-dimethyladrenaline, raising the possibility that quaternary catecholamines may be physiologically important in animals.

N-Ethylation

Man, rat and rabbit have been claimed to form N-ethyl-N-demethylmianserin from mianserin; the data presented are equivocal [B610].

N-(β-N-Acetylglucosaminide) formation

This reaction has been found in monkey, with delaviridine as substrate [J275].

5.9 *Silane anhydrides formation*

Goat acts on bis(*p*-fluorophenyl)methyl(1*H*-1,2,4-triazole-1-ylmethyl)silane to form oxy(bis(bis(*p*-fluorophenyl)(methyl)(silane))) [K144].

6. Elimination of substituents

6.1 *Ester hydrolysis*

Arylesterase (E.C. 3.1.1.2)

$$ArOOCR + H_2O \rightarrow ArOH + RCOOH$$

A human serum enzyme, molecular weight about 43 000 and pI 5.1, is a glycoprotein, with phenyl acetate and paraoxon as substrates [F717]. Liver aspirin esterase (E.C. 3.1.1.55) has an optimum at pH 5–6.5 [C779]. Erythrocyte aspirin esterase is an intracellular cytosolic enzyme, molecular weight 95 000. It appears to be different from 'nonspecific' esterases [C705]. Lens isozymes (molecular weights 200 000 and 30 000) hydrolyze 4-methylumbelliferyl palmitate [J233]. Liver microsomes hydrolyze *p*-nitrophenyl acetate, propionate and butyrate [H465]. Plasma heroin hydrolase is an arylesterase, optimum pH about 7.5, which also acts on *p*-nitrophenyl acetate and *p*-nitrophenyl laurate, but not on *p*-nitrophenyl phosphate [A798, G251].

Rat liver aspirin hydrolase is equally divided between cytosol and particulate fractions. Two soluble isozymes, molecular weight 35 000 (serine esterases) and three high molecular weight enzymes (molecular weight about 220 000) with different immunological properties from the low molecular weight esterases have been detected. The serine esterases both act on 4-methylumbelliferyl acetate and substituted phenyl and naphthyl acetates. Butyrate esters are also hydrolyzed, but caprylate esters only poorly. 4-Acetoxybenzoate is also hydrolyzed [F753]. pH optima are at 5.5 and 7.4 [C779]. Apomorphine is formed from its dipropionyl, diisobutyryl and dipivaloyl esters. Activity is found in most tissues, especially plasma, where activity is 10 times greater than in human plasma [A2013]. Rat liver hydrolyzes phenyl acetate; two enzyme fractions were identified, both with optimum pH 8.5 and a requirement for Ca^{2+}; they exhibit slight stability differences at 35–40°. One was identified as paraoxonase and the other as arylesterase [K194].

In both rat and mouse aspirin esterases I and II are found in all tissues, especially liver and kidney [H921].

Mouse liver aspirin esterase has an optimum at pH 7.4 [C779]. Two isozymes are found in liver and kidney [K148].

Beef plasma phenyl acetate hydrolase (E.C. 3.1.1.2; molecular weight 440 000) activity is markedly reduced by solvent extraction; it may be a lipoprotein [A2388].

Cat liver aspirin esterase has a broad optimum at pH 8 [C779]. Serum hydrolyzes 1-naphthyl acetate, *p*-nitrophenyl acetate, propionate and butyrate. Some of the isozymes do not hydrolyze 1-naphthyl acetate. The major isozyme has an optimum at pH 7.8 [A1598].

Dog liver and kidney enzyme has been separated by electrophoresis into nine bands of activity that hydrolyze 1-naphthyl acetate, and *p*-nitrophenyl acetate, propionate and butyrate. The major bands (optimum pH 7.8) are non-specific carboxylesterases [A868].

Guinea pig liver microsomal carboxylesterase, monomeric molecular weight 55 000 and optimum pH 8, is specific for salicylates with acyl chain length two (aspirin), three, four, five, six, eight and 10. Substrate inhibition is observed with increasing chain length. Thioaspirin and 1-naphthyl acetate are also substrates. It is very sensitive to inhibition by the carboxylesterase inhibitor bis(*p*-nitrophenyl)phosphate [D144]. Cerebral cortex enzyme is composed of two isozymes, optimum pH 7.6, molecular weights 78 000 and 180 000, and pI 5.1 and 5.8 respectively. They are specific in requirement for Mn^{2+}; other divalent cations are inhibitory [K861].

Hamster liver microsomal N,O-acetyltransferase hydrolyzes *p*-nitrophenyl acetate [G744].

Pig pancreas *p*-nitrophenyl acetate hydrolase (a lipase) forms an acetyl lipase as an intermediate [A333]. Liver aspirin esterase, molecular weight 160 000, has an optimum at pH 7.4 [E259].

Rabbit serum arylester hydrolase, molecular weight 150 000–200 000, monomeric molecular weights 40 000–45 000 and 47 000–54 000, which also acts on paraoxon, requires Ca^{2+} [E25]. It also hydrolyzes *p*-nitrophenyl acetate and butyrate [E26]. Rabbit gastric mucosal enzyme is cytosolic, molecular weight 66 000 or 59 000 (depending on method) and optimum pH 8.6 [A3910].

Chicken liver microsomal enzyme, optimum pH 8.6, which is highly specific for α-tocopheryl acetate, requires bile salts [B132].

A general study on birds and mammals detected phenyl acetate-hydrolyzing arylesterase in serum from badger, capybara, cat, goat, mouse, ox, pig, rabbit, rat, rabbit, sheep, bee eater, Canada geese, chicken, cormorant, great tit, guillemot, Japanese quail, mute swan, pigeon, puffin, razorbill, shag, starling, tree sparrow, and in trout. All the mammals (except capybara) also showed paraoxonase activity [K863].

Moniezia expansa and Ascaris lumbricoides aspirin hydrolases, molecular weight 87 000, have optima at pH 7.0. Activity is enhanced by Ca^{2+} and by low molecular weight thiols, but Cd^{2+}, Cu^{2+}, Hg^{2+}, La^{3+}, Zn^{2+}, *p*-chloromercuribenzoate, EDTA, F^-, N-ethylmaleimide, and paraoxon are inhibitory. 2-Naphthyl acetate and 4-methylumbelliferyl acetate are hydrolyzed by enzyme, molecular weights 30 000–300 000; this range suggests that it is a mixture [A3040].

Festuca pratensis leaf naphthyl acetate esterase is composed of five isozymes, molecular weight 55 000. During senescence two additional esterases appear, with the same molecular weight. They do not act on a series of aliphatic esters [A2515].

Petroselinum crispum leaf malonyl esterases, monomeric molecular weight 35 000, exhibit pI 3.8, 3.9, 4.0 and 4.05; all are dimers, except the 'pI 3.8' enzyme, which is monomeric. It acts on 1-naphthyl acetate and propionate; it also forms apigenin-7-O-(6-O-malonylglucoside) from apigenin-7-O-glucoside [C721].

Acinetobacter lwoffii hydrolyzes a large range of phenyl esters including salicylates, *p*-nitrophenyl acetate and higher esters, acetoxybenzoates, diacetoxybenzoates and naphthyl acetates [A962].

Aspergillus oryzae enzyme, molecular weight 35 000, hydrolyzes *p*-nitrophenyl acetate, propionate and butyrate, with the reaction rate decreasing with increasing molecular weight [J389].

Saccharomyces cerevisiae enzyme, a dimer, molecular weight 84 000 and optimum pH 8.0 is moderately stable at 70°. Substrates are 1- and 2-naphthyl esters of fatty acids with 2–10 carbon atom chain [E258].

Yeast (species not stated) carboxypeptidase hydrolyzes *p*-nitrophenyl trimethylacetate [A337].

Glutamate dehydrogenase (from an unspecified source) hydrolyzes 3-acetyloestrone and 3-acetyl-2-nitrooestrone, with a proportion of the acetyl group being incorporated into the enzyme, inactivating it. It is inhibited by ADP, GTP, NADH and especially oestrone, suggesting that hydrolysis takes place at the oestrogen-binding site [A2004].

Megachile rotundata (solitary bee) [F887], bee [G551] and Chromobacterium [A1808] hydrolyse *p*-nitrophenyl acetate.

Arylesterase (carboxylesterase type; E.C. 3.1.1.1)

$$ArCOOR + H_2O \rightarrow ArCOOH + ROH$$

Rabbit serum cocaine esterase (E.C. 3.1.1.1) has an optimum pH of 8.9 [A2507].

Raphanus sativus (radish) sinapine esterase (E.C. 3.1.1.49), which is specific for sinapine, has an optimum at pH 8.5. The products are sinapate and choline. It is not affected by normal esterase inhibitors, such as eserine [B263].

Orsellinate-depside hydrolase (E.C. 3.1.1.40)

Lasallia pustulata (lichen) enzyme, molecular weight 42 000 is composed of four isozymes, stable at 57°. Substrates include lecanoric acid, evernic acid, gyrophoric acid, methyl lecanorate and erythrin [K862].

Aralkyl esters

Rabbit serum atropine esterase, optimum pH 8.9, additionally acts on scopolamine. It is different from the enzyme that hydrolyzes cocaine [A2507].

Streptomyces ferulate esterase hydrolyzes methyl ferulate. There are two components, molecular weight 29 000, optimum pH 5.5, pI 7.9 and 8.5 [G363].

Microorganisms can hydrolyze phenyl-substituted *trans*-2-(alkoxycarbonylethyl)lactams, with the removal of the alkyl group [K110].

Feruloyl esterase

A. niger contains two isozymes, molecular weights 132 000 and 29 000, pI 3.0 and 3.6 respectively, which hydrolyze methyl ferulate and methyl *p*-coumarate. Methyl sinapate is hydrolysed only by the second isozyme and methyl caffeate only by the first isozyme [G915].

Penicillium expansum enzyme, molecular weight 65 000 and optimum pH 5.6, acts on methyl *p*-coumarate, methyl ferulate, and *p*-coumarate and ferulate esters of glycosides [J499]. P. pinophilum enzyme has molecular weight 57 000, pI 4.6 and optimum pH 6.0 [G805].

Neocallimastix enzyme is a dimer, molecular weight 11 000, monomeric molecular weight 5800, pI 4.7 and optimum pH 7.2, which hydrolyses a number of glycoside *p*-coumaroyl esters [G327].

Aspergillus awamori enzyme acts on α-naphthyl esters of acetic, propionic and butyric acids, but activity with the valerate ester is marginal [J831].

Tannase (E.C. 3.1.1.20)

Aspergillus niger enzyme hydrolyzes tannin, chebulinic acid, *m*-digallic acid, methyl gallate and methyl protocatechuate; hydrolysis requires at least two hydroxyls (other than *ortho*) in the acid component of the substrate. It is found only in plants, especially in plant galls rich in tannin, and in bacteria and fungi grown on tannin [K710].

Methylumbelliferyl acetate deacetylase (E.C. 3.1.1.56)

Human erythrocyte enzyme (called esterase D) additionally hydrolyzes the butyrate analogue. It is composed of three electrophoretically separated types determined by two autosomal alleles (one uncommon). It is relatively stable, and was found in all tissues examined, including liver, spleen and fibroblast [K712].

Heroin esterase

Human serum hydrolyzes heroin to 6-acetylmorphine; the only serum esterase that acts on heroin is cholinesterase [B213]. Heroin is hydrolyzed by a plasma arylesterase, optimum pH about 7.5, which also acts on *p*-nitrophenyl acetate and *p*-nitrophenyl laurate, but not on *p*-nitrophenyl phosphate [A798].

Sugar acetates

The Aspergillus oryzae enzyme (Taka diastase) that hydrolyzes *p*-nitrophenyl acetate also hydrolyzes the acetyl groups in polyacetylated oligosaccharide phenolic conjugates [J389].

Chlorogenate hydratase (E.C. 3.1.1.42)

Aspergillus niger enzyme is a tetramer, molecular weight 240 000, stability range pH 3.0–8.5, activation energy 6.0 kcal/mol and a broad optimum at pH 6.5, is composed of several isozymes,

pI 4.0–4.5. It is highly specific; there is slight activity on isochlorogenate. It has been crystallized and the amino acid composition determined [K909, K911].

Meperidine esterase

Rat liver microsomal enzyme, optimum pH 8–9.5 has a heat of activation of 4.6×10^6/mol, with the formation of meperidinic acid [C8].

Bis(2-ethylhexyl)phthalate esterase (E.C. 3.1.1.60) and related reactions

Many studies have demonstrated in animal species, although not at an enzyme level, that phthalate diesters are hydrolyzed stepwise. These include di-(*n*-butyl) phthalate, di-(cyclohexyl) phthalate, di-(9-decenyl) phthalate, di-(2-ethylhexyl) phthalate, di-(5-hexenyl) phthalate and dimethyl phthalate. These reactions have been observed in man [D360], rat, baboon, ferret [A1652, C869, G876], monkey [B579], beef [J718], rainbow trout [A1990], catfish [A2239], minnow, [A2798], earthworm [H9] and microorganisms [K248].

Rainbow trout dealkylates di-(2-ethylhexyl) phthalate. The reaction is inhibited by some methylenedioxy compounds at mM concentrations [A3710].

Wheat contains 12 esterases, only one of which, molecular weight 38 000 (subunit 22 000) acts on the above substrate, to remove one alkyl group. A far better substrate is *p*-nitrophenyl octanoate [D259].

Permethrinase

Bacillus cereus enzyme, molecular weight 61 000 and optimum pH 7.5 hydrolyzes permethrin and a series of α-cyano pyrethroids, fenvalerate, fluvalinate, fastac, deltamethrin, cyfluthrin, flucythrinate, tralocythrin, fenpyrithrin, tralomethrin, cyhalothrin and flumethrin, with release of *m*-phenoxybenzoate or 4-fluoro-3-phenoxybenzoate [G891].

Thiophenyl ester hydrolysis

Rabbit serum arylester hydrolase hydrolyzes phenylthioacetate, propionate and butyrate [E26]. Guinea pig microsomal carboxylesterase also catalyzes this reaction [D144].

CoA thioesterase

p-Hydroxybenzoyl CoA thioesterase (E.C. 3.1.2.23) is found in Corynebacterium sepedonicum [J178] and Pseudomonas [H645]. The latter is a homotetramer, monomeric molecular weight 16 000. It also hydrolyzes benzoyl CoA [K191]. This is the third step in the reaction sequence that converts *p*-chlorobenzoate into *p*-hydroxybenzoate [K798].

Arylsulphatases (E.C. 3.1.6.1)

$$\mathrm{Ar.O.SO_3^-} + \mathrm{H_2O} \rightarrow \mathrm{Ar.OH} + \mathrm{SO_4^{2-}} + \mathrm{H^+}$$

Beef liver sulphatase A is a glycoprotein, molecular weight 107 000 containing eight galactose, 14 mannose, 18 glucosamine and eight sialic acid residues. Neuraminidase removes the sialic acid residues, presumably terminal groups, with little effect on activity [A148]. Brain sulphatase B, a globular protein, molecular weight 60 000, has been separated into 7 fractions by ion-exchange chromatography [A921].

Beef retinal arylsulphatase A, molecular weight 100 000, exhibits optima at pH 4.6 and 5.7, and arylsulphatase B, molecular weight 40 000 has an optimum at pH 5.2 [B247].

Human liver arylsulphatase A is a glycoprotein, molecular weight 104 500 at pH 8.1, which is composed of two different subunits. At pH 5.5 a tetramer is formed [A2801]. Another study found a molecular weight of 134 000, and pI 4.7 [A2918] or 4.3 [A2457]. The heterodimer is composed of monomers, molecular weights variously assessed as 69 000 and 57 000, 66 000 and 53 000, or 59 000

and 49 000, but apparently they are not found in stoichiometric amounts. It is possible that the larger monomer is convertible into the smaller monomer [A2801, B221].

Human placenta arylsulphatase B is composed of three isozymes, optimum pH 5.8, and molecular weights 48 000, 60 000 and 71 500 [A595]. Brain enzyme, solubilized with lysolecithin, has an optimum at pH 6.8, and molecular weight 103 000–105 000, with subunits, molecular weights 25 000 and 47 000. It contains two mol of sialic acid, which is not essential for activity; 4-methylumbelliferyl sulphate is substrate [A942]. Liver arylsulphatase B, molecular weight 50 000, optimum pH 6.1 and pI 7.5, is inactivated by freezing. It hydrolyzes 4-nitrocatechol sulphate and *p*-nitrophenyl sulphate, and is only slightly inhibited by divalent cations [A2457].

Human placental arylsulphatase C is a homotrimer, molecular weight 238 000. It acts on 4-nitrocatechol sulphate and oestrone sulphate [E398].

Human arylsulphatase hydrolyzes both D- and L-tyrosine-4-sulphate at 5 per cent of the rate for nitrocatechol sulphate, with optimum pH 5.3–5.5 [A3839]. Enzyme found in amniotic fluid cells has an optimum pH of 5.0 [A551]. Parotid and submandibular saliva, tears and sweat contain arylsulphatase A, as does rat saliva [A2839].

Rabbit testis sulphatase A is a dimer at pH 7.1, molecular weight 110 000, and a tetramer at pH 5.0. The optimum pH is time dependent; it is 5.2 after five minutes incubation and 4.9 after 90 min. It acts on 4-nitrocatechol sulphate, but not on *p*-nitrophenyl sulphate [A2945]. Sperm enzyme may contain two components, the main one being composed of A and B, but not C, with optima at pH 4.8, 5.6 and 6.0. It acts on 4-nitrocatechol sulphate and *p*-nitrophenyl sulphate [A1145]. Liver sulphatase A, monomeric molecular weight 70 000, is a dimer at pH 7.4 and a tetramer at pH 4.8 [A1585].

Rabbit liver arylsulphatase A is a dimeric glycoprotein, molecular weight 140 000. The amino acid composition has been determined; it also contains 4.6 per cent carbohydrate (mannose, N-acetylglucosamine and sialic acid). 4-Nitrocatechol sulphate is a good substrate, with lower activity towards other substrates [B481].

Rabbit brain enzyme is found in all the subcellular fractions tested. Its activity remains nearly constant at 1/3 of the adult level from 12–30 days post partum [A1221].

Rat liver arylsulphatase IV (tyrosine ester type) has a molecular weight of 30 000 [H483]. Liver arylsulphatase A has an optimum pH of 4.9–5.9, depending on the assay conditions, molecular weight 130 000 at pH 7.5 and 400 000 at pH 5.0. Arylsulphatase B, molecular weight 34 000–66 000 and optimum pH 5.9, appears to be quite different from beef liver arylsulphatase B [A966]. Two rat isozymes, pI 4.0 (minor) and pI 6.4 are active towards 4-nitrocatechol sulphate; they are not heparin sulphamidases [A575]. Arylsulphatase A is found mainly in parenchymal cells, and arylsulphatase B in non-parenchymal cells. Both activities are also found in adrenal, brain, testis, spleen and kidney [A969]. Rat liver enzyme hydrolyzes both protocatechuate mono-O-sulphates [B724].

Rat mast cell enzyme has a molecular weight of 150 000 and optimum pH 5.0 [A2815].

Rat brain enzyme, which acts on 4-methylumbelliferyl sulphate, is found in neurones and glial cells [A512]. It has an optimum at pH 6.8 for 4-methylumbelliferyl sulphate, and pH 7.2 for *p*-nitrophenyl sulphate [A1050].

Sheep brain arylsulphatase A is a glycoprotein containing 25 per cent mannose and glucose, with 0.5 per cent sialic acid [A2374]. Arylsulphatase B is also a glycoprotein [A2068].

Chicken embryo brain activity increases from day 14 to day 18, and then remains steady until hatching [A836].

Helix pomatia enzyme acts on a range of polysulphated flavonoids. Sulphates at positions 4′ and 7 are far more susceptible to hydrolysis than 3-sulphates, which enables the 3-sulphates to be prepared by differential hydrolysis. Quercetin-3,4′,7-tri-O-sulphate yields quercetin-3,4′-di-O-sulphate and quercetin-3,7-di-O-sulphate as intermediates [F102].

Cystoseira tamariscifolia (seaweed) enzyme, molecular weight 166 000 and optimum pH 6.1, hydrolyzes the sulphates of *p*-nitrophenol,

4-nitrocatechol and phloroglucinol. Activity is also found in Fucus, Carpophyllum, Himanthalia, Landsburgia and Sargassum species [G819].

Aspergillus oryzae arylsulphatase II is a homodimer, molecular weight about 95 000 and optimum pH 5.5 [A146]. A. sojae alkaline arylsulphatase III has an optimum at pH 8.5. It is stable at 20° between pH 8 and 10, acts on *p*-nitrophenyl sulphate, and is inhibited by Ag^{+}, Hg^{2+}, Zn^{2+}, borate and fluoride. A. awamori enzyme shows similar properties [B317].

Cyanobacterium plectonema enzyme, which hydrolyzes nitrocatechol sulphate is cytosolic, with optimum pH about 10. It does not require cations for activity [E179].

Comamonas terrigena tyrosine sulphate sulphohydrolase, which exists as two isozymes, is separated electrophoretically from arylsulphatase. One is inducible by tyrosine, and the other is probably constitutive [B159].

Klebsiella enzymes have molecular weights 47 000 and 45 000, with optimum pH 7.5 [A2776].

Streptomyces griseorubiginosus enzyme, molecular weight 45 000, pI 4.95 and optimum pH 8.5, requires Ca^{2+} for the hydrolysis of etoposide-4′-sulphate and *p*-nitrophenyl sulphate [H603].

Glutamate dehydrogenase (E.C. 1.4.1.3 and 1.4.1.4)

This enzyme hydrolyses 3-acetoxy-2-nitrooestrone and 3-acetoxyoestrone, the acetyl group being incorporated into the enzyme molecule, with inactivation. It is inhibited by ADP, GTP, NADH and, especially, oestradiol [A2004].

Nitrate ester hydrolysis

Dog and rat hydrolyze side-chain nitrate esters of a potential calcium-channel blocker [G593].

6.2 *Hydrolysis of glycosides*

β-N-Acetylgalactosaminidase

Human amniotic fluid cell enzyme, which acts on 4-methylumbelliferyl-β-N-acetylgalactosaminide has an optimum pH of 3.6 [A551].

Rat brain enzyme, which hydrolyzes the same substrate, is found in neurones and glial cells [A512].

Rabbit brain enzyme activity increases about threefold from six days gestation to birth, and is then near the adult level [A1221].

Sheep liver enzyme, optimum pH between 5 and 7, is unstable above 50° [B500].

Physarium polycephalum contains two isozymes that act on both 4-methylumbelliferyl-β-N-acetylgalactosaminide and 4-methylumbelliferyl-β-N-acetylglucosaminide [A23].

β-D-N-Acetylglucosamidase

Beef liver enzyme hydrolyzes phenolic substrates substituted with nitro, chloro, hydroxyl, methyl and methoxy groups on the aromatic nucleus [A1940]. It also hydrolyzes 17α-oestradiol-17-β-D-N-acetylglucosamide [A3192].

Human amniotic fluid cell enzyme, optimum pH 4.6, acts on 4-methylumbelliferyl-β-D-N-acetylglucosamide [A551]. Epidermis enzyme, optimum pH 3.7–3.9, hydrolyzes 4-methylumbelliferyl-β-D-N-acetylglucosamide and *p*-nitrophenyl-β-D-N-acetylglucosamide, [A642]. Activity is found in leucocytes [A789] and in urine [A1845].

Rabbit brain enzyme activity rises about threefold from six days gestation to birth, to near the adult level [A1221].

Rat brain enzyme is found in neurones and glial cells, and hydrolyzes 4-methylumbelliferyl-β-D-N-acetylglucosamide [A512].

Sheep liver enzyme, optimum pH between 5 and 7 is unstable above 50° [B500].

Physarium polycephalum contains two isozymes that hydrolyze both 4-methylumbelliferyl-β-N-acetylgalactosaminide and 4-methylumbelliferyl-β-N-acetylglucosaminide [A23].

α-L-Arabinosidase

Penicillium wortmannii extracellular xylosidase (see below) hydrolyzes *p*-nitrophenyl-α-L-arabinopyanoside [A3240].

α-L-Fucosidase

Human epidermis enzyme acts on *p*-nitrophenyl-α-L-fucoside [A642]. The enzyme is also found in urine [A1845].

Rabbit brain enzyme activity increases marginally during gestation, to about the adult level [A1221].

β-D-Fucosidase

Human epidermis enzyme hydrolyzes *p*-nitrophenyl-β-D-fucoside [A642].

Secale cereale β-glucosidase hydrolyzes the same compound [K512].

α-D-Galactosidase (c.f. E.C. 3.2.1.22)

Human amniotic fluid cell enzyme, optimum pH 4.2, hydrolyzes 4-methylumbelliferyl-α-D-galactoside [A551]. Epidermis enzyme, optimum pH 3.7, hydrolyzes 4-methylumbelliferyl-α-D-galactoside and *p*-nitrophenyl-α-D-galactoside [A642]. Activity is also found in leucocytes [A789].

Rat brain enzyme is found in neurones and glial cells, and hydrolyzes 4-methylumbelliferyl-α-D-galactoside [A512].

Castanea sativa (sweet chestnut) seed contains two isozymes, molecular weights 215 000 and 53 000, pH optima 4.5 and 6, respectively, which hydrolyze *p*-nitrophenyl-α-D-galactoside much more effectively than oligosaccharides. The smaller isozyme is the main one in fresh seeds, but the larger one is the major one in 14 week old dry seeds [B759].

Activity in pea embryo increases during germination, but little change is found in cotyledon. Pisum elatus enzyme has a broad optimum pH at 3–5.5, and P. sativum at pH 3–7 [A3137].

Poteriochromonas malhamensis enzyme, molecular weight 360 000 and optimum pH 7, has maximal stability at pH 8. Substrates are *p*-nitrophenyl-α-D-galactoside and 4-methylumbelliferyl-α-D-galactoside [B486].

Secale cereale β-glucosidase hydrolyzes *p*-nitrophenyl-β-galactoside [K512].

Bacillus stearothermophilus contains two isozymes, molecular weights 280 000 and 325 000. Both appear to be homotetramers, and hydrolyze *p*-nitrophenyl-α-D-galactoside [B544].

2- And 6-deoxy-*p*-nitrophenyl-α-galactoside, but not 3- or 4-deoxy-*p*-nitrophenyl-α-galactoside, are hydrolyzed by enzyme from Coffea, Mortierella vinacea and A. niger [K437].

β-D-Galactosidase (c.f. E.C. 3.2.1.23)

Human amniotic fluid cell enzyme, which hydrolyzes 4-methylumbelliferyl-β-D-galactoside has an optimum pH of 3.6 [A551]. Epidermis enzyme hydrolyzes 4-methylumbelliferyl-β-D-galactoside and *p*-nitrophenyl-β-D-galactoside, optimum pH 4.5 [A642]. Activity is found in leucocytes [A789].

Rabbit brain enzyme activity remains fairly constant prior to birth, at about twice the adult level [A1221].

Rat brain enzyme, with 4-methylumbelliferyl-β-D-galactoside as substrate, is found in neurones and glial cells [A512].

Queen scallop contains an isozyme, molecular weight 148 000 and optimum pH near 6, and a second isozyme, which is active at pH 3 [A376].

Activity in pea embryo increases during germination, but little change in activity is found in cotyledon. Pisum elatus and P. sativum enzymes have an optimum pH 4–4.5 [A3137].

Petunia hybrida enzyme, optimum pH 4.3, is composed of five isozymes, pI 5.1, 5.65, 5.9, 6.1 and 6.5. It hydrolyzes 5-bromo-4-chloro-3-indolyl-β-D-galactoside [B495].

Sugar cane enzyme, optimum pH 4.25, which is found primarily in cell walls hydrolyses phenyl- and *o*-nitrophenyl-β-D-galactosides [B488].

Macrophomina phaseoli enzyme is a glycoprotein, containing about 12 per cent of carbohydrate. Its optimum pH is 5.0, and is stable up to 55° and between pH 4 and 8. It hydrolyses *o*- and *p*-nitrophenyl-β-D-galactosides, but not N-acetyl-β-D-glucosaminides, α-D-galactosides, α-fucosides or β-xylosides. It is inhibited slightly by Hg^{2+}, but not by other heavy metals [A1758].

Sclerotium tuliparum contains two isozymes, with optimum pH 2.0. It is stable up to 50° and between pH 3 and 6. It acts on *o*-nitrophenyl-β-D-galactoside but only poorly on *p*-nitrophenyl-β-D-galactoside. It is inactivated by N-bromosuccinimide but not by heavy metals [A1759].

α-D-Glucosidase (E.C. 3.2.1.20)

Human amniotic fluid cell enzyme hydrolyzes 4-methylumbelliferyl-α-D-glucoside [A551]. Epidermis enzyme optimum pH 3.7, hydrolyzes 4-methylumbelliferyl-α-D-glucoside and *p*-nitrophenyl-α-D-glucoside [A642].

Rat brain enzyme is found in neurones and glial cells, with 4-methylumbelliferyl-α-D-glucoside as substrate [A512].

Buckwheat enzyme hydrolyzes phenyl-α-maltoside to phenyl-α-glucoside [A3873].

β-D-Glucosidase (c.f. E.C. 3.2.1.21)

Beef liver enzymes hydrolyze 3-glucosides of 17α- and 17β-oestradiol (95 per cent cytosolic) and 17α-oestradiol-17-β-D-glucoside (95 per cent microsomal); the 3-glucosidase is much more active than the 17-glucosidase [A3192].

Human epidermis enzyme, optimum pH 4.8, hydrolyzes 4-methylumbelliferyl-β-D-glucoside and *p*-nitrophenyl-β-D-glucoside [A642].

Pig liver enzyme, molecular weight 55 000, acts on 7-glucosides of several flavonoids, but some other flavonoid glucosides are not substrates, nor are 7-rhamnoglucosides [K309].

Rat brain enzyme, which hydrolyzes 4-methylumbelliferyl-β-D-glucoside, is found in neurones and glial cells [A512].

Pinus banksiana lignifying xylem contains two glycoprotein isozymes, molecular weights 110 000 and 90 000, both pI 3.8, which hydrolyze *E*-coniferin to coniferyl alcohol [H308].

Secale cereale (rye) enzyme, pI 4.9–5.1, molecular weight about 300 000 and monomeric molecular weight 60 000, hydrolyzes glucosides as well as fucosides, galactosides and xylosides [K512].

Triglochin maritima contains two isozymes, both of which hydrolyze β-D-glucosides of *o*- and *p*-nitrophenol, 4-methylumbelliferone and salicin, as well as *p*-nitrophenyl-β-D-galactoside. One, molecular weight 125 000 and optimum pH 5.2, hydrolyzes the aliphatic natural product triglochinin, and the other, molecular weight about 250 000 and optimum pH 5.0 in addition hydrolyzes taxiphyllin to *p*-hydroxymandelonitrile [A3756].

Amygdalin-β-glucosidase (E.C. 3.2.1.117)

Prunus serotina (cherry) enzyme, optimum pH 5.5 forms prunasin, but prunasin is not a substrate. It acts on *o*- and *p*-nitrophenyl-β-glucosides, but not α-glucosides [K910].

Coniferin-β-glucosidase (E.C. 3.2.1.126)

Cicer arietinum enzyme, optimum pH 5, isozymes pI 8.5–10, which all appear to be heterodimers, molecular weight 110 000 and monomeric molecular weights 63 000 and 43 000. Other β-glucosides (poorer substrates) and β-galactosides are also hydrolyzed [K832].

Spruce (Picea abies) enzyme, optimum pH 4.5–5.5, is composed of several isozymes, one of which is monomeric, molecular weight 58 000, found in cell wall particulates from root and seed.

Several other glycosides as well as some galactosides are also substrates [K833].

Prunasin-β-glucosidase (E.C. 3.2.1.118)

Prunus serotina (cherry) enzyme, optimum pH 6.5 hydrolyses prunasin. It acts on *o*- and *p*-nitrophenyl-β-glucosides, but not α-glucosides [K910].

Strictosidine-β-glucosidase (E.C. 3.2.1.105)

Catharanthus roseus cell culture enzyme, optimum pH 6.2, forms strictosidine aglycone. It is also found in C. pusilus, C. trichophyllus and Amsonia salicifolia [K868].

Vicianin-β-glucosidase (E.C. 3.2.1.119)

Davallia trichomanoides enzyme, optimum pH 6.0, hydrolyzes vicianin to mandelonitrile and vicianoside. It also acts slowly on (*R*)-amygdalin and (*R*)-prunasin to release mandelonitrile [K910].

β-D-Glucuronidase (E.C. 3.2.1.31)

Beef liver enzyme has an optimum pH of 4–5, according to one study. It hydrolyzes phenolic substrates, benzyl-β-D-glucuronide and acyl glucuronides of benzoate, veratrate and indole-3-acetate [A1029]. In another study, the optimum pH was found to be 4.4 and molecular weight 290 000, and composed of two isozymes, pI 5.1 and 5.9. It is a glycoprotein, containing mannose, galactose, glucose, glucosamine and sialic acid [A1583]. It also hydrolyzes 17α-oestradiol-3-β-D-glucuronide [A3192].

Human amniotic fluid cell enzyme, optimum pH 3.6, hydrolyzes 4-methylumbelliferyl-β-D-glucuronide [A551]. Epidermis enzyme hydrolyzes 4-methylumbelliferyl-β-D-glucuronide and *p*-nitrophenyl-β-D-glucuronide, optimum pH 4.5 [A642]. Activity is also found in leucocytes [A789] and platelets [A810].

Rabbit brain enzyme activity declines by about 50 per cent to the adult level between 12 days gestation and birth [A1221].

Rat brain enzyme is found in neurones and glial cells; 4-methylumbelliferyl-β-D-glucuronide is substrate [A512]. Five liver isozymes are heterotetramers composed of 3 different subunits, molecular weights 58 700, 60 200 and 62 900, which appear to be glycoproteins. The isozymes differ in inactivation rates in 3M guanidinium solution. 4M urea inhibits reversibly, and sodium dodecyl sulphate inactivates irreversibly [A1629].

Juglans regia enzyme, molecular weight 64 000 and pI 8.9, hydrolyzes hydrojuglone-β-D-glucuronide [J695].

Scutellaria baicalensis enzyme (baicalinase), molecular weight 55 000, pI 5.4 and optimum pH 4.7, hydrolyzes wogonin-β-D-glucuronide, and baicalin to baicalein [H747].

Alcaligenes isozymes I and II, molecular weights 75 000 and 300 000 and optimum pH 7.5 and 6.0, respectively, are both inhibited by saccharo-1,4-lactone, the classical β-glucuronidase inhibitor. Besides phenolic glucuronides, oestrone, oestriol and oestradiol glucuronides, with the substituent at the 3-, 16α- and 17β- positions, are hydrolyzed by one or both isozymes [E323].

E. coli enzyme hydrolyses phenolic substrates (optimum pH 5.5–6.5), benzyl-β-D-glucuronide and acyl glucuronides of benzoate, veratrate and indole-3-acetate (optimum pH 5.5) [A1029].

N-Glucuronide hydrolysis

The quaternary glucuronide of croconazole is hydrolyzed by β-glucuronidase [F490].

α-D-Mannosidase (c.f. E.C. 3.2.1.24)

Human amniotic fluid cell enzyme, optimum pH 4.0, hydrolyses 4-methylumbelliferyl-α-D-mannoside [A551]. Epidermis enzyme, optimum pH 4.3, hydrolyzes 4-methylumbelliferyl-α-D-mannoside and *p*-nitrophenyl-α-D-mannoside

[A642]. The enzyme is also found in urine [A1845].

Rabbit brain enzyme activity increases about sevenfold between 12 and 18 days gestation, and then remains constant near the adult level [A1221].

Rat brain enzyme is found in neurones and glial cells; 4-methylumbelliferyl-α-D-mannoside is substrate [A512]. Gastrocnemius muscle activity is found between pH 5 and 7. The activity above pH 6 is mostly destroyed above 55°, and the main residual enzyme is active below pH 6. Some is residual activity found in heated enzyme preparations above pH 6; this is activated by Co^{2+} and Cd^{2+}, but these ions do not activate the (thermally stable) activity observed below pH 6 [A1842].

Dictyostelium (slime mould) enzyme, which hydrolyzes *p*-nitrophenyl- and 4-methylumbelliferyl-α-D-mannosides, has been separated into two isozymes that are active below pH 4.5. Both lose activity rapidly at 55°, but a residual activity is much more thermally stable [A1774].

β-D-Mannosidase (E.C. 3.2.1.25)

Human epidermis enzyme hydrolyzes *p*-nitrophenyl-β-D-mannoside [A642].

Rat brain enzyme, with 4-methylumbelliferyl-β-D-mannoside as substrate, is found in neurones and glial cells [A512].

Quercitrinase (E.C. 3.2.1.66)

Aspergillus flavus enzyme, optimum pH 6.4, acts on quercitrin to release quercetin and L-rhamnose. It is fairly specific, but myricitrin and robinin are also substrates [K866].

Tetra-N-acetylchitotetraosidase

Vibrio alginolyticus chitinase, optimum pH 5.5, hydrolyzes 3,4-dinitrophenyl tetra-N-acetylchitotetraoside to 3,4-dinitrophenol. It is inhibited by α-chytin or colloidal chitin, is stable at 40°, but is inactivated at 60° [A2722].

β-D-Xylosidase

Mouse fibroblasts probably contain this enzyme [C77].

Secale cereale β-glucosidase hydrolyzes *p*-nitrophenyl-β-xyloside [K512].

Penicillium wortmannii extracellular enzyme, molecular weight 100 000, pI 5.0 and optimum pH 3.3–4.0, hydrolyzes *o*- and *p*-nitrophenyl-β-D-xylosides. Its amino acid composition has been determined. It is inactivated by N-bromosuccinimide [A3240].

Bacillus pumilus enzyme is inducible (not stated how) and hydrolyzes *p*-nitro- and *p*-fluorophenyl-β-D-xylosides [A2061].

6.3 *Hydrolysis of amides*

Primary amides

Few studies appear to have been carried out on this reaction at an enzyme level.

Pseudomonas chlororaphis enzyme, a dimer, molecular weight 105 000 and optimum pH 7.0–8.6, hydrolyzes benzamide and phenylalaninamide, but not N-methylbenzamide [H435].

Benzamide is hydrolyzed by mouse and sheep liver [A2037], Rhodococcus rhodochrous [J857], and Nocardia globerula [G343]. Benzamide and several mono- and dichlorobenzamides are hydrolyzed in Aspergillus flavus and A. niger [A640].

Formylase (kynurenine formamidase; E.C. 3.5.1.9)

Mouse enzyme, molecular weight 60 000–70 000, is probably a dimer. Eserine is inhibitory [B251].

Pig enzyme has been separated into three bands of activity [A2893].

Rat liver enzyme, molecular weight about 35 000 and pI 4.9, hydrolyses formyl-L-kynurenine [A2893]. Brain enzyme, optimum pH about 7.6, hydrolyzes formyl-L-kynurenine and 5-hydroxyformyl-L-kynurenine; it is unclear whether 5-hydroxyformyl-D-kynurenine is a substrate [A1284].

Chicken yolk sac membrane contains two isozymes, molecular weights 73 000 (major) and 78 000 (minor); only the latter is inhibited by eserine. The major isozyme disappears from liver after hatching and is replaced by greatly increased levels of the other isozyme [B251].

Drosophila melanogaster contains two isozymes, one with molecular weight 60 000 and a broad optimum, pH 6.7–7.8, and the other, molecular weight 31 000 and optimum pH 6.5–8.0. They are not interconvertible [A2269]. In eye the enzyme is mainly cytosolic [A1194].

A study on molecular weights obtained values of 60 000 and 36 500 for Drosophila virilis isozymes. The larger form in beef liver has molecular weight 59 000, with 58 500 in yeast (species not stated), 59 000 in chicken liver and 60 000 in Musca domestica. The smaller form has molecular weight 30 500 in Rana pipiens liver and 36 000 in mouse liver [A2269].

Microorganisms contain two classes of isozyme, molecular weights 54 000–59 000 and 25 000–30 000. Both are found in Candida lipolytica, C. guilliermondii, Hansenula henricii, Pichia guilliermondii, Rhodotorula rubra, Rhodosporidium toruloides and R. sphaerocarpum. The larger isozyme is found in H. fabiani, C. utilis and Saccharomyces cerevisiae [A3880]. H. henricii formamidase I, molecular weight 56 000 and optimum pH 7–8 may be a dimer of formamidase II, optimum pH 5.5–7.0, with N-formylanthranilate and N-formylkynurenine as substrates [A3776]. In Streptomyces parvulus the molecular weights are 42 000 and 24 000 [B788].

A study on 90 strains of Mycobacterium found activity only in M. fortuitum and other rapidly growing strains [A584].

Formyltetrahydrofolate deformylase; (E.C. 3.5.1.10)

An E. coli enzyme, which converts this compound into tetrahydrofolate and formate is a hexamer, monomeric molecular weight 32 000. It is activated by methionine [H380].

An enzyme, source unstated, but possibly from microorganisms, expresses two different mechanisms. One is hydrolysis, and the other is a dehydrogenase reaction with NAD^+ as co-substrate. Mutation studies have shown that the full molecular length is required for the dehydrogenase activity, but the hydrolysis reaction requires only part of the molecule [K316].

Acetyl aminoacid hydrolysis

Rat liver mercapturic acid deacylase (which differs from other classes of acylase) is a tetramer, molecular weight about 145 000. It deacetylates *p*-nitrobenzyl-, benzyl- and *p*-bromophenylmercapturates (i.e., S-substituted N-acetyl-L-cysteines), as well as N-acetyl-L-tyrosine and N-chloroacetyl-L-tyrosine. Acylase III, molecular weight 55 000, also hydrolyzes all these compounds [C29].

Rat kidney enzyme, which is not acylase I, hydrolyzes N-acetyl-L-phenylalanine, N-acetyl-L-tryptophan and N-acetyl-L-tyrosine [A3520].

Brevibacterium enzyme, which may be a homodimer, molecular weight 50 000 and optimum pH 7.5, hydrolyzes α-acetamidocinnamate (α,β-dehydro-N-acetylphenylalanine). It is inhibited by Hg^{2+}, Cd^{2+} and *p*-chloromercuribenzoate. Slight activation is found with dithiothreitol, which appears to be entirely due to protection from inactivation. The product is an iminoacid that can be hydrolyzed to phenylpyruvate or reduced enzymatically to L-phenylalanine. Other substrates include a range of dipeptides [E587].

Hippurate hydrolase (E.C. 3.5.1.32)

Streptococcus enzyme has a molecular weight in excess of 70 000 and optimum pH 7.1–9.0 [A824].

Corynebacterium equi N-benzoyl-L-alanine amidohydrolase (E.C. 3.4.17.6) hydrolyzes hippurate and a number of *para*-substituted hippurates (see above) [E145]. Only some strains of Streptomyces hydrolyze hippurate [A435].

Hydrolysis of L-aminoacid β-naphthylamides

Human lens enzyme hydrolyzes alanyl, arginyl, glycyl, leucyl, lysyl, methionyl and phenylalanyl-β-naphthylamides (βNA), with optimum pH 6–8, depending on substrate. It is activated by Co^{2+} and Mn^{2+}, and (less) by Ca^{2+}. Thiols stimulate, dithiothreitol stabilizes it, and *p*-chloromercuribenzoate inactivates [A1397]. Synovial membrane and fluid contain two isozymes, activated slightly by Co^{2+} and Mn^{2+}, and inhibited by puromycin and Cu^{2+} [A751]. Two muscle isozymes have been shown to hydrolyze some β-naphthylamides; a third (main) hydrolyzes aspartyl, glycyl, lysyl and phenylalanyl-βNA as well as some *p*-nitroanilides. The enzyme is inactivated by EDTA, and activity is restored by several divalent ions [A1219].

Human and pig epidermal enzymes, which are both soluble and membrane-bound, hydrolyse leucyl-βNA. The particulate enzymes, optimum pH 7.0 (man) and 6.6 (pig), are inhibited by puromycin or (partially) by EDTA. They do not require heavy metals or thiols for activity. Pig enzyme is moderately stable at 70°. The soluble enzymes, which are inhibited by puromycin and thiol-binding reagents and activated by dithiothreitol, are inactivated at 60° [A3067].

Rabbit small intestinal enzyme, which hydrolyzes α-L-glutamyl-βNA is found mainly in brush border. It is a different enzyme from L-leucyl-βNA arylamidase [A2347]. Its molecular weight is 225 000, optimum pH about 7 and hydrolyzes alanyl, arginyl, α-glutamyl, leucyl, lysyl, phenylalanyl, alanyl-alanyl, alanyl-leucyl, leucyl-alanyl-βNAs [A1589]. Lung enzyme, which is apparently an aminoendopeptidase, hydrolyzes alanyl, arginyl, α-glutamyl, histidyl, leucyl, lysyl, methionyl, phenylalanyl, seryl and valyl-βNAs, but not prolyl nor isoleucyl-βNAs [B334]. Skeletal muscle enzyme, molecular weight 340 000, is composed of three subunits, molecular weights 51 000, 72 000 and 92 000, and optimum pH 7.5–8, is also an aminoendopeptidase designated Hydrolase H; it requires 40 mM mercaptoethanol for maximal activity. It hydrolyses α-N-benzoylarginyl-βNA and leucyl-βNA, but other α-N-benzoylaminoacid-βNas are not hydrolyzed [B524, B787].

Rat brush border enzyme hydrolyzes alanyl, α-glutamyl, γ-glutamyl, histidyl, isoleucyl, leucyl, lysyl, phenylalanyl, tyrosyl, valyl, alanyl-alanyl and seryl-tyrosyl-βNAs. Except for γ-glutamyl-βNA, hydrolysis is inhibited by puromycin or EDTA [A523].

Intestinal enzyme activity is maximal in jejunum from Pottos monkey and tamarin, and maximal in ileum from tree shrew, slow loris, capuchin, owl monkey and macaque. It is evenly spread through the gut of squirrel monkey, one species of tamarin and baboon. [A977].

Chick skeletal muscle enzyme aminopeptidase H, molecular weight 400 000 with subunit molecular weight 55 000 and optimum pH 8.0 is activated by reducing agents. It hydrolyzes α-N-benzoylarginyl-βNA and leucyl-βNA as well as many small peptides, such as L-tryptophanylglycine and L-phenylalanylglycine [G654].

Penaeus setiferus (shrimp) muscle lysyl-βNA arylamidase, optimum pH 6.5, is activated by Co^{2+} and Mn^{2+}, and inhibited by puromycin [A1286].

Mytilus edulis L-leucyl-βNA arylamidase, optimum pH 7.2, is found in hepatopancreas, mantle, gills, foot, siphuncles and adductor muscle. Phenylalanyl, tyrosyl and tryptophanyl-βNA are hydrolyzed, apparently by the same enzyme. 8M urea, *p*-chloromercuribenzoate, iodoacetamide and mercaptoethanol are inhibitory [A1514].

Nemertean worm enzymes have optimum pH in the range of 6.9–10.5, depending on species, and are activated by Ca^{2+} [A1622].

Agave americana enzyme, optimum pH 7–8, hydrolyzes alanyl, glycyl, isoleucyl, lysyl, phenylalanyl, prolyl, seryl, tryptophanyl, tyrosyl and valyl-βNA. It is inhibited by low concentrations of ascorbate, and by diethyl pyrocarbonate [A2745].

Euonymus enzyme, molecular weight 62 000 and optimum pH 7.6, hydrolyzes leucyl, phenylalanyl and tyrosyl-βNA [D216].

Glycine max root enzyme, molecular weight 63 000 and optimum pH 8, acts on N^{α}- alanyl, arginyl, benzoylarginyl, histidyl, isoleucyl, lysyl, methionyl, ornithyl, seryl, tyrosyl and valyl-βNA (in decreasing order of activity) as well as on leucyl-phenylalanyl and leucyl-tyrosyl-βNA [A1596].

Pisum sativum germinating seeds contain two isozymes that hydrolyze leucyl-βNA, only one of which is inhibited by *o*-phenanthroline. The activity of both increases to a plateau after 24 h germination, and then from six days it decays to zero at 20–24 days [A3213].

E. coli enzyme, molecular weight 80 000, pI 5.7 and optimum pH 7.5, hydrolyzes leucyl-βNA [E586].

Flavobacterium meningosepticum enzyme, molecular weight 500 000 is composed of subunits, molecular weight 62 000. The optimum pH is 7.5 for leucyl-βNA and 6.2 for cysteine di-βNA [C73].

Streptococcus durans β-naphthylamidase hydrolyzes leucyl, alanyl, tyrosyl and aspartyl-βNA. Two forms are found, an arylamidase, molecular weight 80 000 and an aminopeptidase, molecular weight 300 000 [C277].

Hydrolysis of L-aminoacid *p*-nitroanilides

Guinea pig kidney enzyme, molecular weight 120 000 and optimum pH 8.0, which hydrolyses succinyl-trialanyl-*p*-nitroanilide(pNA) but only acts poorly on other analogues, requires Ca^{2+} for activity. Liver enzyme is composed of 2 isozymes, optimum pH 7.0 and 8.0 [C178, D230].

A major human muscle enzyme hydrolyzes lysyl, leucyl and glutamate-pNA as well as some amino acid β-naphthylamides. It is inactivated by EDTA, and activity is restored by several divalent ions [A1219]. The optimum pH is 7.3 [A2450].

Human uterus enzyme, molecular weight 71 000 and optimum pH 7.4–7.5, hydrolyzes succinyl-trialanyl-pNA, but not a series of other peptides; it is claimed to be different from other enzymes of this type [C391]. A kidney enzyme of this type, pI 4.9 and optimum pH 8.0, is activated by Ca^{2+}, and inhibited by EDTA or *o*-phenanthroline [B946]. The analogous serum enzyme, molecular weight 200 000–10 000 000, is apparently a series of polymers of the 200 000 monomer. It is inhibited by EDTA, and reactivated by Ca^{2+}; a second enzyme is not inhibited by EDTA [C213].

Rat cardiac muscle contains two isozymes, molecular weights 257 000 and 105 000, optimum pH 7.0 and 7–8 respectively, and they hydrolyze leucyl-pNA. They are inhibited by puromycin, *p*-hydroxymercuribenzoate, *o*-phenanthroline and bivalent cations [A3126]. Skeletal enzyme is a mixture of a monomer, molecular weight 122 000, a dimer and a polymer, molecular weight greater than 1 000 000. The dimer pI is 5.2, and the monomer pI a triplet at about 4.9; the optimum pH is 7.3. No cations are required. Substrates are alanyl, leucyl, lysyl, phenylalanyl and tyrosyl-pNA [C173].

Glycine max root enzyme, optimum pH 8 and molecular weight 63 000, acts on N^{α}-benzoylarginyl, glycyl, leucyl and lysyl-pNA [A1596].

Vigna unguiculata enzyme, molecular weight 60 000, is stable at pH 7–9 and 40°. It hydrolyses leucyl and N^{α}-benzoylarginyl-pNA [C171].

Streptococcus durans β-naphthylamidase (see above) also hydrolyzes leucyl, alanyl, glycyl, and lysyl-pNA [C277].

Nocardia globerula aryl acylamidase is a homodimer, molecular weight 126 000 and optimum pH about 9.5–10.5. It hydrolyses alanyl, arginyl, glycyl, leucyl, lysyl, methionyl, phenylalanyl, prolyl and valyl-pNA, and also a range of aryl-substituted acetanilides, amides and esters [G343].

Bacillus sphaericus enzyme, molecular weight 75 000, optimum pH 7.0–8.5, is stable at −15°, but it is rapidly inactivated at 40°. It is inhibited by mM heavy metal ions. It hydrolyses L-alanyl-pNA as well as many other anilides [A1006].

Aminopeptidases (E.C. 3.4.11 group)

Aspergillus oryzae aminopeptidase IV, molecular weight 130 000 and optimum pH 7.0, hydrolyses a number of tyrosine-containing dipeptides, but not L-amino acid β-naphthylamides [A3658].

Brevibacterium acylase (see Acetyl amino acid hydrolysis, below) hydrolyzes a range of phenylalanine, tyrosine and tryptophan-containing dipeptides [E587].

Glutathione conjugate hydrolysis

Many xenobiotics are converted into mercapturates prior to excretion. It is considered that conjugation with glutathione is a prerequisite, and these conjugates are then hydrolyzed to the corresponding S-cysteinyl conjugates. These reactions have received little study at the enzyme level.

A compound or mixture described as (−)-*anti*-benzo[a]pyrene-(7*R*, 8*S*)-diol 9*S*, 10*R* epoxide glutathione conjugate is hydrolyzed by a commercial γ-glutamyltranspeptidase to form the corresponding cysteinylglycine conjugate [K286].

Pteroyl-γ-oligoglutamyl endopeptidase (E.C. 3.4.19.8)

Chicken intestine enzyme, optimum pH 80 000 and pI 4.8, yields pteroylglutamyl-γ-glutamate from the corresponding oligoglutamates with 5 or 7 glutamyl residues, but not with three residues [A1339].

N-Benzoyl-L-alanine amidohydrolase (E.C. 3.4.17.6)

Corynebacterium equi enzyme is a homohexamer, molecular weight 230 000, pI 4.6 and optimum pH 8.0. It hydrolyzes N-benzoyl-L-alanine and several *para*-substituted analogues as well as hippurates and N-benzoyl-L-aminobutyrate [E145].

Indole-3-acetyl-L-aspartate hydrolase

Enterobacter enzyme, molecular weight 45 000 and optimum pH 8–8.5, is specific for this peptide [J254].

Non-aminoacid arylamidases

Small intestine enzyme hydrolyzes 2-acetamidofluorene as well as butyric, benzoic and succinic analogues, and 4-acetamidobiphenyl. Activity is found in rat, man, mouse and guinea pig. Acetanilides are not substrates [A808].

Mouse liver enzyme, which hydrolyzes 2-acetamidofluorene and 2,4-diacetamidotoluene is mainly microsomal, with some cytosolic [A3949].

Rat liver microsomal enzyme is solubilized with phospholipase A, and precipitated without inactivation by a rabbit antibody [A738].

Sheep brain enzyme hydrolyzes *o*-nitroacetanilide. The optimum is somewhere between pH 6.5 and 8, probably about 7.5; the data are imprecise. It is inhibited by 1 mM choline, succinylcholine, benzoylcholine, acetylcholine and (best) butyrylcholine, and by serotonin and 5-hydroxytryptophan [A2177].

Ascaris lumbricoides enzyme, molecular weight 90 000 and optimum pH 7.4, hydrolyzes acetanilides substituted on the aromatic nucleus. The enzyme is cytosolic, with good activity in intestinal epithelium, with less in reproductive organs. Best substrates, hydrolyzed at a similar rate to acetanilide are *meta*-substituted; *ortho*-substituted substrates are least hydrolyzed. It is inhibited by Cu^{2+}, Zn^{2+}, N-ethylmaleimide,

p-chloromercuribenzoate, and especially by anthelmintic organophosphates [A2036].

Moniezia expansa (tapeworm) cytosolic enzyme, molecular weight 95 000 and optimum pH 7.4, hydrolyzes acetanilide and a series of *o*-, *m*- and *p*-substituted acetanilides. It is inhibited by Cu^{2+}, Zn^{2+}, N-ethylmaleimide, *p*-chloromercuribenzoate, and anthelmintic organophosphates [A1755].

Moniezia expansa, Ascaris lumbricoides, mouse and sheep liver enzymes hydrolyze a range of substituted benzanilides. Reaction rates are similar for all compounds tested, except that an *ortho* hydroxyl group markedly reduces the reaction rate, and the rate is increased 10-fold in *p*-nitrobenzoyl analogues [A2037].

Red rice enzyme, optimum pH about 8.3, hydrolyzes propionanilides substituted with one or two chloro groups on the aromatic nucleus. The enzyme hydrolyzes propionanilides, acetanilides, valeranilides and butyranilides in reducing order, but is not active towards 2-methacrylanilides. It is inactivated at above 40° [A3773].

Taraxacum officinale (dandelion) enzyme, optimum pH 7.4–7.8, hydrolyzes propionanilides substituted with one or two chloro groups on the aromatic nucleus. The enzyme hydrolyzes 3,4-dichloropropionanilide and its acetanilide, valeranilide, butyranilide and 2-methacrylanilide analogues in reducing order. It is inhibited by mM Hg^{2+}, Cu^{2+}, catechol, *p*-chloromercuribenzoate, *p*-quinone, *o*-iodosobenzoate and N-ethylmaleimide, and is inactivated at above 50° [A230].

Bacillus sphaericus enzyme, molecular weight 75 000 and optimum pH 7.0–8.5, is stable at −15°, but it is rapidly inactivated at 40°. It is inhibited by mM heavy metal ions. It hydrolyzes linuron, propanil, karsil, dicryl, solan and prophan, most of which are anilides, as well as L-alanyl-pNA [A1006].

Nocardia globerula aryl acylamidase not only hydrolyzes L-aminoacid *p*-nitroanilides (see above), but also a range of aryl-substituted acetanilides [G343].

Pseudomonas fluorescens enzyme is monomeric, molecular weight 52 500 and optimum pH 8.6; it hydrolyzes acetanilides. It is unstable at 60° [C691].

Rat gut flora hydrolyze a range of acetanilides [A261].

Arylalkyl acylamidase (E.C. 3.5.1.76)

Pseudomonas putida enzyme, optimum pH 8 and molecular weight 150 000, appears to be a homotetramer. It shows strict specificity; it hydrolyzes N-acetyl arylalkylamines such as N-acetyl-2-phenylethylamine, but is inactive towards acetanilides. It is activated by Zn^{2+}, Mg^{2+} and Mn^{2+}; other heavy metals are inhibitory. The amino acid composition has been determined [K790].

Phthalyl amidase (3.5.1.79)

Xanthobacter agilis enzyme, whose activity is enhanced by growth on phthalate, is monomeric, molecular weight 49 900 (49 724 calculated from DNA sequence) and pI 5.5. It acts on a wide range of *o*-phthalylamides as well as numerous other amides. This reaction has been suggested as a synthetic method for completion of hydrolysis of the phthalimido protecting group used in the Gabriel synthesis of primary amines. The phthalimido group is notoriously difficult to remove chemically, whereas hydrolysis to phthalylamide by classical chemical techniques is easier [J253, K793].

β-Lactamase (E.C. 3.5.2.6)

Klebsiella oxytoca enzyme, molecular weight 27 000, pI 5.34 and optimum pH 7.0, acts on benzylpenicillin [G193].

Dihydropyrimidinase (E.C. 3.5.2.2)

Rat and calf liver enzymes, molecular weight 252 000 (subunit 59 000) and 266 000 (subunit 62 000), respectively, hydrolyze 5-phenylhydantoin and α-phenylsuccinimide [A3462].

γ-Glutamyl transpeptidase (E.C. 2.3.2.2)

Rat kidney enzyme acts on γ-glutamyl-*p*-nitroanilide and glycylglycine to form *p*-nitroaniline; the other product is presumably a tripeptide [A3043].

Indomethacin hydrolysis

Pig liver hydrolyzes the benzoyl moiety on the indole nitrogen. The purified enzyme is inactive toward esters [J248].

6.4 *Hydrolysis of phosphates*

Acid phosphatase (E.C. 3.1.3.2)

The enzyme is found in human platelets [A810], leucocytes (phenyl phosphate as substrate) [A789] and in epidermis with optimum pH 5–6, the value depending on substrate (*p*-nitrophenyl and 1-naphthyl phosphates) [A642].

Rabbit brain enzyme activity increases about twofold from 6–14 days gestation, and then remains constant at the adult level [A1221].

Spinach leaf enzyme is a dimer, molecular weight 92 000. It contains Mn and a polysaccharide component, and hydrolyzes *p*-nitrophenyl phosphate [A2623].

Polysphondylium pallidum (slime mould) acid phosphatase I, molecular weight 150 000 and optimum pH 3.5, is stable at 4°. It hydrolyzes *p*-nitrophenyl phosphate and, better, sugar phosphates [A158].

E. coli enzymes, pI 4.9, 5.3 and 6.4, hydrolyze *p*-nitrophenyl phosphate [A1511].

Alkaline phosphatase (E.C. 3.1.3.1)

Enzyme is found in human leucocytes, with phenyl phosphate as substrate [A789]. Kidney enzyme, molecular weight 180 000, pI 4.7 and optimum pH 11.4, is activated by Mg^{2+} and Ni^{2+}, whereas most other divalent cations are slightly inhibitory. Monovalent ions activate at low concentration. It is inhibited by N-bromosuccinimide, *p*-chloromercuribenzoate, iodoacetate, EDTA, L-cysteine and *o*-phenanthroline, and is inactivated at 37° [A1807]. Placental and intestinal enzymes, which hydrolyze phenyl phosphate, is inhibited by inorganic phosphate at 10–50 mM, particularly the placental enzyme. It is activated, with *p*-nitrophenyl phosphate as substrate, by Mg^{2+} and inactivated by Zn^{2+}, whereas biliary, bone, liver and kidney enzymes are activated by both ions [A1943, A2543].

Rat intestinal enzyme is composed of isozymes, molecular weights 64 000, 79 000 and 92 000, but another measurement method gives a value of about 160 000, suggesting that it may be dimeric. It contains about 20 per cent polysaccharide that contains glucose, galactose and mannose residues [A1650]. Rat placental enzyme, a dimer, molecular weight 135 000, hydrolyzes *p*-nitrophenyl phosphate. It is activated by Mg^{2+}, but only in the presence of Zn^{2+}; excess Zn^{2+}, sufficient to block the Mg^{2+}-binding sites inactivates it [A240].

Intestinal enzyme activity is greatest in duodenum or proximal jejunum in tree shrew, capuchin, squirrel monkey, Pottos monkey and tamarin. It is evenly spread through jejunum and proximal ileum in slow loris, macaque and baboon. Peak activity is found in proximal ileum of owl monkey. Activity is partially lost in 10 minutes at 56° [A977].

Egg yolk enzyme which hydrolyzes *p*-nitrophenyl phosphate with optimum pH 9.2–9.6, is composed of three fractions, pI 3.65, 3.95 and 4.25, with maximal stability at pH 5–8.5. It is activated by Mg^{2+}, but less so by other divalent cations [A2063].

E. coli enzymes, pI 4.8 and 5.3, hydrolyse *p*-nitrophenyl phosphate [A1511]. In another study three isozymes were detected, with a broad optimum at pH 8–11. It is inactivated irreversibly at pH 2.3, but is stable at 80° [A251].

Serratia marcescens enzyme has a sharp optimum at pH 9. It is inactivated reversibly at pH 2.3, and is unstable at 80° [A251].

4-Nitrophenylphosphatase (E.C. 3.1.3.41)

Saccharomyces cerevisiae enzyme molecular weight 60 000 and optimum pH 8.0–8.2, is highly specific; it requires Mg^{2+} and is stimulated by some other divalent cations; others antagonise Mg^{2+} activation [K864, K865].

FMN phosphatase

This activity, which produces riboflavine from FMN, has been detected in mouse [A3780].

FAD pyrophosphatase (E.C. 3.6.1.18)

$$FAD + H_2O \rightarrow AMP + FMN$$

This activity has been detected in mouse [A3780].

Protein-tyrosine phosphatase (E.C. 3.1.3.48)

Rat muscle membrane vesicle and liver enzyme acts on phosphorylated IgG heavy chain [K867, K919].

Phosphodiesterase (E.C. 3.1.4.1)

E. coli enzymes, pI 5.0, 5.3, 5.6 and 6.3, hydrolyze bis(*p*-nitrophenyl) phosphate [A1511]. A similar reaction has been observed in rat [A2591].

Paraoxonase (E.C. 3.1.8.1)

$$\text{Aryl dialkyl phosphate} + H_2O \rightarrow \text{dialkyl phosphate} + \text{hydroxyaryl}$$

Human serum arylesterase that acts on paraoxon has a molecular weight of 380 000, with monomeric molecular weight 46 000 [F717, G892].

A general study on birds and mammals detected paraoxonase activity in badger, capybara, cat, goat, mouse, ox, pig, rabbit, rat and sheep, but not in capybara, trout or birds [K863].

Activity has been detected in cow, dog, guinea pig, horse, human, rabbit, rat and sheep serum. A phosphorylphosphatase, molecular weight about 500 000 catalyzes the reaction. A study on a large number of rabbits found that the serum activity is monophasic, whereas a similar study in humans showed a biphasic distribution [A1296, J553]. The rat liver enzyme is microsomal, optimum pH 7.5–7.8, and probably requires Ca^{2+} [D72]. Activity is also found in mouse liver [D804].

Cat serum enzyme appears to be carboxylesterase [A1598].

E. coli enzymes have pI 5.3, 5.6 and 6.2 [A1511].

6.5 *Miscellaneous reactions*

Nitrilase (E.C. 3.5.5.1)

Brassica campestris enzyme, optimum pH 7.5, hydrolyzes indole-3-acetonitrile [A3986].

Agrobacterium tumefaciens enzyme is a homotetramer, molecular weight 102 000, which acts on indole-3-acetonitrile to form indole-3-acetamide. A Rhizobium specoes shows similar activity [H366].

Fusariun solani enzyme, molecular weight 620 000, subunit molecular weight 76 000, pI 4.2 and optimum pH 7.8–9.1, hydrolyzes benzonitrile to benzoate with an activation energy of 48.4 kJ/mol. A range of halogen, nitro, hydroxy and methylbenzonitriles and other nitriles are substrates. The rates are greatest for *para*-substituted benzonitriles and least for *ortho*-substituted compounds, except for tolunitriles where *m*-tolunitrile is most rapidly hydrolysed. The enzyme is inhibited by thiol-binding reagents as well as by some heavy metals [A3364].

Nocardia enzyme, molecular weight 560 000, is composed of monomers, molecular weight 45 000. It forms benzoates and ammonia, apparently without the intermediate formation of amides. Subunits form an active dodecamer with substrate as catalyst; this polymerization is highly dependent on temperature, pH and enzyme concentration, with maximal rate at pH 7.2. The optimum pH for the enzyme is 8.0 or 7–9.5, with activation energy for the reaction of 51.8 kJ/mol

above 20°; below 20° it increases to 119 kJ/mol, the increase possibly being caused by enzyme association. Thiol-binding reagents are inhibitory. Substrates are benzonitriles substituted with halogens, nitro, methyl and hydroxyl groups, although *o*-substituted compounds are usually not substrates; the nitrile group must be substituted directly onto the aromatic nucleus. The rates for *m*- and *p*-substituted compounds are usually similar, except for nitro-substituted compounds, where the *p*-substituent eliminates the reaction. With benzonitrile, benzamide is not an intermediate. The reaction shows a lag period. The enzyme is unstable at 0° or on freezing [A1367, A3420, D725].

Rhodococcus rhodochrous amidase hydrolyzes benzonitrile quantitatively, but much more slowly than benzamide [J857].

Cysteine conjugate β-lyase (E.C. 4.4.1.13)

Gut and other microflora, especially Eubacterium limosum act on 2-(S-cysteinyl)-N-isopropylacetamide and S-(2-benzothiazolyl)cysteine to form the corresponding mercapto analogues. An enzyme is found in rat liver and gut, pig liver and kidney, onion root and corn root that acts on S-(2-benzothiazolyl)cysteine, but not on 2-(S-cysteinyl)-N-isopropylacetamide; there appears to be an inverse relationship between species that contain the enzyme and the presence of glutathione-S-transferase [D356]. Although this reaction type may be involved in the degradation of many glutathione conjugates, the reaction is poorly documented.

Glutathione elimination

Rat liver acts on S-(2,4-dichlorophenacyl)glutathione to form 2,4-dichloroacetophenone and 1-(2,4-dichlorophenyl)ethanol [A1752].

7. Transfer reactions

7.1 *Transamination*

D-Phenylglycine aminotransferase

Pseudomonas stutzeri enzyme is a homodimer, molecular weight 92 000, pI 5.0 and optimum pH 9–10. The co-substrate is α-oxoglutarate; the reverse reaction requires L-glutamate. Another substrate is *p*-hydroxy-D-phenylglycine; otherwise the enzyme is specific [J353, K503].

D-*p*-Hydroxyphenylglycine aminotransferase (E.C. 2.6.1.72)

Pseudomonas putida acts on D-*m*- and *p*-hydroxyphenylglycine to form the corresponding phenylglyoxylates; the reaction appears to be reversible [K716].

L-Tyrosine α-oxoglutarate transaminase (E.C. 2.6.1.5)

This enzyme is the first in the sequence that leads to the oxidation of tyrosine to CO_2 and water, and was one of the first biochemical systems studied in mammalia. Most key studies were carried out prior to the period covered here. Many enzymes of this class show a broad specificity.

Rat small intestinal enzyme is a dimer, molecular weight 90 000 and optimum pH 7.5–8.0. The pure enzyme acts on tyrosine, phenylalanine, tryptophan and aspartate [A1580]. Another publication claims that the enzyme is a homodimer, molecular weight about 100 000, and each monomer has a pyridoxal phosphate-binding site [B12]. In a further study two major components (TATI and TATII) were found to be immunologically identical. Both are dimers, molecular weights about 90 000; acrylamide electrophoresis detected one component, molecular weight 44 000 in TATI, and two components, molecular weight 44 000 and 46 000 in TATII [A2916]. Another study found the molecular weight for the soluble dimer to be 104 000, and the monomer 52 000, pI 4.3, and with no saccharide content [A2930]. Four isozymes have been separated from rat, one of which is found in all tissues [A816].

Rat brain enzyme acts on tyrosine as well as other amino acids [A894]. It is mainly mitochondrial, molecular weight 63 000, acting on tyrosine, phenylalanine, tryptophan, 5-hydroxytryptophan, kynurenine and 3-hydroxykynurenine, but much less rapidly than for aspartate; it is suggested that it is L-aspartate α-oxoglutarate transaminase (E.C. 2.6.1.1) [A2342]. Another study found that it is associated with the inner mitochondrial membrane. It is a tetramer, molecular weight 100 000 and monomeric molecular weight 25 000, containing two mol of pyridoxal phosphate. Both serine and alanine were found to be N-terminal amino acids, suggesting that it contains two moles of each monomer. Tyrosine and 3-iodotyrosine were the best substrates, which are transaminated by a ping-pong bi-bi mechanism. Homogentisate, fumarate, maleate and noradrenaline are inhibitory [A1383].

Soluble rat liver enzyme, molecular weight 50 000, has been separated into three isozymes, and occasionally a fourth has been found [A3388]. Multiple peaks of activity were found in one study, and these were altered considerably by the preparative procedures, suggesting that the enzyme may be particularly susceptible to artifact formation [A382]. One of at least two rat liver

cytosolic isozymes is a small molecule, molecular weight about 23 000, inducible by cortisol or by a high dose of tyrosine and methionine [A462]. It is inhibited by MK486, which also inhibits transamination of L-dopa and 3-methoxytyrosine; both liver and kidney mitochondrial enzymes are unaffected by MK486 [A456].

Rat liver enzyme shows its highest activity at birth [A771]. Activity rises slightly during gestation to the adult level at birth, it then decreases rapidly by 60 per cent, followed by an increase to the adult level at weaning. There may be a further decrease before adulthood [A71]. Liver enzyme shows a diurnal rhythm, with low daytime levels, commencing when the pups eyes open at 11–15 days after birth. During weaning high activity is found throughout the whole cycle, and after weaning a high amplitude diurnal rhythm is established [A527]; the activity increases 300 per cent at night [D196]. Rat liver enzyme is induced by the action of corticosteroids [A462, D196]; it is induced by hydrocortisone or quinolinate during the phase in the diurnal rhythm in which activity is normally rising. Tryptophan also induces, poorly, possibly functioning through the formation and action of quinaldic acid. The diurnal activity is eliminated by cycloheximide [A1060].

Trypanosoma bruceri enzyme requires pyridoxal phosphate for activity; phenylalanine is not a substrate [A1619]. T. cruzi enzyme is dimeric, monomeric molecular weight 45 000, pI 4.6–4.8 and optimum pH 7.0. It has a broad specificity [G894].

Anchusa officinalis enzyme, optimum pH about 9, transaminates tyrosine and phenylalanine, but not tryptophan or L-dopa. Oxaloacetate can replace α-oxoglutarate as co-substrate [E436].

Bushbean (Phaseolus vulgaris) seedling enzyme, molecular weight 128 000 and optimum pH 8.3, transaminates tyrosine, phenylalanine and tryptophan; aspartate appears to be the best substrate. Glyoxylate cannot substitute for α-oxoglutarate as co-substrate, and no requirement for pyridoxal phosphate was found. The Stokes radius is 4.3 nm. Highest activity is found 8–14 days after germination, depending on the organ and light conditions [A566]. This appears to be the same enzyme described under phenylalanine α-oxoglutarate transaminase.

Activity is found in Drosophyllum lusitanicum [A1149].

Bacillus brevis enzyme is dimeric, molecular weight 71 000 and optimum pH 6.5–8.6. It contains one pyridoxal phosphate/monomer. Phenylalanine, tyrosine and tryptophan are substrates, but it is much less effective with aliphatic amino acids [E385]. B. subtilis contains two aromatic acid transaminases, molecular weights 64 000 and 73 000 and optimum pH about 7.2, which act on tyrosine and phenylalanine, and are stable at 55°. Histidinol phosphate transaminase (E.C. 2.6.1.9), molecular weight 54 000 and optimum pH also about 7.2, acts on both these substrates with pyridoxal phosphate as coenzyme, with histidinol phosphate or (poorer) α-oxoglutarate as amino acceptor. It is rapidly inactivated at 55° [A2791, A3546].

Brevibacterium linens enzyme acts on phenylalanine and tryptophan as well as on tyrosine; pyruvate cannot substitute for α-oxoglutarate. Two isozymes are found, optimum pH 9.0; one is L-aryl amino acid aminotransferase, molecular weight 126 000, and the other is L-aspartate aminotransferase, molecular weight 81 000 [D724].

Brevibacterium flavum and Corynebacterium glutamicum both contain two isozymes, molecular weights 155 000 and 260 000, with a pyridoxal phosphate content. They act on phenylpyruvate and *p*-hydroxyphenylpyruvate, with glutamate, tyrosine or phenylalanine as co-substrate, and with leucine also active with the larger enzyme [B266].

E. coli aromatic amino acid transaminase (E.C. 2.6.1.57), molecular weight 90 000 and optimum pH 7.2–7.6 or 8.0, acts on tyrosine and phenylalanine, and at far higher concentrations tryptophan and aliphatic amino acids are also substrates, all with a similar V_{max}, with pyridoxal phosphate as co-enzyme and oxaloacetate (best) or α-oxoglutarate as amino acceptors. The reverse reaction, with glutamate as co-substrate, transaminates phenylpyruvate and

p-hydroxyphenylpyruvate at 50 μM concentration, and on oxaloacetate and 4-methylpentanoate at 3 mM. Aspartate aminotransferase (E.C. 2.6.1.1), molecular weight 84 000 and optimum pH 6.6–7.8 or 8–9, has a similar specificity, but it is active towards all the substrates at about 1 mM concentration. The amino acid compositions of both enzymes are similar, and both are dimers [A3548, K715].

Thermococcus litoralis enzyme is composed of two isozymes, molecular weights 45 000 and 47 000 that require pyridoxal phosphate (which forms a pyridoxamine intermediate in the transamination) and α-oxoglutarate. Tyrosine, phenylalanine and tryptophan, but not aliphatic amino acids are substrates. The enzymes are inactive at 30°, but active at 95–100° [H116].

Pyrococcus furiosus enzyme, molecular weight 44 000 acts on tyrosine, phenylalanine and tryptophan, with pyridoxal phosphate and α-oxoglutarate as co-substrates. It loses 50 per cent of its activity at 95° in 16 h [H437].

Phenylalanine α-oxoglutarate transaminase (E.C. 2.6.1.64)

Rat small intestine mucosal enzyme is a homodimer, molecular weight 100 000, pI 8.5 and optimum pH about 8, is induced in vitamin B_6 deficiency. It has no aspartate transaminase activity; aliphatic amino acids are not substrates, and tryptophan, tyrosine and 5-hydroxytryptophan are relatively poor substrates. It is specific for α-oxoglutarate. This activity is not found in other tissues [B379]. Liver enzyme (cytosolic) is separable from phenylalanine pyruvate transaminase (E.C. 2.6.1.58), is more heat labile, and is probably not inducible by glucagon [A478, A2304]. Small intestinal tyrosine α-oxoglutarate transaminase acts on phenylalanine, tryptophan and aspartate [A1580]. Activity has also been found in rat brain [A894].

Bushbean transaminases I and II, molecular weights 100 000 and 110 000 respectively and optimum pH 8.5, can substitute oxaloacetate for α-oxoglutarate as co-substrate. Substrates include phenylalanine, mono- and dichlorophenylalanines, monofluorophenylalanines and other *p*-substituted phenylalanines, but because aspartate is the best substrate these enzymes are classified as L-aspartate transaminase. The co-substrate is α-oxoglutarate; oxaloacetate can substitute for it, but only with a few substrates [E500, E640].

Bacterium enzyme, molecular weight 90 000 and pI 4.4, transaminates only phenylalanine and tyrosine. It is not activated by pyridoxal phosphate, and the enzyme shows no indication of a pyridoxal phosphate content or requirement. Oxaloacetate, but not pyruvate can substitute for α-oxoglutarate [A2005].

Candida guilliermondii enzyme requires pyridoxal phosphate [A2483].

Glutamine-phenylpyruvate transaminase (E.C. 2.6.1.64)

Rat kidney enzyme appears to be a homodimer, monomeric molecular weight 48 000, and is found both in the cytosol and mitochondria. It contains firmly bound pyridoxal phosphate and is identical with L-phenylalanine-α-keto-γ-methiolbutyrate transaminase (the best substrate) [K718, K719].

L-Dopa transamination (E.C. 2.6.1.49)

Rat liver transaminase, part of which is particulate, converts 3,4-dihydroxyphenylpyruvate into L-dopa, with glutamate, aspartate, tyrosine, phenylalanine or tryptophan (best) as co-substrate [A1393]. Activity on L-dopa is found in brain, with α-oxoglutarate or pyruvate as co-substrate [A894].

Alcaligenes faecalis transaminase converts 3,4-dihydroxyphenylpyruvate into L-dopa, with glutamate, aspartate or phenylalanine as co-substrate, with optimum pH about 10, 9.5 and 7.5 respectively, possibly involving different enzymes. The stability range is pH 7–9.5 [A956].

Enterobacter cloacae enzyme converts 3,4-dihydroxyphenylpyruvate into L-dopa, with

glutamate or glycine as co-substrate; other amino acids are poor co-substrates. The optimum pH is 7.5–8.5, depending on co-substrate. Activity is rapidly lost at 45° outside the pH range 7–9 [A1616].

L-Kynurenine (3-hydroxykynurenine) aminotransferases

Human brain activity has been separated from other transaminases, with pyruvate, oxaloacetate or α-oxoglutarate (E.C. 2.6.1.7) as co-substrates [A894]. Two isozymes have been separated. One, optimum pH 9.6 requires pyruvate, and the other, optimum pH 7.4, requires pyruvate or α-oxoglutarate as co-substrates [G141].

Human liver kynurenine: glyoxylate aminotransferase (E.C. 2.6.1.63), molecular weight 90 000–100 000, also acts on phenylalanine and many aliphatics; many compounds are amino acceptors. It is identical with serine pyruvate transaminase (E.C. 2.6.1.51) and alanine transaminase (E.C. 2.6.1.2) [B677].

Rat liver enzymes are found mainly in mitochondria with smaller amounts in nuclei, lysozomes and cytosol, but not in microsomes [A2892]. They can utilize pyruvate (optimum pH 8.0–8.5) and α-oxoglutarate (optimum pH 6.0–6.5) [A2275, A2892]. Another study found the latter activity in liver, brain and small intestine; enzymes in these tissues appear to be identical. Other substrates, tyrosine, phenylalanine, tryptophan and 5-hydroxytryptophan, are appreciably better than kynurenine; pyruvate is not a co-substrate. The molecular weight is 88 000 with optimum pH 8–8.5. This activity may be identical with mitochondrial tyrosine transaminase and aspartate α-oxoglutarate transaminase. A second liver isozyme, molecular weight 100 000 and optimum pH 6–6.5, which is specific for kynurenine and α-oxoglutarate, is not found in brain or small intestine [A2339]. Identity of the mitochondrial activity (which requires pyridoxal phosphate) with α-aminoadipate transaminase (E.C. 2.6.1.39) has also been suggested [C557], and in another study, with 3,5-diiodotyrosine transaminase (E.C. 2.6.1.24). Both kidney and liver enzymes are inactivated at 70°. They are inhibited by straight chain dicarboxylic acids; a study on the relationship between inhibitory potential and chain length of these acids found that acids with three or fewer methylene units were almost inactive, a maximum in potential was found with four methylene units, a minimum for six, and a further maximum for eight, but longer chain compounds were not studied [A3398]. The same researchers conclude that this activity is the same as α-aminoadipate transaminase, based on subcellular distribution and differences between the sexes and inhibition by dicarboxylates. Highly purified enzyme is active towards α-aminoadipate, which is also a competitive inhibitor [A338].

Rat kidney enzymes are both mitochondrial and cytosolic. One, which requires α-oxoglutarate as co-substrate has an optimum at pH 6–6.5, and the other, requiring pyruvate as co-substrate has an optimum at pH 8–8.5 [A2273]. A cytosolic enzyme is considered to be identical with α-aminoadipate aminotransferase. It appears to be a homodimer, molecular weight 85 000 and pI 6.56, and is inactivated irreversibly by L-seryl-O-sulphate [A3094]. The pyruvate-requiring isozyme appears to be identical with the corresponding brain enzyme, which is found in astrocyte-like cells. It may be a homodimer with monomeric molecular weight 48 000. Phenylpyruvate, oxaloacetate and a range of other 2-oxo-fatty acids can also act as co-substrates [F800, G423].

Rat brain enzyme has been separated into two isozymes. The preferred co-substrate for one, optimum pH 9.1, is pyruvate and is inhibited by glutamine. The preferred substrate for the other is 3-hydroxykynurenine, optimum pH about 7, and shows a broad specificity for oxo co-substrates [J470]. Kynurenine/glutamine aminotransferase K is both cytosolic and mitochondrial, and requires pyruvate as co-substrate [H608].

Rat intestinal enzyme appears to be identical with tyrosine α-oxoglutarate transaminase (see above) [A1580]. In another study other substrates were 3- and 5-hydroxykynurenine, optimum

pH 8.0–8.5; but α-oxoglutarate was a poor co-substrate [A1005].

A study on rat and monkey liver enzymes (E.C. 2.6.1.63), both molecular weight 80 000, pI 8.0 and optimum pH 8–8.5 are mitochondrial, with glyoxylate as coenzyme; this can be replaced by α-oxoglutarate only in rat. It is induced by glucagon, at least in rat. Aromatic amino acids are substrates including kynurenine, especially phenylalanine [K717].

Aedes aegypti (mosquito) enzyme transaminates 3-hydroxykynurenine and pyruvate [J668].

Activity is found in several species of Saccharomyces, and in Pichia, Debaryomyces and Hansenula, with optimum pH 8 for Hansenula. Co-substrates are glyoxylate, pyruvate or α-oxoglutarate, but oxaloacetate is poor. It is inhibited by 1 mM D-cycloserine and hydroxylamine, partially reversible by pyridoxal phosphate, which is probably the coenzyme [A2337].

Hansenula schneggii enzyme, optimum pH 8.0, is a homodimer, monomeric molecular weight 52 000, and each monomer contains one mol of pyridoxal phosphate. The amino acid composition has been determined. The specificity is broad; other (poorer) substrates include phenylalanine and tyrosine and their nitro-substituted analogues, 3-hydroxykynurenine, dopa, benzoylalanine and many aliphatic amino acids, with α-oxoglutarate, α-oxoadipate, phenylpyruvate, *p*-hydroxyphenylpyruvate or indole-3-pyruvate as co-substrates [D978].

L-Tryptophan transaminases

Rat brain enzymes use pyruvate and α-oxoglutarate as co-substrates [A894]. In midbrain phenylpyruvate is 150 times better than α-oxoglutarate as co-substrate; *p*-hydroxyphenylpyruvate is less effective [A3026]. A brain enzyme found in cytosol and synaptosomes, but not in mitochondria, molecular weight about 55 000, pI 6.2 and optimum pH 8.0, transaminates tryptophan, 5-hydroxytryptophan and tyrosine, but not phenylalanine or histidine. The activity with aspartate is much greater than for these amino acids; it is considered to be identical with L-aspartate: 2-oxoglutarate aminotransferase (E.C. 2.6.1.1). Oxaloacetate is co-substrate; α-oxoglutarate is less good [A2847].

Rat liver cytosol contains three isozymes, one of which is specific for tryptophan, a second also acts on aspartate and the third on tyrosine [A644].

Enzyme is found in most plant families including Amaranthaceae, Balsaminaceae, Compositae, Cruciferae, Labiatae, Leguminosae, Moraceae, Papaveraceae, Solanaceae and Umbelliferae. It is present mainly in stem tips and leaves, but less in stem and root. It is not found in Fucus spiralis (an algal seaweed) [A753].

Phaseolus aureus enzyme requires α-oxoglutarate as co-substrate [A463].

Zea mays contains two isozymes, molecular weights 45 000 and 80 000 and optimum pH 8–9, which require α-oxoglutarate as co-substrate [G888].

Agrobacterium tumefaciens tryptophan phenylpyruvate aminotransferase (E.C. 2.6.1.28) has an optimum at pH 9.6 [B568].

Klebsiella aerogenes aminotransferase I is probably a dimer, monomeric molecular weight 42 000, pI 6.64 and a broad optimum at pH 8. It requires pyridoxal phosphate, and it is considered to be a flavoprotein. Substrates are tryptophan, phenylalanine and phenylpyruvate, with oxaloacetate and α-oxoglutarate as co-substrate for the forward reaction, and glutamate for the reverse. For tryptophan, oxaloacetate is the better co-substrate. Aminotransferase IV, molecular weight 100 000 and optimum pH 9, is probably aspartate aminotransferase. Substrates and co-substrates are the same as for aminotransferase I. It is stable at 55° [B732].

Pseudomonas L-tryptophan α-oxocaproate aminotransferase (E.C. 2.6.1.27) and molecular weight 90 000–110 000, additionally transaminates tyrosine and 5-hydroxytryptophan. Several long-chain pyruvates as well as phenylpyruvate

and indole-3-pyruvate are also co-substrates, but pyruvate and α-oxoglutarate are inactive [B672].

Rhizobacterium enzyme, optimum pH 8.0, requires α-oxoglutarate and pyridoxal phosphate [E982].

Saccharomyces cerevisiae contains two transaminases, one of which acts on tryptophan, phenylalanine and tyrosine with pyruvate, phenylpyruvate or α-oxoglutarate as co-substrate. The other acts on tryptophan, with pyruvate as co-substrate [C533].

Streptomyces griseus enzyme, which is involved in indolmycin biosynthesis, requires α-oxoglutarate and pyridoxal phosphate. Other substrates are β-methyltryptophan, phenylalanine and tyrosine [A2307].

L-Phenylalanine pyruvate aminotransferases

Rat liver enzyme is found in peroxisomes and mitochondria, and probably represents several isozymes [A3416]. It is induced by cAMP [A1248]. Induction by tetraiodoglucagon is blocked by cycloheximide and actinomycin D, demonstrating that induction involves protein synthesis [A981]. Glucagon increases activity fourfold in 24 h or eightfold in eight days, and this is enhanced by theophylline, which is an inhibitor of cAMP hydrolysis [A478]. In addition to glucagon induction it is activated twofold by heating at 40°–70° (it is inactivated at higher temperature) [A2459]. It is claimed to be asparagine-pyruvate aminotransferase (E.C. 2.6.1.14) [E331]. Another study which claims that it is probably identical with histidine-pyruvate aminotransferase, found two isozymes, molecular weight about 74 000. One is a homodimer, pI 7.8, monomeric molecular weight 42 000, and the other is a heterodimer, pI 7.3, subunit molecular weights 42 000 and 44 000. Both are immunologically identical, but with different amino acid composition. Several aliphatic amino acids are better substrates than histidine, but not as good as phenylalanine [A3606]. It is separable from phenylalanine-α-oxoglutarate aminotransferase (see above) [A2304].

It is also found in brain [A369, A894]. Rat brain kynurenine/glutamine aminotransferase K (above) also acts on phenylalanine [H608].

Rat liver activity increases about fivefold just before birth, followed by a decrease of about 30 per cent at five days post partum, and then it slowly doubles to the adult level. A similar pattern is observed in kidney, but with smaller fluctuations. Brain enzyme shows minimal changes in activity, with a small fluctuation at birth. In human adult liver the activity is 10 times greater than in foetal liver [A3020].

Monkey and rat liver enzymes, molecular weight 80 000, pI 8.0 and optimum pH 8–8.5, act on phenylalanine, tyrosine, tryptophan, 5-hydroxytryptophan and kynurenine (in decreasing order of activity in rat) with glyoxylate, pyruvate, hydroxypyruvate, 2-oxo-4-methylthiobutyrate and (in rat) 2-oxoglutarate as co-substrates. It is different from kynurenine transaminase [A3570].

Tyrosine-oxaloacetate aminotransferase

E. coli enzyme contains two isozymes, molecular weights 82 000 and 88 000; the pI, about 4.5, differs by 0.05 unit between isozymes. Growth on tyrosine repressed one isozyme, but not the other [A1224].

Aromatic amino acid: oxaloacetate aminotransferase (E.C. 2.6.1.60)

Monkey and rat liver enzyme, molecular weight 80 000, pI 8.0 and optimum pH 8.0–8.5, is induced by glucagon; it is different from kynurenine transaminase. Co-substrates are glyoxylate, pyruvate, hydroxypyruvate and 2-oxo-4-methylthiobutyrate; α-oxoglutarate is active only in rat [K714, K907].

L-Tyrosine: phenylpyruvate aminotransferase

Rat liver enzyme is not induced by cortisol or by other agents that activate tyrosine-α-oxoglutarate

aminotransferase in vivo. Its activity increases by 40 per cent at night [D196].

Diiodotyrosine transaminase (E.C. 2.6.1.24)

Rat kidney mitochondrial enzyme, optimum pH 6.4 requires pyridoxal phosphate and α-oxoglutarate, and is specific for L-acids. Substrates include diiodotyrosine, dibromotyrosine, dichlorotyrosine; monoiodotyrosine (optimum pH 7.2), phenylalanine, tryptophan and *p*-fluorophenylalanine are poor substrates [K925].

Thyroid hormone transaminase (E.C. 2.6.1.26)

Rabbit enzyme, molecular weight 95 000 appears to be a homodimer, and is found mainly in liver and kidney, with smaller amounts in heart, brain, lung and skeletal muscle, but none in serum. It acts on T_3, 3-iodotyrosine, 3,5-diiodotyrosine and 3,5-dinitrotyrosine, with α-oxoglutarate as co-substrate; oxaloacetate and pyruvate are alternative co-substrates, except for 3,5-dinitrotyrosine, which is specific for α-oxoglutarate [K713].

D-Tryptophan aminotransferase

Alaska pea contains a D-tryptophan aminotransferase with pyruvate or α-oxoglutarate as co-substrate. It is specific for the D-isomer [F405].

A D-tryptophan aminotransferase, molecular weight 55 000, which requires pyruvate as co-substrate, is found in Zea mays, optimum pH 8–9 [G888].

5-Hydroxytryptophan aminotransferases

Rat brain contains this activity, with pyruvate and α-oxoglutarate as co-substrates [A894, A2339, A2342, A2847]. Activity has also been found in Hansenula schneggii [D978], monkey and rat liver [A3570] and rat small intestine [B379]. This activity is associated with non-specific aminotransferases.

(*S*)-α-Phenethylamine: pyruvate transaminase

A patent has described the formation of acetophenone from (*S*)-α-phenethylamine, apparently with pyruvate forming optically-active alanine as the second product. The source of the enzyme was not stated in Chemical Abstracts [K449].

Phenylacetone transamination

p-Methyoxyphenylacetone is transaminated to (*S*)-(+)-*p*-methoxyamphetamine, optimum pH about 6. The most effective amino donor is L-alanine. Activity is found in Brevibacterium, Chromobacterium, Flavobacterium, Mycobacterium, Pseudomonas and Sarcina. B. linens enzyme also acts on 3,4-dimethyoxyphenylacetone and 4-(*p*-methoxyphenyl)-2-butanone, again to form (*S*)-amphetamine analogues [F813].

Amination with L-hydroxyisocaproate dehydrogenase

Lactobacillus confusus L-hydroxyisocaproate dehydrogenase forms L-phenylalanine from phenylpyruvate, NADH and NH_4^+ [H954].

7.2 *Isomerization*

Many stereoisomerisation reactions are carried out with the formation of well-defined intermediates, such as oxo compounds for amino acids and mandelic acids. These are described elsewhere.

Phenylpyruvate tautomerase (E.C. 5.3.2.1)

$$R.\ CH_2\text{–}CO.CO_2H \leftrightarrow R.CH{=}CHOH.CO_2H$$

Since its discovery the tautomerase has been an enzyme looking for a role, since no physiological or biochemical role has been discovered for this tautomerization. It may be an activity not associated with its primary function.

Human lymphocyte enzyme, molecular weight 12 000, acts on phenylpyruvate and *p*-hydroxyphenylpyruvate. It functions as a macrophage migration inhibitory factor [J475].

The enzyme that converts D-dopachrome into 5,6-dihydroxyindole enolizes indole-3-pyruvate and *p*-hydroxyphenylpyruvate; it is suggested that these two activities are associated with the same protein [J514].

Mouse enzyme (additionally acts as macrophage migration inhibition factor) is inhibited competitively by (*E*)-2-fluoro-*p*-hydroxycinnamate; its activity is profoundly affected by mutation at Pro-1 [K274, K559].

Mandelates from phenylglyoxals

$$R.CO.CHO \rightarrow R.CHOH.CO_2H$$

Administration of phenylglyoxals to rats results in the formation of the corresponding mandelates. Potential intermediates, e.g. phenylglyoxylates were not detected, nor did their administration result in the formation of equivalent quantities of mandelates. This reaction involves an internal oxidation-reduction, apparently in a single step [J287].

Styrene oxide isomerase (E.C. 5.3.99.7)

Xanthobacter forms phenylacetaldehyde from styrene oxide [F440]. The same reaction is found in Corynebacterium [H881] and Pseudomonas putida [H369]. The Corynebacterium enzyme, optimum pH 7, is highly specific and acts preferentially on the (*S*)-isomer. The reaction is irreversible [J517].

Quinone methide isomerase

Sarcophaga bullata larval haemolymph 4-alkyl-*o*-quinone/2-hydroxy-*p*-quinone methide isomerase is a dimer, molecular weight 98 000 and optimum pH 6.0, which acts on quinones of N-acetyldopamine, N-β-alanyldopamine and 3,4-dihydroxyphenylethanol to form quinone methides. These then spontaneously hydrate to form, for instance, N-acetylnoradrenaline. The quinones formed from these products can react further, finally to form, for instance, N-acetyl-β-oxophenethylamine. Dihydrocaffeoyl methylamide quinone forms caffeoyl methylamide and a little 3,4-dihydroxyphenyl-hydracryloyl methylamide [F792, F793]. The reaction sequence for N-acetyldopamine involves, firstly quinone formation by the action of phenoloxidase, followed by quinone methide formation, which then either hydrates to form N-acetylnoradrenaline or, by the action of a tautomerase forms β-acetamido-3,4-dihydroxystyrene [F386].

This reaction has also been observed in Manduca sexta and Periplaneta americana [F68].

***Cis-trans* isomerisation**

Cis- and *trans*-cinnamates are isomerized in plants in which phenylalanine ammonia lyase is active, by the action of UV radiation in sunlight; this may be important in the formation of cinnamates and their metabolic products, such as flavonoids [H615].

(−)-Epigallocatechin epimerase

Musa accuminata fruit converts this compound into (−)-gallocatechin; the reaction involves *R*/*S*-isomerisation of the phenyl moiety [K423].

Cicloprofen and analogue isomerization

Rat converts (*R*)- ibuprofen to (*S*)-ibuprofen, with quantitative loss of one hydrogen atom at

C-2 without isotope effect, as one step in the sequence. It is postulated that the mechanism involves CoA conjugation, followed by reversible enolization and hydrolysis. All the reaction steps except, perhaps, the final one are considered to be reversible [F733, G304].

Rat, dog, man and monkey convert (−)-cicloprofen into (+)-cicloprofen. The reverse reaction is, at best, slow [A1696, A1767, A2111].

Rat and sheep convert (*R*)-(−)-fenoprofen to (*S*)-(+)-fenoprofen [H597].

7.3 *Migrations*

Formation of (*S*)-tropic acid

Datura innoxa forms tropate from cinnamate. Labelling experiments show that C-2 of the side chain is converted into the hydroxymethyl moiety [A2557]. Starting with L-phenylalanine, isotope studies show that the carboxyl group migrates, with retention of the configuration [E420].

Isoflavone synthase

The reaction is important in the formation of this major class of plant natural products from flavones.

Glycine max isoflavone synthase is microsomal, and requires NADPH and oxygen. The reaction involves the migration of the benzene ring from C-2 to C-3 of the coumarin ring, with the formation of a double bond at position 2–3; a quinonoid intermediate linked to C-2 and C-3 is postulated. Substrates include naringenin and liquiritigenin, which form genistein and daidzein respectively [D468].

Glycyrrhiza echinata 2-hydroxyisoflavanone synthase is a P450 enzyme, with liquiritigenin and genistein as substrates; the reaction appears to be a 'NIH'-type of reaction, involving hydroxylation and migration of the substituent. Usually daidzein and genistein are found as the products; it is unclear whether these are artifacts in all experiments, or whether they are always formed enzymatically, since they can be formed from the 2-hydroxy intermediates by treatment with acid [K308].

Pueraria lobata microsomes convert liquiritigenin into 2,4′,7-trihydroxyisoflavanone, with NADPH as cofactor [F845].

Tyrosine 2,3-aminomutase (E.C. 5.4.3.6)

Bacillus brevis enzyme, optimum pH 8.5, pI 4.6 and molecular weight 75 000, converts L-tyrosine into β-tyrosine, with ATP as co-substrate. It is suggested that there may be a Schiff base intermediate [B316, K824].

A similar reaction may occur with phenylalanine in the formation of the phenylisoserine moiety found in taxol [G738].

Side chain migration without hydroxylation

Human anaerobic faecal organisms convert *p*-hydroxyphenylpropionate into *m*-hydroxyphenylpropionate [A2767, A3990].

7.4 *Racemization*

Amino acid racemase (E.C. 5.1.1.10)

Pseudomonas putida enzyme, molecular weight 62 000–65 000, pI 7.6 and optimum pH about 8, acts on D- and L-phenylalanine as well as on aliphatic amino acids [F110]. The enzyme does not racemize phenylglycine, but it catalyzes α-D labelling in the presence of D_2O, with configuration retention [J883].

Phenylalanine racemase (E.C. 5.1.1.11)

Bacillus brevis enzyme, molecular weight 100 000, requires ATP, its activity is enhanced by dithiothreitol and is reversible. The optimum pH for the

reaction on the L-isomer is 8.5, and for the reverse 7.9 [K860].

Mandelate racemase (E.C. 5.1.2.2)

Pseudomonas enzyme acts on the (*R*)-isomer [K310]. It was originally detected in P. fluorescens; both isomers were converted into the DL mixture [K950]. In view of other research it must be considered that this reaction is the consequence of reversible formation of phenylglyoxylic acid.

8. Formation and reactions of non-aryl double and triple bonds

8.1 *Double and triple bond formation*

L-Phenylalanine ammonia lyase (E.C. 4.3.1.5)

L-Phenylalanine $\leftrightarrow$ *trans*-cinnamate + NH_3

Aesculus hippocastanum enzyme is composed of two isozymes [A1632].

Bamboo (Bambusa oldhami) shoot enzyme, pI 4.7 and molecular weight 360 000, monomeric molecular weight 86 000, is probably tetrameric. After harvesting, there is a sharp increase in activity that is only partly due to *de novo* synthesis. Two minor fractions have a molecular weight of at least 600 000 [E983].

Brassica juncea enzyme, optimum pH 9.0, is a tetramer, monomeric molecular weight 40 000 [J513].

Cucumis sativus enzyme is inhibited by D-phenylalanine, cinnamate, *o*-coumarate, gallate, quercetin and kaempferol [A173].

In gherkin an inhibitor is present that reversibly binds to the enzyme. The inhibitor is a small molecule associated with a larger molecule (molecular weight greater than 12 000); the association breaks down during storage [A224].

Hordeum vulgare enzyme is found in chloroplasts. In etiolated seedlings four minutes exposure to red light results in increased activity some hours later [A223].

Melilotus alba enzyme, optimum pH 8.7, is found in apical buds and axillary leaves. It is inhibited by cinnamate and *o*-coumarate, but not by *p*-coumarate, coumarin, melilotate or *o*-coumarate glucoside [B369].

Nicotiana tabacum enzyme is inhibited by 0.1–0.25 M D-mannitol, D-sorbitol, D-glucose, D-mannose and D-sorbose [A1925].

Osimum basilicum enzyme is a homotetramer, molecular weight 152 000 [J243].

Parsley enzyme contains a dehydroalanine group that is essential for activity; it is formed after protein synthesis. *m*-Tyrosine, unlike tyrosine, is also a substrate [H647].

Pisum sativum seedling enzyme is composed of two isozymes, one of which is formed in the dark, and the other in the light [A847].

Quercus pedunculata roots contain two isozymes, one of which is microsomal, and the other is associated with mitochondria and microbodies [A622].

Radish enzyme, pI 4.9 and molecular weight 280 000, is found only when grown in light. In the absence of light an inactive protein is found, with identical properties including immunoelectrophoresis, pI and sedimentation velocity [A1083].

Wheat enzyme, molecular weight 325 000 is composed of monomers, molecular weights 75 000 and 85 000. The amino acid composition has been determined [A464].

Activity has been found in barnyard grass (Echinochloa crusgalli), bracken fern (Ptreridium spp.), cocklebur (Xanthium pensylvanicum), corn (Zea mays), cotton (Gossypium hirsutum), crabgrass (Digitaria sanguinalis), green and yellow foxtail (Setaria viridis and S. glauca respectively), johnsongrass (Sorghum halepeuse), morning glory (Ipomoea purpurea), yellow and purple nutsedge (Cyperus esculentus and C. rotundus), pigweed (Amaranthus retroflexus) soya (Glycine max) and wheat (Triticum vulgare) [A189].

Alternaria cultures produce two different isozymes. One, designated 68 (the age of the culture in hours), molecular weight 560 000 and optimum pH 8.2, is inhibited by benzoate,

whereas the other, designated 116, molecular weight 380 000 and optimum pH 8.8, is inhibited by cinnamate, *p*-coumarate, benzoate and *p*-hydroxybenzoate [A20].

In Rhizoctonia solani the enzyme only develops in the presence of phenylalanine [A1466].

Rhodotorula glutinis enzyme is a tetramer, monomeric molecular weight 83 000. It is inactivated by nitromethane, apparently by bonding with the dehydroalanine imine prostheic group [A1642].

Ustilago maydis (fungus), molecular weight 320 000 (monomer 80 000) has an optimum at pH 8.8–9.2. Phenylalanine, but not tyrosine is the substrate [J231].

Enzyme activity is modulated by *cis-trans* isomerisation of the product by UV radiation [H615].

L-Tyrosine ammonia-lyase

L-Tyrosine ↔ *p*-coumarate + NH_3

Activity has been found in barnyard grass, bracken fern, cocklebur, corn, cotton, crabgrass, green and yellow foxtail, johnsongrass, yellow and purple nutsedge, pigweed, soya bean and wheat. The ratio relative to phenylalanine ammonia-lyase activity is different for each species. Green foxtail enzyme is not separated chromatographically from phenylalanine ammonia-lyase [A189].

Zea mays enzyme (which also acts on phenylalanine) eliminates the 3-*pro-S* hydrogen [A607].

Cinnamates

Although some studies implying the formation of cinnamates from phenylpropionates have been carried out, the enzymes involved remain obscure.

Phenyllactate dehydratase

Clostridium sporogenes enzyme, which is a trimer, monomeric molecular weights 40 000, 43 000 and 46 000, interconverts (*R*)-phenyllactate and *trans*-cinnamate. The 46 000 component is a cinnamoyl CoA: phenyllactate CoA transferase, and the rest of the complex, which retains dehydratase activity, requires FAD, Mg^{2+}, NADH and cinnamoyl CoA [K534].

Phenylserine dehydratase

Pseudomonas pickettii enzyme forms ammonia and phenylpyruvate from L-*threo*-phenylserine [H569].

Substituted acetaldoxime dehydratase
(indoleacetaldoxine dehydratase, E.C. 4.2.1.29)

e.g. Indole-3-acetaldoxime → indole-3-acetonitrile

Chinese cabbage, Isatis tinctoria, Helianthus annuus and Zea mays catalyze this reaction with indole-3-acetaldoxime as substrate [D896].

Bacillus acts on (*Z*)-3-phenylpropionaldoxime [J508]. Further studies found that the enzyme, phenylacetaldoxime dehydratase, is monomeric, molecular weight about 40 000 and optimum pH 7.0, which is stable at neutral pH up to 45°. It contains loosely bound protohaem IX and requires FMN. Activity is also enhanced by Fe^{2+}, Sn^{2+}, SO_3^{2-} or azide and by the absence of oxygen. It is inhibited by chelators, carbonyl-binding reagents, electron donors, ferrocyanide and ferricyanide. The gene codes for 351 amino acid residues, corresponding with a molecular weight 40 018. The (*Z*)-isomer is the preferred substrate; other substrates include phenylacetaldoxime, 4-phenylbutyraldoxime, *p*-chlorophenylacetaldoxime, *p*-methoxyphenylacetaldoxime and indole-3-acetaldoxime, as well as an unspecified naphthoaldoxime and aliphatic analogues [K411].

This activity has been detected in banana and Aspergillus niger [K882].

Sorghum bicolor cytochrome P450 acts on (*Z*)-*p*-hydroxyphenylacetaldoxime [A2914, J504].

Flavone formation from flavanone (flavonol synthase)

Antirrhinum majus enzyme, optimum pH about 7, is found in microsomes from flowers; it requires NADPH. It converts naringenin into apigenin and eriodictyol into luteolin, with the formation of a double bond in the heterocyclic ring. The enzyme is also found in Verbena hybrida and Taraxacum officinale, plants that form flavones; the enzyme has not been found in species that do not contain flavones [C65].

Petunia hybrida flower bud enzyme, optimum pH 6.5, requires α-oxoglutarate, ascorbate and Fe^{2+}. Substrates are dihydrokaempferol and dihydroquercetin, but not dihydromyricetin; kaempferol and quercetin are the products [D950].

Dianthus caryophyllus enzyme, optimum pH 7.4, requires α-oxoglutarate, ascorbate and Fe^{2+}. Substrates are dihydrokaempferol and dihydroquercetin [G761].

DDT dehydrochlorinase (E.C. 4.5.1.1)

$$(p\text{-}ClC_6H_4)_2CHCCl_3 \rightarrow (p\text{-}ClC_6H_4)_2C{=}CCl_2 + H^+ + Cl^-$$

Two dimeric isozymes are found in housefly, both with pI 7.1. The subunits in the main isozyme have molecular weights 23 000 and 25 000, and in the minor isozyme both have a molecular weight of 25 000. They exhibit marked glutathione S-transferase activity towards chloronitrobenzenes, but another glutathione S-transferase (E.C. 2.5.1.18) has no DDT dehydrochlorinase activity [D332].

Schistocerca gregaria (desert locust) enzyme activity is highest in cuticle, moderate in fat body and low in gut and flight muscle [A3185].

A DDT dehydrochlorinase contained phosphatidylcholine, phosphatidylserine and their lyso- analogues. Both saturated and unsaturated C_{12}–C_{18} (especially C_{16} and C_{18}) fatty acid components were found [A2258].

8.2 *Reactions of double bonds*

Double bond reductases

a. Cinnamate

Cinnamate → phenylpropionate

Although studies on this reaction have demonstrated that *m*- and *p*-coumarates are reduced to the corresponding phenylpropionates in rat [Al334], Lactobacillus, Proteus and Clostridium [A653], little has been discovered relating to the enzymes involved. Cinnamate is reduced in Streptomyces setonii [C818] and in mixed microorganisms [J12], and indole-3-acrylate may be reduced in Clostridium [A2571].

Arthrobacter coumarate reductase (E.C. 1.3.1.11) requires NADH and is specific for *o*-coumarate, with very low activity for some analogues. The reaction is not reversible [K870].

b. Muconate (E.C. 1.3.1.40)

Pseudomonas cruciviae enzyme is composed of three isozymes. One, molecular weight 170 000 requires NADPH. It reduces one of the double bonds in 2-hydroxy-6-oxo-6-phenylhexa-2,4-dienoate (its methyl ester is also a substrate) to form 2,6-dioxo-6-phenylhexanoate [E156].

c. 3-Methyleneoxindole reductase (E.C. 1.3.1.17)

Pea enzyme, which requires NADP, is composed of four or five isozymes; it forms 3-methyloxindole [K875].

d. Biochanin-A reductase (E.C. 1.3.1.46)

Fusarium javanicum enzyme, a homodimer, molecular weight 87 000, monomeric molecular weight 43 000 and optimum pH 7.5, requires NADPH. It converts biochanin A into 5,7-dihydroxy-4′-methoxyisoflavanone by reducing the double bond in the heterocyclic ring. It is highly specific for biochanin A,

although it will act on pratensein and genistein [E724].

Styrene monooxygenase

Styrene → styrene oxide

Rat enzyme is found in liver with some in lung, but little in heart, spleen or brain. It requires NAD(P)H, and is inhibited by metyrapone or SKF 525-A [A1796].

Human leucocyte myeloperoxidase and Coprinus cinereus peroxidase convert styrene and peroxide into styrene oxide and benzaldehyde. Coprinus enzyme forms benzaldehyde as the main product, and a significant amount of benzaldehyde is formed by myeloperoxidase. Substituted styrenes are also substrates [K431].

Horseradish peroxidase forms styrene oxide from styrene in the presence of glutathione, oxygen and peroxide; the incorporated oxygen comes from molecular oxygen. It is suggested that a glutathione thiyl radical is involved [E308].

Pseudomonas fluorescens forms epoxides from styrene, methyl *trans*-cinnamate, *trans*-cinnamyl alcohol and its acetate ester [K167].

Methylococcus capsulatus soluble methane monooxygenase (E.C. 1.14.13.25) converts styrene into styrene oxide [F278].

Dehydrocyclopeptine epoxidase

Penicillium cyclopium enzyme, molecular weight in excess of 480 000, forms an epoxide with the side chain double bond. The enzyme is a mixed function oxidase that may contain flavin, and requires oxygen. NAD(P)H, ascorbate or 6-methyltetrahydropteridine are cofactors. It is inhibited by cyanide, thiocyanate, heavy metals and iron-chelating reagents, but is stimulated by Fe^{2+} [A2734].

Dioxetane formation

Garbanzo and horseradish peroxidase act on 2′,4,4′-trihydroxychalcone to form a dioxetane (peroxide) ring with the double bond. It uses oxygen stoichiometrically, with peroxide as catalyst. It is inhibited by Mn^{2+} and a range of reducing agents, especially *p*-phenylenediamine [A1729].

Hydration of double bonds in unsaturated fatty acids

This type of reaction, which is analogous to one of the steps in the β-oxidation of fatty acids, is implicit in the degradation of cinnamates and longer chain phenolic fatty acids and hydrocarbons. Little information at an enzyme level is available.

Kievitone hydratase

Fusarium solani kievitone hydratase is composed of two isozymes, both of which are dimeric. It hydrates the prenyl double bond to form a tertiary alcohol. Although there have been technical problems in assessing their molecular weights, the molecular weights of the monomers appear to be 47 000 and 49 000. They are glycoproteins, pI 5.1 and optimum pH 5.5. Fusarium also hydrates phaseollidin, but a different enzyme appears to be involved [C58, C713, F687].

Phaseollidin hydratase (E.C. 4.2.1.97)

Fusarium solani enzyme forms phaseollidin hydrate by addition of water to the side-chain double bond. It is separable from kievitone hydratase, which catalyzes a similar reaction [K797].

1,2-Dehydroreticulinium reductase (E.C. 1.5.1.27)

Papaver somniferum enzyme, molecular weight 30 000 and optimum pH 8.5, requires NADPH and is highly specific, reducing the carbon-nitrogen double bond to form (*R*)-reticuline. Its activity is highest four days after germination, and then declines; it is present only where morphinan alkaloids are found [K771].

Halogenation

Bromoperoxidase (non-haem type) from the red alga Corallina pilulifera catalyzes a series of reactions: styrene and *trans*-cinnamyl alcohol add HBr to form 1-phenyl-2-bromoethanol and 2-bromo-1-phenylpropane-1,3-diol respectively, and cinnamate yields a mixture of 2-bromophenylhydracrylate and ω-bromostyrene. In addition anisole and other compounds are halogenated on the aromatic nucleus. It is postulated that the reaction proceeds via a halonium cation intermediate [E597].

Sulphonation

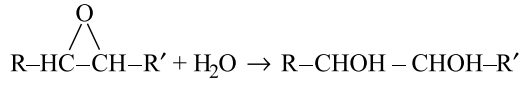
In rat N-(4-chloro-2-fluoro-5-((1-methyl-2-propynyl)oxy)phenyl)-3,4,5,6-tetrahydrophthalimide forms 4-chloro-2-fluoro-5-hydroxyphenyl-1-sulpho-1,2-cyclohexanedicarboximide and several other metabolites containing a sulpho group, in which a C-sulphonic acid is formed by addition at the double bond. It is postulated that a glutathione adduct may be involved [G568].

Amination of hydrocarbon double bonds

Rat liver has been claimed to aminate myristicin to form an amphetamine [A699, A975]. Another study failed to confirm this reaction type (Goodwin, B.L., Ruthven, C.R.J., unpublished).

9. Hydration of epoxides

Epoxide hydratase; styrene oxides (E.C. 3.3.2.3)



This reaction converts styrene oxide and analogues into side-chain diols.

Solubilized horse liver microsomal enzyme has a molecular weight of 50 000 [H905].

Human liver cytosolic enzyme exists in two forms. One, monomeric molecular weight 49 000 and pI 9.2, hydrolyzes *cis*-stilbene oxide. The other, a dimer, monomeric molecular weight 61 000, hydrolyzes the *trans*-isomer [G195]. Another study with liver enzyme that hydrolyzes the *trans*-isomer found a molecular weight of 58 000 for the soluble enzyme and 50 000 for microsomal hydroxylase. The soluble enzyme was very active towards stilbene oxide and naphthalene-1,2-oxide, but inactive towards benzpyrene-4,5-oxide, and almost inactive towards *p*-nitrostyrene oxide. Another enzyme, which hydrolyzed *p*-nitrostyrene oxide, was less active towards *trans*-stilbene oxide. The specificity of microsomal enzyme was similar to that from rat liver (below), with good activity towards styrene oxide, *p*-nitrostyrene oxide and *trans*-stilbene oxide, but naphthalene-1,2-oxide was the best substrate studied and with significant activity towards benzpyrene-4,5-oxide. All the enzymes studied showed low activity towards *trans*-β-ethylstyrene oxide, and *cis*-β-ethylstyrene oxide was scarcely hydrolyzed [C386].

Mouse liver nuclear envelope enzyme hydrolyzes *trans*-stilbene oxide, optimum pH 6.5. Induction and inhibition studies demonstrate that this enzyme is different from the one hydrolyzing benzpyrene-4,5-oxide [D609, E56]; antibodies to it do not cross-react with other epoxide hydrolases [C861]. In kidney and liver the activity is both cytosolic and particulate, the latter being found in peroxisomes [D643]; another study found activity in both cytosol and the mitochondrial fraction. The mitochondrial enzyme was found mainly in the matrix and the intermembrane space fraction. Both mitochondrial and soluble enzymes have a molecular weight in the range 120 000–140 000 [B648]. An enzyme that acts on 1-(4′-ethylphenoxy)-3,7-dimethyl-6,7-epoxy-*trans*-2-octene is found in liver, especially in the soluble and mitochondrial fractions. The soluble enzyme is also found in kidney, lung, testes and spleen (in order of reducing activity). The level differs between male and female animals, and increases about four-fold between five and 10 weeks post partum. The molecular weight is 130 000 [A3955]. Microsomal enzyme, molecular weight 50 000, cross-reacts with antiserum prepared with rat liver enzyme [A2006].

Rabbit enzyme activity is highest in liver (optimum pH 7), slightly lower in kidney but with good activity in lung (optimum pH 7.5) and intestine [A2509]. Liver activity is low at birth, and increases steadily after weaning to the adult level. Gut and kidney enzyme activities follow a similar time course, but lung activity increases twofold to the adult level at weaning, decreases slightly for two to four months, and then increases [A2132]. *cis*-Stilbene oxide hydrolysis is inhibited competitively by *trans*-stilbeneimine [A86].

Rat enzyme is found in liver, kidney, spleen (only in males), but little or none is found in lung, heart or brain [A1796]. It acts on *cis*-β-ethyl-, *n*-propyl-, *n*-butyl- and *n*-hexylstyrene oxides to form the analogous (*R*, *R*)-*threo*-diols [J17]. *trans*-Stilbene oxide is also a substrate for liver cytosolic enzyme, which differs from the

microsomal enzyme; it is a homodimer, molecular weight 120 000, and optimum pH 7.4 [E759]. Another publication claims that the molecular weight of the microsomal enzyme is 53 000–54 000, and is polymerizable. The amino acid composition has been determined [A3421]. The specificity is essentially the same as for the human enzyme (above).

Activity towards styrene oxide has been found in liver and kidney from Atlantic stingray, black drum, bluntnose ray, dogfish, eel, southern flounder, winter flounder, jack crevalle, king of Norway, mangrove snapper, mullet, nurse shark, redfish, sea bass, sheepshead, large skate, small skate, thorny skate, lobster, spiny lobster, blue crab, rock crab and clam [B69].

Teleost species show activity in liver at a similar level to that found in rabbit liver [A1694].

Aspergillus enzyme acts only on the (*R*)-isomer of *p*-nitrostyrene [H922].

Pseudomonas enzyme, pI 5.5, hydrolyzes styrene oxide and a series of aliphatic epoxides [G429].

Streptomonas antibioticus enzyme hydrolyzes (*S*)-styrene oxide to (*S*)-phenylglycol [K394].

Epoxide hydratase; polynuclear hydrocarbons

This activity is a key step in the metabolism of polynuclear hydrocarbons in animals. *In vivo* studies usually fail to detect the epoxide metabolites because of their instability, and the final products, *trans*-dihydrodiols and glutathione conjugates are those usually detected; phenolic metabolites are often assumed to be products arising from epoxide intermediates.

Human liver enzyme exhibits an optimum at pH 8.6–8.9. Substrates (in decreasing order of activity) include phenanthrene-9,10-oxide, benzpyrene-4,5-, 7,8- and 9,10-oxides, benzanthracene-5,6-oxide, naphthalene-1,2-oxide, 3-methylcholanthrene-11,12-oxide, dibenzo[*a*,*h*]anthracene-5,6-oxide and benzpyrene-11,12-oxide; the latter is only marginally active. Styrene oxide is also a substrate [A95, A3217]. Human enzyme is found in liver (best), kidney, lung, spleen and gut (least) [C507]. Its molecular weight is 49 000; it is immunologically distinct from rat liver enzyme, although the specificity is identical [A3031, B63].

Mouse liver enzyme, with benzpyrene-4,5-oxide as substrate, is found in microsomes, with negligible activity in the soluble and mitochondrial fractions [B648].

Studies on rat liver enzyme have found that the addition of water to naphthalene- and anthracene-1,2-oxides occurs exclusively at the 2 position. When (−)-(1*R*,2*S*)-naphthalene-1,2-oxide is used as substrate, both (−)-(1*R*,2*R*)- and (+)-(1*S*,2*S*)-naphthalene-1,2-dihydrodiols are formed in nearly equal amounts [D261]. Specificity for both nuclear and mitochondrial enzymes is similar to that for human enzyme (above), but with much lower activity in the nucleus. Although both these enzymes have molecular weights of 49 000, their properties, especially induction, indicate that the enzymes are different [B142]. Studies on microsomal enzyme, both in rat and man (including activity towards styrene oxide) indicate the presence of multiple forms [B220]. Studies in rats found that (−)-benzpyrene-7,8-dihydrodiol yields tetrahydro-7β,8α,9β,10β-, 7β,8α,9α,10β-, 7β,8α,9β,10α- and 7β,8α,9α,10α-tetrahydroxybenzpyrenes, in reducing amounts [A3093]. Benzpyrene-4,5-oxide (racemic) yields the 4,5-dihydrodiol highly enriched in (−) isomer, with oxygen from water incorporated almost equally at positions 4 and 5, whereas hydrolysis of 7,8- and 9,10- oxides shows almost no stereospecificity, with water incorporated almost exclusively at position 8 with 7,8-oxide as substrate [A3166]. Liver microsomal enzyme has optimum pH values between 7.4 and 8.9, depending on the substrate used [A3031]. Highest activity is found in liver, with lower but significant activity in testis, kidney and ovary. Low or trace activity is found in lung, adrenal, fat, bladder, prostate, trachea, tongue, oesophagus, membraneous and glandular stomach, small intestine, caecum, colon, epidermis, cutis, subcutis, submaxillay gland, spleen, thymus, brain, heart and triceps. It is absent from blood [A1894].

Rat adrenal enzyme activity remains approximately constant after about eight days

post-partum. Ovarian enzyme activity is low before weaning; at weaning the activity increases eightfold to the adult level [A3461]. Immunological studies indicate that liver microsomal activity towards benzpyrene-4,5-oxide and styrene oxide reside on the same molecule [A2445]. Inhibition with styrene oxide allows benzpyrene-4,5-oxide to accumulate as a metabolite of benzpyrene [A739].

Skin microsomal enzyme, which has been found in man, rat and mouse, acts on all of a range of epoxides tested. Rat enzyme has a broad optimum with maximal activity at pH 9, whereas human enzyme has a constant activity between pH 7 and 10. 1,1,1-Trichloropropene and cyclohexene oxides are inhibitory [A2486].

Activity towards benzpyrene-4,5-oxide has been found in liver and kidney from Atlantic stingray, dogfish, eel, sheepshead, small skate, winter flounder, lobster, spiny lobster, blue crab, rock crab and clam [B69].

The quinoline verlukast is epoxidized at positions 5 and 6 in rat *in vivo*, and the dihydrodiol formed from this is found in rhesus monkey [G839].

10. Light-forming reactions

Cypridina-luciferin 2-monooxygenase
(E.C. 1.13.12.6)

Cypridina hilgendorfii enzyme, molecular weight 68 000 with monomeric molecular weight 10 000–13 700 (method-dependent) requires oxygen, and produces a bluish luminescence. The amino acid composition has been determined [K803, K815].

Firefly luciferase (Photinus-luciferin 4-monooxygenase (ATP-hydrolyzing); E.C. 1.13.12.7)

The enzyme, molecular weight 50 000 with one luciferin-binding site, readily dimerizes. The dimer binds one ATP and one $ATPMg_2$ [A905].

Both D- and L-luciferin (a benzthiazole) produce light; with the latter substrate L-luciferyladenylate is an intermediate; presumably D-luciferyladenylate is an intermediate with the oxidative decarboxylation of D-luciferin. The reaction is stimulated by pyrophosphate and pyrophosphatase [J204, K850]. Three luminescent components have been separated chromatographically; one is associated with the enzyme, a second behaves like luciferyl adenylate, but the third was not characterized. ATP is required for their formation [K447]. The visible spectrum is dependent on the environment [K849].

Treatment with 2-benzothiazolesulphonate, a luciferin analogue, changes the emission to red light after a short exposure, whereas longer exposure totally inhibits light emission.

L-1-Chloro-4-phenyl-3-(*p*-tolylsulphonamido)-2-butanone inhibits without changing the emission wavelength [A1522].

Renilla-luciferin 2-monooxygenase
(E.C. 1.13.12.5)

This reaction has been reviewed; the products are carbon dioxide and oxyluciferin [K812, K813, K926]. It is found in Renilla, Aequorea, Carvernularia, Leioptilus, and probably Pelagia and other phyla such as cephalopod molluscs [K884].

Watasenia-luciferin 2-monooxygenase
(E.C. 1.13.12.8)

This squid enzyme opens an amide bond with decarboxylation [K899].

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Part 2 Index

Some entries in the index are duplicates, differing only in names that are in common use for the same enzyme

ORGANIC CHEMISTRY

"The book will be indispensable for my work, and for researchers involved in a variety of fields in academia and industry."

— ***Dr. Iqbal Gill,*** Head of Biotransformations/Biocatalysis Department, Roche Vitamins Inc.

Handbook of
BIOTRANSFORMATIONS OF AROMATIC COMPOUNDS

B.L. Goodwin

Understanding the biotransformations of aromatic compounds and how they are metabolized in animals, plants, and microbes, is central to the applications in a wide range of industries, such as the design and testing of natural and synthetic pharmaceuticals, oil refining, the development of agrochemicals, bioremediation, and for use in functional genomics and xenobiotics.

Presenting the most complete resource of its kind, the ***Handbook of Biotransformations of Aromatic Compounds*** examines 20,000 aromatic compounds researched since 1972 and assembled from all the major, relevant journals. The author focuses his coverage on the biotransformation in animals, plants, and microbes while remaining within the scope of aromatic compounds that contain, or are fused with, at least one aromatic C6 ring. Part One lists each compound alphabetically along with the forward and reverse mechanisms of its metabolism in specific organisms. Part Two characterizes the different types of organic reactions that have been identified — including formation and degradation, oxidations and reductions, substitution, and transfer reactions — and the enzymes associated with those reactions. The author cites selected references for enzymes that are well documented while filling in the details for those with little research literature. This book also contains a searchable CD-ROM of the author's previous work covering aromatic compounds researched from 1900 through 1972.

Features:

- Synthesizes data from all of the major resources over the past 30 years
- Describes the metabolism of of 20,000 aromatic compounds
- Includes a CD-ROM of the author's previous work for complete historical coverage

About the Author

Dr. B.L. Goodwin has held several respected research and teaching positions from 1961 through 1997 at Cambridge University; Oxford University; the Fels Research Institute in Ohio; Queen Charlotte's Maternity Hospital in London; the Royal Botanic Gardens in Kew; and most recently, Kings College in London. Currently retired, Dr. Goodwin's main research has centered on the metabolism of aromatic amino acids and amines and their connection with disease, the metabolic pathways of aromatics, and the development of potential drugs.

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