Microbial Siderophores

Herbert Budzikiewicz

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H. Budzikiewicz
Institut für Organische Chemie, Universität zu Köln, Greinstr. 4, 50939 Köln, Germany
e-mail: aco88@uni-koeln.de

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1. Introduction

Iron is of great importance for many metabolic processes since the redox potential between its two valence states Fe^{2+} and Fe^{3+} lies within the range of physiological processes. Actually, iron is not a rare element, it is fourth in abundance in the earth crust, but it is not readily available for microorganisms. In the soil ferric oxide hydrates are formed at *pH* values around seven and the concentration of free Fe^{3+} is at best 10^{-17} mol/dm^3 while about 10^{-6} mol/dm^3 would be needed. In living organisms iron is usually strongly bound to peptidic substances such as transferrins. To increase the supply of soluble iron microorganisms other than those living in an acidic habitat may circumvent the problem by reduction of Fe^{3+} to Fe^{2+} (*182*), which seems to be of major importance for marine phytoplankton (*151*); see also amphiphilic marine bacteria (Sect. 2.8) and Fe^{2+} binding ligands (Sect. 7) below. An important alternative is the production of Fe^{3+} chelating compounds, so-called siderophores. Siderophores are secondary metabolites with masses below 2,000 Da and a high affinity to Fe^{3+}. Small iron-siderophore complexes can enter the cell via unspecific porins, larger ones need a transport system that recognizes the ferri-siderophore at the cell surface. In the cell, iron is released mostly by reduction to the less strongly bound Fe^{2+} state (*137*), and the free siderophore is re-exported ("shuttle mechanism"); for a modified shuttle system see pyoverdins (Sect. 2.1) and amonabactins (Sect. 2.7). Rarely the siderophore is degraded in the periplasmatic space as, *e.g.* enterobactin (Sect. 2.7). Alternatively Fe^{3+} is transferred at the cell surface from the ferri-siderophore to a trans-membrane transport system ("taxi mechanism"). A probably archaic and unspecific variety of the taxi mechanism comprises the reduction of Fe^{3+} at the cell surface (see ferrichrome A, Sect. 2.6 (*99*, *105*)). The terms "shuttle" and "taxi mechanism" were coined by *Raymond* and *Carrano* (*296*).

A microbial strain may produce more than one siderophore. There are variations in fatty acid chains of a lipophilic part or in the amino acids making up the backbone, as well as released intermediates of the biosynthetic chain. These variations belong all to the same structural pattern. However, there is also the possibility that so-called secondary siderophores are encountered. They constitute a different structural type, usually less complex in their constitution but also less efficient in binding Fe^{3+} than the primary ones. Secondary siderophores will be produced when the demand for iron is not so severe or in case there is a genetic defect impeding the production of the primary ones. Examples will be found throughout the review.

Obviously siderophores can be potent virulence factors of pathogenic bacteria. Siderophores in many cases have elaborate structures providing recognition only by the receptor site of the producing species. This renders a pirating by competing microorganisms more difficult. The structural specificities of siderophores have been used for classification purposes of bacterial species (see especially pyoverdins, Sect. 2.1).

Whether a Fe^{3+} binding metabolite is actually involved in the iron transport has not always been established firmly. Criteria are the pronounced production under iron starvation and growth after feeding, or labeling studies (at best simultaneously of Fe^{3+} and of the ligand, see, *e.g.* parabactin, Sect. 3.2, and schizokinen, Sect. 4.1). Chelators whose function is uncertain will be included in this review with an explanatory remark. Incompletely characterized siderophores will be mentioned when at least some structural elements have been identified. However, the mere statement that color reactions for catecholates (*8a*) or hydroxamates (*9a*) were positive will not be sufficient. Not included will be the sideromycins, conjugates of siderophores with antibiotically active residues, produced mainly by *Streptomyces* spp., which use the iron transport paths for "Trojan Horse" strategies. For further references see (*34*, *97*, *187*).

Due to its high charge density, small ion radius, and low polarizability, Fe^{3+} is a hard *Lewis* acid and can bind strongly to hard *Lewis* bases such as oxide ions. It forms octahedral d^5 high spin complexes providing six coordination sites, which can accommodate three bidentate ligands. The major ligands types are catecholates, hydroxamates, and α-hydroxy carboxylates; other ligands are encountered occasionally. Siderophores containing different ligand types are not uncommon. Three bidentate ligands are often connected by aliphatic segments keeping them in place for complexation. This results in an entropic advantage over three non-connected ligands. Siderophores containing only two binding sites form either $(Fe^{3+})_2Lig_3$ complexes or the remaining two octahedral loci accommodate some external ligand (see, *e.g.* pyochelin, Sect. 5). For $(Fe^{3+})_2Lig_3$ structures with three bridges or with one bridging ligand have been discussed. The latter variety has been proven for alcaligin (Sect. 3.3). Three bidentate ligands can be arranged around the Fe^{3+} nucleus in two ways forming a left-handed or a right-handed screw, designated as Λ or Δ. Three identical ligands can point all in the same direction (*cis*) or one of them is reversed (*trans*). The chiral arrangement of the Fe^{3+} complex can be determined by X-ray analysis or can be deduced from the sign of the broad CD extremum at *ca.* 500 nm correlated with the metal-to-ligand charge transfer band. A positive $\Delta\varepsilon$ indicates a Λ configuration.

Ga^{3+} complexes are frequently analyzed for two reasons. Ga^{3+} also forms octahedral structures and it has almost the same ion radius as Fe^{3+} (62 *vs.* 65 pm). In contrast to Fe^{3+} it is diamagnetic and its complexes are therefore amenable to NMR analysis. Also in contrast to Fe^{3+} it cannot be reduced and therefore it is used for uptake studies interested in the fate of the complex in the cell.

Siderophores can be classified by different criteria. In this review related structural types will be grouped together. Some arbitrariness cannot be avoided due to the occurrence of "mixed types". Cross-references will then be given. Trivial names

have either been given to the free ligands or to their iron complexes. In the latter case the free ligands are referred to as "desferri" or "deferri" (sometimes in a shortened form as "desferrioxamines" for "desferriferrioxamines") or as "pro" (see Sect. 3.3). Occasionally the name applied originally to the iron complex was used later for the free ligand (*e.g.* ferribactins, Sect. 2.1). These variations should be kept in mind when literature search programs are used.

For earlier compilations of siderophores see (*97*, *255a*, *276*), specifically for fungal siderophores (*157a*, *300*, *383*), and for biosynthesis pathways (*19*, *63*, *403*). Reviews for specific classes of siderophores will be mentioned where applicable.

2. Peptide Siderophores

In this group the ligands are incorporated in a peptide chain usually containing both D- (underlined in the structural formulas below) and L-configured amino acids. Frequently the two ends of the peptide chain are blocked by the formation of cyclic structures or otherwise. This prevents the degradation by proteolytic enzymes. Non-proteinogenic amino acids are encountered (homoserine, Hse; ornithine, Orn; 2,4-diaminobutyric acid, Dab; 2,3-dehydrobutyric acid, Dhb), lysine and ornithine may be incorporated in the chain by their ε/δ- rather than by their α-amino group, and amino acids may be modified to form ligand sites (3-hydroxy-aspartic acid, OHAsp; 3-hydroxy-histidine, OHHis; N^5-acyl-N^5-hydroxy-ornithine, acylOHOrn; *N*-hydroxy-*cyclo*-ornithine, *i.e.* 3-amino-1-hydroxy-piperidone-2, cOHOrn). Diaminobutyric acid frequently condenses with the preceding amino acid (Chart 1) giving a tetrahydropyrimidine ring (*116*). These condensation products are indicated below by a parenthesis as *e.g.* (Hse-Dab) in azoverdin (Sect. 2.2).

2.1. *Pyoverdins and Related Siderophores from Pseudomonas spp.*

The most thoroughly investigated representatives are the pyoverdins, also spelled pyoverdines and occasionally named pseudobactins (*353*), produced by the fluorescent members of the genus *Pseudomonas*. For reviews see (*44*, *231*); for a detailed

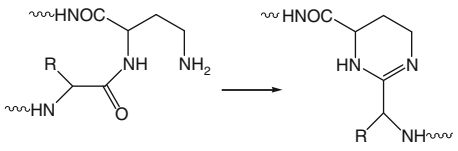


Chart 1. Condensation of a Dab residue with the preceding amino acid residue

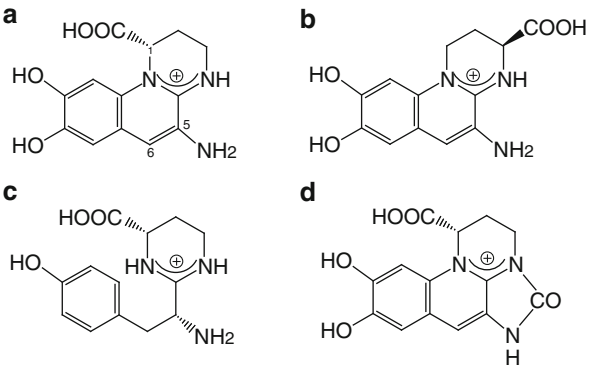


Fig. 1. Chromophore types: (**a**) pyoverdin, (**b**) isopyoverdin, (**c**) ferribactin, (**d**) azotobactin

study of the siderophores of this genus (*37*). Pyoverdins consist of three distinct structural parts, a chromophore (Chr**a**) (Fig. 1, **a**), a peptide chain comprising six to twelve amino acids, and a dicarboxylic acid (succinic acid – Suc-, malic, glutamic, and 2-oxoglutaric acid) or monoamides (succinamide, malamide). For glutamic and 2-oxoglutaric acid the binding to the chromophore by their γ-carboxyl groups has been established by chemical degradation (*124*). For malic acid some not really convincing and partially contradictory NMR arguments have been advanced (*319*) for the binding by the carboxyl group neighboring the CH_2 group. Recently mass spectrometric arguments were reported suggesting a binding *via* the other carboxyl group (*45*).

The about fifty pyoverdins for which structures have been proposed can be divided into three structural types exemplified by the three pyoverdins of *Pseudomonas aeruginosa* (*234*) (Fig. 2), *viz*. pyoverdins (a) with a C-terminal tri- or tetra-cyclopeptidic substructure (lactam formation between the C-terminal carboxyl group and an in-chain lysine or ornithine), *e.g*. ATCC 15692 (PAO1) (**1**), (b) with a C-terminal cOHOrn, *e.g*. ATCC 27853 (**2**), and (c) with a C-terminal free carboxyl group, *e.g*. Pa6 (R) (**3**). The free carboxyl group is probably the hydrolysis product of a depsipeptidic substructure (ester formation between the C-terminal carboxyl group and an in-chain serine or threonine). In several cases both the cyclic and the hydrolyzed open-chain form were found (*e.g*. (*50*)). Binding sites for Fe^{3+} are the catecholate part of the chromophore Chr**a** and two units in the peptide chain, hydroxamate (acylOHOrn, cOHOrn) and/or α-hydroxycarboxylate (OHAsp, OHHis).

Complete structural analysis requires mass spectral and NMR data as well as chemical degradation and analysis of the chirality of the constituent amino acids, determination of the mode of linkage of lysine (α- or ε-), the size of the cyclopeptide or cyclodepsipeptide ring, *etc*. (*37*). In some cases structures have been proposed based only on mass spectral data. Difficulties arising in this approach were discussed (*44*). To determine the three-dimensional structure an X-ray

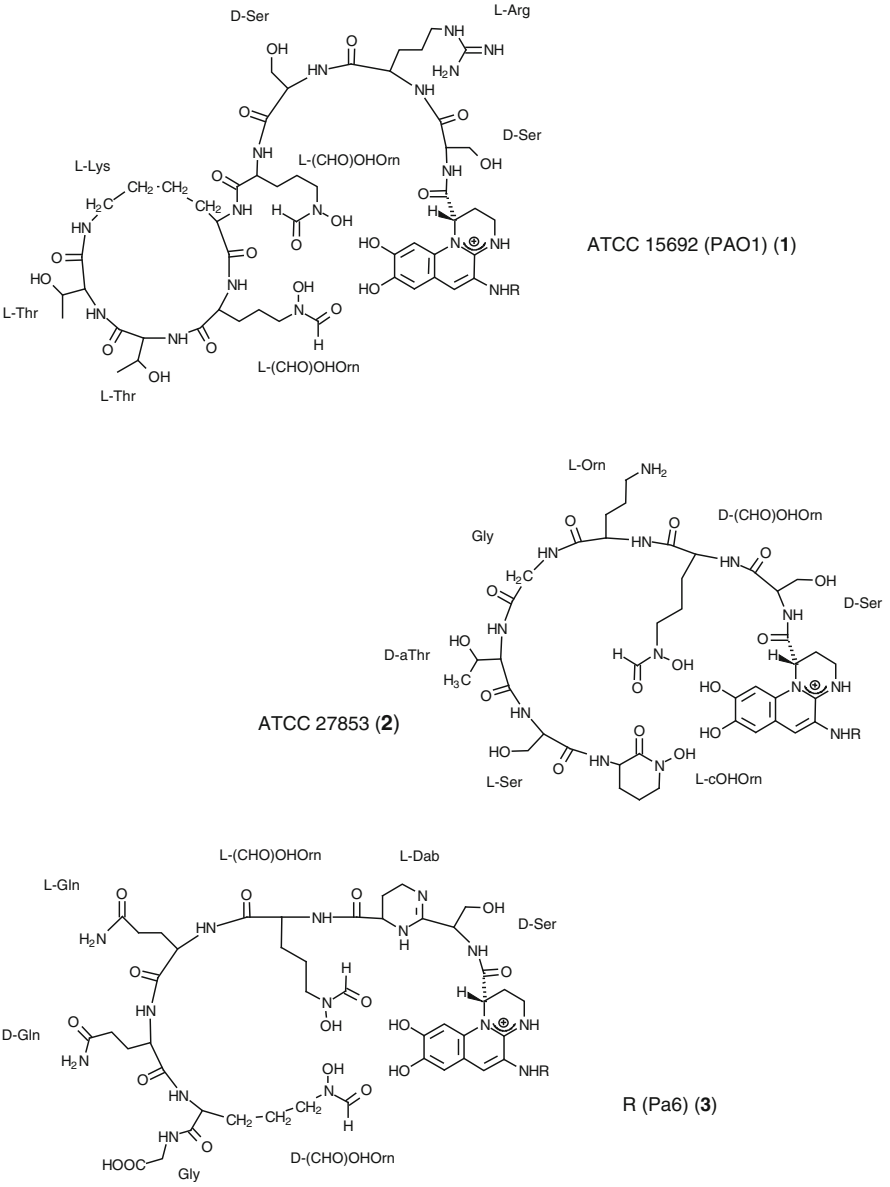


Fig. 2. Pyoverdins from *Pseudomonas aeruginosa* representing the three structural types

analysis (Plate 1) so far only of the Fe^{3+} complex of the pyoverdin B10 (**4**) was performed (*353*).

4 Suc-Chr**a**-εLys-OHAsp-Ala-aThr-Ala-cOHOrn

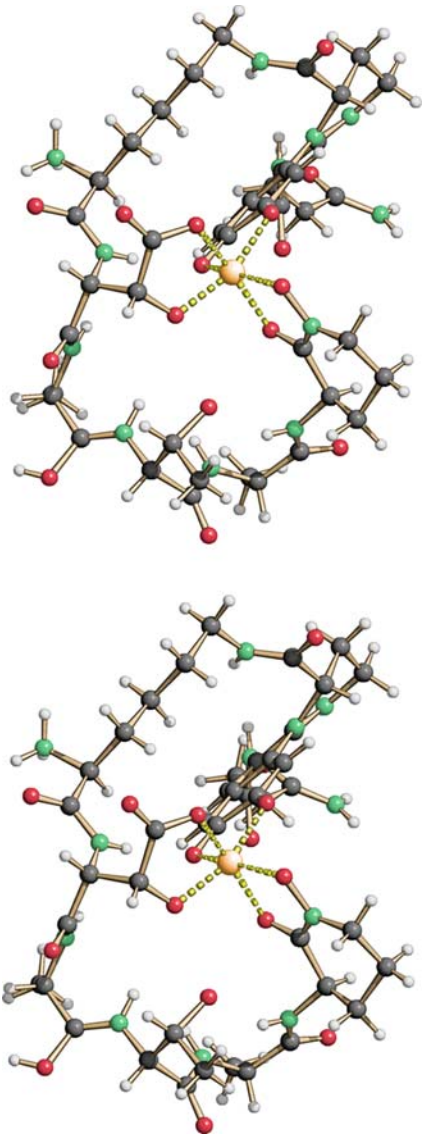


Plate 1. X-ray structure (stereo view) of ferri-pyoverdin B10 (ferri-**4**)

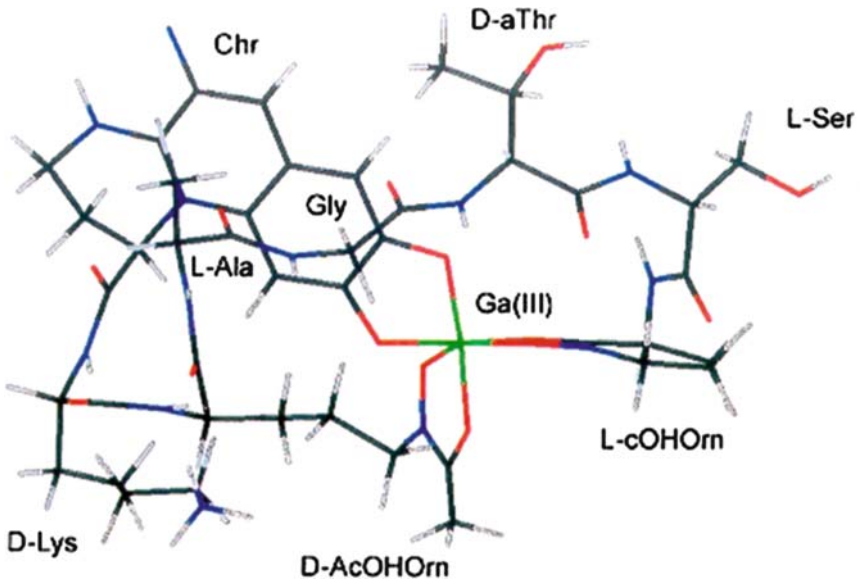


Plate 2. Calculated three-dimensional structure of the Ga^{3+}-complex of pyoverdin PL8 (without side chain) Chr**a**-Lys-acetylOHOrn-Ala-Gly-aThr-Ser-cOHOrn

As an alternative strategy the investigation of the isomorphic Ga^{3+} complexes by NMR analysis was developed (*241*) for the pyoverdin GM-II (**5**) and extended to other pyoverdins, *e.g.* PL8 (*16*) (Plate 2) (*H. Budzikiewicz*, unpublished).

5 Suc-Chr**a**-Ala-Lys-Gly-Gly-OHAsp-Gln-Ser
-Ala-Ala-Ala-Ala-cOHOrn

In all cases the metal ion was found to lie at the surface of the complex. This facilitates its uptake and release. For the pyoverdins both Λ and Δ arrangements have been reported (*37*).

Iron transport through the cell membrane follows a modified shuttle mechanism. Evidence has been presented that the iron-free siderophore of *P. aeruginosa* PAO1 (**1**, Fig. 2) binds strongly to the receptor protein (*67*, *314a*). This suggests two scenarios for the subsequent steps of iron transfer, an exchange of the ligands or a transfer or Fe^{3+} between them. By ^{3}H- and ^{55}Fe-labeling as well as fluorescence studies it was shown that an exchange between the approching ferri-pyoverdin and the bound iron-free pyoverdin occurs and that the former one enters the cell, *i.e.* that no Fe^{3+} exchange between the two ligands takes place (*314b*). Model studies with *Aeromonas* (Sect. 2.7) demonstrated there the iron-exchange variety. Binding of the iron-free siderophore to the receptor protein seems to be a common feature of the transport systems of *P. aeruginosa* and *Escherichia coli* (*145a*).

The peptide chains of the pyoverdins are responsible for the recognition of the ferri-siderophore at the cell surface of the producing species. It is usually highly strain specific. Cross-recognition between two strains is only observed when structurally closely related pyoverdins are produced (*125*, *233*). An exception seems to be *P. aeruginosa* ATCC 15692, which besides its own ferripyoverdin (Fe-**1**), accepts several foreign ones (*128a*).

Without going into structural details, the pyoverdins stemming from the saprophytic group *Pseudomonas aeruginosa/fluorescens/putida* contain either two hydroxamic acid units or one hydroxamic and one α-hydroxycarboxylic acid, and those from the phytopathogens *P. syringae etc.* two α-hydroxycarboxylic acids. Structural differences of pyoverdins have been used recently to characterize species newly defined by breaking up the classical cluster of *P. fluorescens/putida* (*e.g.* (*229*, *231*)). A listing of all pyoverdins from *Pseudomonas* spp. for which structural data have been published up to December 2009 is contained in the Appendix.

Pyoverdin-like siderophores with other chromophores have also been observed (see Fig. 1) (*45*). The 5,6-dihydropyoverdins (Chr**a** without the 5,6-double bond) and the ferribactins (Chr**c**) are considered to be biogenetic precursors of the pyoverdins (*318*) (the term "ferribactin" was originally used for the Fe^{3+} complex (*221*) and later for the free ligand). An azotobactin chromophore (Chr**d**, see also below Sect. 2.2) is occasionally found in *Pseudomonas* isolates (*e.g.* (*146*)). Siderophores produced by a specific *Pseudomonas* strain but differing in the chromophore always have identical peptide chains.

Isopyoverdins contain the siderophore Fig. 1, Chr**b** with aspartic acid as the first amino acid. They have been encountered so far only in isolates from *Pseudomonas putida* strains, *e.g.* BTP1 (*168*) (**6**).

6 Glu-Chr**b**-Asp-Ala-Asp-acetylOHOrn-Ser-cOHOrn

2.2. *Azomonas and Azotobacter Siderophores*

For a detailed discussion of this class of compounds see (*37*).

Azomonas macrozytogenes produces a siderophore with an isopyoverdin chromophore, azoverdin, but with a peptide chain **7** related to those of azotobactins, *viz.* (*236*).

7 Suc-Chr**b**-Hse-(Hse-Dab)-acetylOHOrn-Ser-acetylOHOrn

The three-dimensional structure of the Ga^{3+} complex was determined by NMR techniques as outlined above. Also here the metal ion lies at the surface of the complex (*377*).

From *Azotobacter vinelandii* the structures of two siderophores were elucidated. They contain the chromophore Chr**d** (Fig. 1) and Hse units: azotobactin 87-I (**8**) (from the three Hse in this sequence two are L and one D configured) from the strain ATCC 12837 (*314*), and azotobactin D (**9**) (*76*) from the strain CCM 289.

8 Chr**d**-Ser-Ser-Hse-Gly-OHAsp-Hse-Hse-Hse
-β-hydroxybutyrylOHOrn-Hse

9 Chr**d**-Asp-Ser-Hse-Gly-OHAsp-Ser-Cit-Hse-acetylOHOrn-Hse

Both of them are accompanied by compounds where the C-terminal Hse forms a γ-lactone ring (azotobactin 87-II and δ). An azotobactin O for which also a structure had been proposed (*120*) was shown later to be identical with azotobactin D (*272*). For secondary metabolites see protochelin and its constituents (Sect. 3.2).

Azotobacter chroococcum produces ornithine-containing hydroxamate siderophores with molecular masses 800 and 844 Da (difference of one carboxyl group?) of unknown structure (*115a*).

2.3. Anachelin

Cyanobacteria were probably the first organisms to perform oxygenic photosynthesis resulting eventually in the oxidation of environmental Fe^{2+} to Fe^{3+} with all its consequences. To cope with this problem the production of siderophores was initiated. Not much is known about the siderophores of cyanobacteria. Schizokinen (see below under citrate siderophores, Sect. 4.1) (*326*) found to be produced by several bacterial species may have been acquired by gene transfer; see however also the citrate siderophores synechobactins.

Certainly of genuine origin is anachelin, a strange compound whose biosynthesis requires *inter alia* steps from the peptide and polyketide paths. It exists in an open (anachelin H, Fig. 3, (**10**)) and two cyclic forms arising from an interaction of the carbonyl group of the salicylic acid residue with one of the neighboring

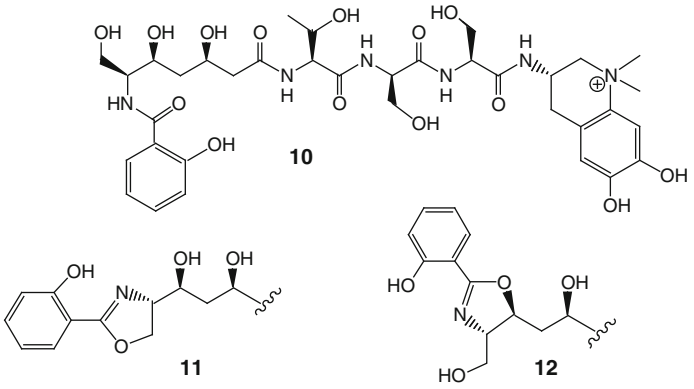


Fig. 3. Anachelin H (**10**), anachelin 1 (**11**), anachelin 2 (**12**)

hydroxy groups (anachelin 1 and 2, Fig. 3, (**11**) and (**12**)) (*22*, *167*). The relative and absolute stereochemistry of all chiral centers was established (*22*, *166*) and confirmed by synthesis (*121*) (see Sect. 8.1). In solution anachelin forms a β-turn arrangement (*122*). Mass spectrometric analysis of the Fe^{3+} complex suggests a 1:1 ratio.

2.4. Actinomycetal Metabolites

Desferrimaduraferrin is a Fe^{3+} complexing metabolite of *Actinomadura madurae* (*185*). It consists of salicylic acid, β-Ala, Gly, L-Ser and N^5-hydroxy-N^2-methyl-L-Orn, with the latter incorporated in a heterocyclic system (Fig. 4, **13**). From the same species the madurastatin group was obtained (*136*). The main representative **A1** shows the sequence salicylic acid, D-azaridine carboxylic acid, L-Ala, β-Ala, N^5-hydroxy-N^2-methyl-Orn, L-cOHOrn (Fig. 4, **14**). In **A2** the azaridine ring is opened giving a Ser residue, **A3** is an isomer of the open form with the salicylic acid bound to the hydroxy group of Ser. **B1** and **B2** are the precursors *N*-salicyloyl-azaridine carboxylic acid and *N*-salicyloyl-Ser. The madurastatin species **A1** forms a 1:1 Fe^{3+} complex as shown by mass spectrometry.

Asterobactin from *Nocardia asteroides* (*257*) contains salicylic, 2,3-dihydroxy-propionic, and 2-methyl-3-hydroxyundecanoic acid as well as derivatized Orn and Arg residues (Fig. 4, **15**). It forms a Fe^{3+} complex. The stereochemistry of the various centers was not determined but L-configuration is proposed for Orn and Arg for biosynthetic reasons (general amino acid pool) and a negative $[\alpha]_D^{25}$ of asterobactin. Whether the three compounds are involved in metal transport has not been investigated.

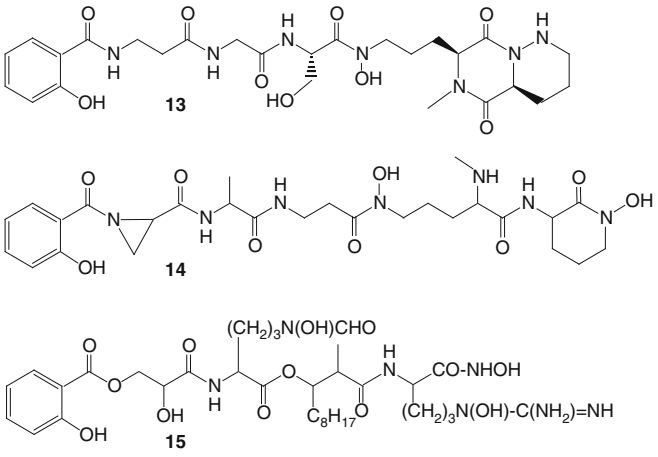


Fig. 4. Desferrimaduraferrin (**13**), madurastatin A1 (**14**), asterobactin (**15**)

2.5. *Bacterial Hydroxamate Siderophores*

Exochelins (*322*, *323*) are peptidic siderophores from *Mycobacterium* spp. (see also below mycobactins). Exochelin MS (**16**) from *M. smegmatis* comprises β-Ala and three N^5-OHOrn units, which are linked by their N^5 atoms to acyl groups thus forming hydroxamic acids.

16 N^5-formyl-N^5-OHOrn-β-Ala-N^5-OHOrn-aThr-N^5-OHOrn

Exochelin MN (**17**) from *M. neoaurum* contains N^2-methyl-N^5-hydroxy-Orn linked by its N^5 to β-Ala and by its carboxyl group to N^2 of Orn, which in turn is bound amidically to cOHOrn; all amino acids are L configured.

17 OHHis-β-Ala-β-Ala-MeOHOrn-Orn-cOHOrn

The Fe^{3+} chelating properties of exochelin MN (**17**) were investigated in detail (pK_a values, chelation constants, redox equilibria, *etc.*) (*87*). In one publication (*128*) siderophores from *Mycobacterium tuberculosis* otherwise referred to as carboxymycobactins (see below Sect. 2.8) were also named exochelins.

Vicibactin (**18**) (previously called hydroxamate K (*61a*)) from *Rhizobium leguminosarum* is a macrocyclic trilactone consisting of N^2-acetyl-N^5-hydroxy-D-Orn and (*R*)-3-hydroxybutyric acid (*91*).

18 $[\text{-O-CH(CH}_3\text{)-CH}_2\text{-CO-NOH-(CH}_2\text{)}_3\text{-CH(NHCOCH}_3\text{)-CO-}]_3$

Vicibactin 7101 from a mutant strain lacks the N-acetyl groups but shows comparable siderophore activity as demonstrated by $^{55}Fe^{3+}$ uptake studies (*91*). The answer to the question why vicibactin is biosynthesized if vicibactin 7101 is as efficient in iron sequestering may be the greater stability of the acetylated compound (*cf.* fusarinines, Sect. 2.6). Vicibactin is identical with neurosporin produced by the fungus *Neurospora crassa* for which X-ray data of the Fe^{3+} complex are available. CD spectroscopy indicates a Λ-*cis* configuration both for crystals and for solution (*108*).

A hydroxamate siderophore from *Salmonella typhimurium* is described as containing isoleucine/leucine, phenylalanine and valine, but not serine and lysine. Further details are not given (*290a*). For other *Salmonella* siderophores see Sect. 2.7.

2.6. *Fungal L-Ornithine-Based Hydroxamate Siderophores*

For other fungal siderophores see neurosporin above, pistilarin (a spermidine derivative, Sect. 3.2) and rhizoferrin (a citrate siderophore, Sect. 4.4); siderophores

produced by marine fungi are treated in (*147*). The siderophores to be discussed here can be divided in three groups, the fusarinines, the ferrichromes, and the coprogens, all based on N^5-hydroxy-N^5-acyl-L-Orn. There exist some earlier reviews (*204*, *300*, *383*); for the early days see also (*395*). Lists of sidrophores and the producing fungi have been assembled (*384*, *385*) to which the marine yeast *Aureobasidium pullulans* may be added (*374a*); see also (*139*). Chromatographic separation techniques were established (*175*, *192*). For a number of siderophores and their Fe^{3+} complexes X-ray and other structural analyses are reported (*366*). In the text and the figures, the desferri ligands will be presented without adding the prefix "desferri" to their names.

Fusarinines (**19**) produced by several fungal genera comprise the acyl unit (*Z*)-5-hydroxy-3-methyl-pent-2-enoic acid (anhydromevalonic acid) (Fig. 5, **a**) bound to N^5-hydroxy-L-ornithine. They can be a linear monomer, dimer (fusarinine A) or trimer (fusarinine B) (the monomer can also be (*E*)-configured) (*172*). Fusarinine B is possibly identical with coprogen C (*89*).

19 HO-[CO-CHNH$_2$-(CH$_2$)$_3$-NOH-CO-CH = CCH$_3$-(CH$_2$)$_2$-O]$_{1-3}$-H

The trimer by forming an ester bond between the two terminal functions results in a lactone ring (fusarinine C or fusigen) (*88*, *313*). Since the fusarinines are rather labile it is not clear whether the open forms are genuine siderophores, precursors of fusigen or just hydrolysis products (*204*). The monomers (*Z*)- and (*E*)-fusarinine form in aqueous solution at neutral *pH* (Fe^{3+})Lig_3 complexes, which are mixtures of Λ and Δ isomers (*172*).

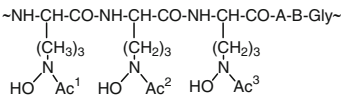
The free α-amino groups of the ornithine units were also found in an acetylated form (*90*, *243*). Since triacetylfusigen is resistant to hydrolysis, formation of the acetylated mono-, di-, and trimeric linear acetylfusarinines is assumed to be effected by enzymatic cleavage (*103a*, *243*). X-ray and CD data of the Fe^{3+} complex of triacetylfusigen have been obtained (*152*). Depending on the solvent used for crystallization the crystals show Λ-*cis* or Δ-*cis* configuration, while in solution Δ-*cis* prevails.

The members of the ferrichrome group are cyclohexapeptides with the general structure [-(N^5-acyl-N^5-hydroxy-L-Orn)$_3$-A-B-Gly-] where A and B can be Gly, Ala, or Ser (Table 1); the various acyl groups are depicted in Fig. 5. Exceptions are tetraglycylferrichrome, a cycloheptapeptide with four Gly units in sequence and three acetyl residues in the Orn part (ferrichrome with an additional Gly) (*82*), and des(diserylglycyl)ferrirhodin, a linear tripeptide containing only the three Orn units

a. (*Z*)-CO-CH=CCH$_3$-(CH$_2$)$_2$-OH
b. (*E*)-CO-CH=CCH$_3$-(CH$_2$)$_2$-OH
c. (*E*)-CO-CH=CCH$_3$-CHOH-CH$_2$OH
d. (*E*)-CO-CH=CCH$_3$-(CH$_2$)$_2$-OCOCH$_3$
e. CO-CH$_2$-CH(CH$_3$)OH-(CH$_2$)$_2$-OH
f. (*E*)-CO-CH=CCH$_3$-CH$_2$-COOH
g. CO-CH$_2$-COOH
h. CO-(CH$_2$)$_{14}$-CH$_3$
i. COCH$_3$

Fig. 5. Acyl residues encountered in fungal hydroxamate siderophores

Table 1. The ferrichrome family[a]



Name	A	B	Ac^1	Ac^2	Ac^3	References
ferrichrome	Gly	Gly	**i**	**i**	**i**	(*106*)
ferrichrome A	Ser	Ser	**f**	**f**	**f**	(*106*, *383*, *396*)
ferrichrome C	Gly	Ala	**i**	**i**	**i**	(*209*, *383*)
ferrichrysin	Ser	Ser	**i**	**i**	**i**	(*170*, *174*, *184*, *383*)
ferricrocin	Gly	Ser	**i**	**i**	**i**	(*184*, *383*)
ferrirubin	Ser	Ser	**b**	**b**	**b**	(*170*, *174*, *383*)
ferrirhodin	Ser	Ser	**a**	**a**	**a**	(*383*)
malonichrome	(Gly	Ala)	**g**	**g**	**g**	(*104*)
sake colorant A	Ser	Ala	**i**	**i**	**i**	(*209*)
asperochrome A	Ser	Ala	**b**	**b**	**b**	(*155*, *174*)
asperochrome B_1	Ser	Ser	**i**	**b**	**b**	(*170*, *174*)
asperochrome B_2	Ser	Ser	**b**	(**b**	**i**)	(*170*, *174*)
asperochrome B_3	Ser	Ser	**b**	(**b**	**i**)	(*170*)
asperochrome C	Ser	Ser	(**b**	**b**	**d**)	(*174*)
asperochrome D_1	Ser	Ser	**b**	**i**	**i**	(*170*, *174*)
asperochrome D_2	Ser	Ser	**i**	(**b**	**i**)	(*170*, *174*)
asperochrome D_3	Ser	Ser	**i**	(**b**	**i**)	(*170*, *174*)
asperochrome E	Ser	Ser	(**a**	**b**	**b**)	(*177*)
asperochrome F_1	Ser	Ser	(**b**	**b**	**e**)	(*177*)
asperochrome F_2	Ser	Ser	(**b**	**b**	**e**)	(*177*)
asperochrome F_3	Ser	Ser	(**b**	**b**	**e**)	(*177*)

[a]Parentheses indicate that the position of the residues is not certain. For the designation of the acyl residues see Fig. 5. Where the chirality of Ala or Ser was determined it was found to be L

of ferrirhodin (*169*). One of the members of this group, ferricrocin was identified as an intra- and intercellular iron transporter for *Aspergillus fumigatus* (*374*).

Ferrichrome (as do also at least the members of the group for which structural data are available ((*366*) and references noted in Table 1) shows Λ-, synthetic *enantio*-ferrichrome based on D-Orn Δ-configuration (*253*). Uptake studies performed with *Ustilago sphaerogena* (*103*) using $^{59}Fe^{3+}$ and [^{14}C]-ferrichrome under optimal conditions (30°C, *pH* 7) showed rapid resorption of both labels during the first 30 min. The uptake of $^{59}Fe^{3+}$ continued for further 30 min, then the level of radioactivity stayed constant, while the level of ^{14}C dropped to a lower constant value. Desferri-[^{14}C]-ferrichrome is not taken up or even bound to the cell surface. These findings are in agreement with shuttle mechanism and re-export of the ligand after detachment of iron. See also analogous experiments with parabactin (Sect. 3.2) and with schizokinen (Sect. 4.1). In contrast, ferrichrome A does not enter the cell. Fe^{3+} is rather reduced and given off at the cell surface and subsequently transported into the cell (*99*, *105*). ^{55}Fe uptake studies performed with *Neurospora crassa* showed the same incorporation rate for ferrichrome and tetraglycylferrichrome indicating that the peptide ring size is of minor importance for the acceptance by the transport system (*82*).

The third group comprises the coprogen family. Their characteristic element is a diketopiperazine ring formed by the head-to-head condensation of two N^5-acyl-N^5-hydroxy-L-Orn units. Rhodotorulic acid (**20**) first isolated from the yeast *Rhodotorula pilimanae* and subsequently found to be produced by many yeasts (*9a*) contains two acetyl groups (Fig. 6) (*9*), and dimerum acid (**21**) from *Fusarium dimerum* (*89*) and other fungi (*172*) two (*E*)-anhydromevalonyl residues (Fig. 6). An acetyl-dimerum acid of unknown structure has been encountered (*157b*). In the coprogens a third variously substituted (*E*)-fusarinine unit is added by means of an ester bond (Table 2) (*300*). Rhodotorulic and dimerum acid form $(Fe^{3+})_2Lig_3$ complexes, but also a mixed 1:1:1 complex of Fe^{3+} with dimerum acid and (*Z*)-fusarinine was observed. Various coprogens were shown to yield 1:1 complexes with Fe^{3+} (*60*, *153*, *172*). The CD-spectra of the coprogen and neocoprogen I/II Fe^{3+} complexes demonstrate Δ-configuration for the solutions and for the crystals of neocoprogen I

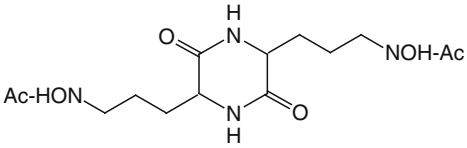
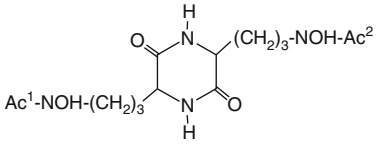


Fig. 6. Rhodotorulic acid (Ac = Fig. 5, **i**) (**20**) and dimerum acid (Ac = Fig. 5, **b**) (**21**)

Table 2. The coprogen family[a,b]



Ac^2 = CO-CH=C(CH_3)-$(CH_2)_2$-O-CO-CH(NR^1R^2)-$(CH_2)_3$-NOH-Ac^3

Name	Ac^1	Ac^3	R^1	R^2	References
coprogen	**b**	**b**	$COCH_3$	H	(*117*, *184a*)
coprogen B	**b**	**b**	H	H	(*89*)
triornicin (isoneocoprogen I)	**b**	**i**	$COCH_3$	H	(*117*)
isotriornicin (neocoprogen I)	**i**	**b**	$COCH_3$	H	(*118*, *153*)
neocoprogen II	**i**	**i**	$COCH_3$	H	(*153*)
N^2-methyl coprogen B	**b**	**b**	CH_3	H	(*30c*, *157b*)
N^2-dimethyl coprogen	**b**	**b**	CH_3	CH_3	(*173*)
N^2-dimethyl neocoprogen I	**i**	**b**	CH_3	CH_3	(*173*)
N^2-dimethyl isoneocoprogen I	**b**	**i**	CH_3	CH_3	(*173*)
hydroxycoprogen	**b**	**c**	$COCH_3$	H	(*176*)
hydroxyneocoprogen I	**i**	**c**	$COCH_3$	H	(*176*)
hydroxyisoneocoprogen I	**c**	**i**	$COCH_3$	H	(*176*)
palmitoylcoprogen	**b**	**b**	**h**	H	(*5*)

[a]For the designation of the acyl residues see Fig. 5
[b]Coprogen C is possibly identical with fusarinine B (*89*)

(*153*). Palmitoylcoprogen (Table 2 last entry) from *Trichoderma* spp. is retained in the fungal mycelium and may therefore be considered as a candidate for an iron uptake taxi mechanism (*5*).

Relationships between the structure of the siderophores and the iron transport were investigated for the fungus *Neurospora crassa* (*160*, *160a*). Apparently two different receptors exist for ferrichromes and for coprogenes. For the recognition and the binding to the cell surface the iron configuration and the nature of the acyl chains is of importance. However, the transport system seems to be the same for both siderophore types dependent on the peptide part of the molecules.

2.7. *Catecholate Siderophores*

For other catecholate siderophores see di-/tri-aminoalkane (Sect. 3.2) and citric acid (Sect. 4.3) derivatives below; for a review see (*38*).

2,3-Dihydroxybenzoic acid is produced by a series of microorganisms, *viz*. *Aerobacter aerogenes* (*291*), *Azotobacter vinelandii* (*70*, *273*), *Bacillus subtilis* (*282*), *Escherichia coli* (*261*, *291*), *Klebsiella oxytoca* (*196*), *Micrococcus denitrificans* (*347*), *Nocardia asteroides* (*112*), *Rhizobium* sp. (*74*), and *Salmonella typhimurium* (*290*), 3,4-dihydroxybenzoic acid by a mutant of *Aerobacter aerogenes* (*291*), *Azomonas macrocytogenes* (*380*), *Bacillus anthracis* (*123*), *Escherichia coli* (*291*), *Magnetospirillum magneticum* (*54*), and *Mycobacterium smegmatis* (*291*). Both dihydroxybenzoic acids can act as siderophores.

Condensation products of DHB (which usually is found also in the fermentation broth) with amino acids were reported, *viz*. with glycine from *Bacillus subtilis* (*164*) named subsequently itoic acid (*282*); with serine from *Escherichia coli* (*261*) and *Klebsiella oxytoca* (*196*); with threonine from *Klebsiella oxytoca* (*196*) and *Rhizobium* spp. (*275*, *327*); with arginine from *Pseudomonas stutzeri* (*62*); with glycine and threonine from *Rhizobium* sp. (*240*); with threonine and lysine as well as with leucine and lysine from *Azospirillum lipoferum* (*312*, *320*). In most cases the isolate (sometimes designated as being a siderophore) was hydrolyzed and the constituents were determined by paper chromatography. The relative amounts of the constituents, the chiralities of the amino acids and the molecular mass of the isolate have not been determined. Hence it is not known whether condensation products of the enterobactin type exist.

Ideally suited for Fe^{3+} complexation – exemplified by the extremely high complexing constant of 10^{49} (originally estimated as 10^{52}) (*210*) – is enterobactin (enterochelin) first isolated from *Salmonella typhimurium* (*286*) and *Escherichia coli* as well as from *Aerobacter aerogenes* (*261*) and recently from *Enterobacter cloacae* (*368*). It is a cyclic trilactone of *N*-2,3-dihydroxybenzoyl-L-serine (DHB-Ser) (Fig. 7, **22**). Syntheses have been reported (*71*, *321*). DHB-Ser by itself can act as a siderophore. In the culture medium degradation products of enterobactin also were found, and are open-chain compounds comprising two or three constitutional units. Iron release in the cell is effected by degradation of

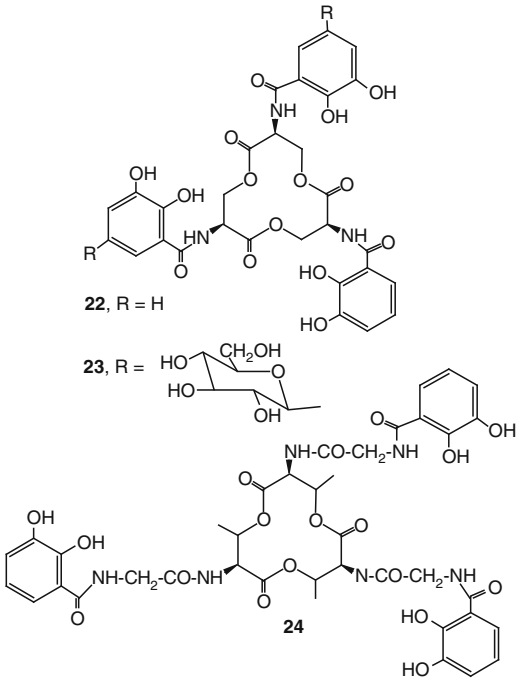


Fig. 7. Enterobactin (**22**), salmochelin S4 (**23**), corynebactin (**24**)

enterobactin. Ferri-enterobactin shows a Δ-*cis* configuration, with the synthetic ferri-*enantio*-enterobactin based on D-Ser Λ-*cis*-configuration (*256*).

Escherichia coli and *Salmonella enterica* produce a derivative of enterobactin, salmochelin S4, where two of the aromatic rings are *β*-C-glucosylated in the 5-position (Fig. 7, **23**). Also glycosylated degradation products or precursors (monomer: salmochelin SX, dimers: S1 and S5, linear trimer: S2) could be isolated (*31*, *135*, *247*). Salmochelin S4 is identical with pacifarin, a compound active against salmonellosis (*378*), and SX with pacifarinic acid, glucosylated DHB-serine (*247*).

From *Corynebacterium glutamicum* the siderophore corynebactin was obtained (*41*). It differs from enterobactin in being composed of three DHB-Gly-L-Thr units (Fig. 7, **24**). Later the same siderophore was found to be produced also by *Bacillus subtilis* and named bacillibactin (*223*). Its complexation constant is ~10^{48} (*84*). The monomeric unit DHB-Gly-Thr was isolated from *Bacillus licheniformis* (*357a*).

Azospirillum brasilense under iron starvation produces spirilobactin. Hydrolysis yields DHB, ornithine, and serine of unknown chirality in a ratio of 1:1:1. The molecular mass was not determined and hence it is not known whether spirilobactin forms a (cyclic) trimer. Iron uptake was studied with the $^{59}Fe^{3+}$ complex (*10*).

Erwinia chrysanthemi (*278*) and *Serratia marcenscens* (*101*) produce N^2-DHB-D-Lys-L-Ser named chrysobactin. The structure was confirmed by synthesis. At physiological *pH* values 2 or 3 chrysobactin residues are associated with Fe^{3+} (*280*).

From *Chryseomonas luteola* in addition to chrysobactin a derivative (chrysomonin) was isolated where C-6 of the DHB unit is substituted with the N-atom of a pyridinium cation. Chrysomonin could be synthesized from chrysobactin (*1a*).

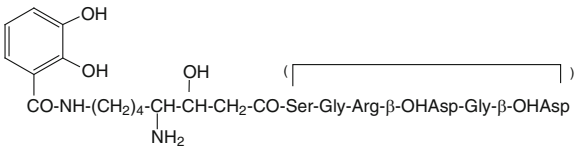
Amonabactins (**25**) were found to be excreted by *Aeromonas hydrophila* (*355*, *356*) and by *Pseudomonas stutzeri* (*398*). They are based on the peptides Lys-Lys-Phe and Lys-Lys-Trp; N^6 of the first L-Lys residues is derivatized by DHB or by a DHB-Gly residue, and that of the second L-Lys by a DHB group (Table 3). At high *pH* values and excess ligand a $(Fe^{3+})_2Lig_3$ complex is formed, while at neutral *pH* a 1:1 ratio prevails with H_2O molecules satisfying the remaining coordination sites. The 2:3 complex is preferentially Δ-configured, and the 1:1 complex is achiral (*357*). Model uptake studies with *Aeromonas* were performed with $^{55}Fe^{3+}$ and a ^{14}C-labeled artificial synthetic siderophore. They demonstrate a modified shuttle mechanism. An iron-free siderophore molecule is strongly bound to the receptor protein and Fe^{3+} exchange occurs between an approaching ferri-siderophore and the bound one, which then is transported into the cell (*337*); *cf.* the pyoverdins (Sect. 2.1).

Alterobactin A is a cyclodepsipeptide from *Alteromonas luteoviolacea*, with N^8-DHB-(4*S*),8-diamino-(3*R*)-hydroxy-octanolyl-D-Ser-Gly-L-Arg-L-*threo*-3-hydroxy-Asp-Gly-L-*threo*-3-hydroxy-Asp having an ester bond between the C-terminal carboxyl group and Ser. It is accompanied by its hydrolysis product alterobactin B (Fig. 8, **26**, **27**) (*298*). Alterobactin A forms a 1:1 complex with Fe^{3+} with an

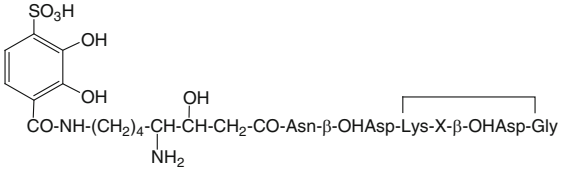
Table 3. Amonabactins (**25**)

R^1-NH-$(CH_2)_4$-CH(NH_2)-CO-NH-CH(COR_2)-$(CH_2)_4$-NH-DHB

Name	R^1	R^2
Amo T 789	DHB-Gly	D-Trp
Amo P 750	DHB-Gly	D-Phe
Amo T 732	DHB	D-Trp
Amo P 693	DHB	D-Phe



26: with ester bond between OHAsp and Ser
27: without ester bond between OHAsp and Ser



28: X = Lys, **29**: X = Arg

Fig. 8. Alterobactins (**26, 27**), pseudoalterobactins (**28, 29**)

unexpectedly high complexing constant (between 10^{49} and 10^{53}), higher than that of enterobactin above, despite the fact that two complexing sites are α-hydroxy acids which bind Fe^{3+} less efficiently than DHB units (*148*). A synthesis has been reported (*83*) (see Sect. 8.2).

Related structures are the pseudoalterobactins A and B from *Pseudoalteromonas* sp. (Fig. 8, **28**, **29**) (*183*), one of the rare examples of bacterial metabolites containing an aromatic sulfonic acid (*40*). Chiralities of the constituents were not determined.

Heterobactin A and B (**30**) are produced by *Rhodococcus erythropolis* (*59*). They are based on the sequence Orn-Gly-cOHOrn. The N^5-amino group of Orn is substituted by a DHB group. In heterobactin B, the α-amino group of Orn is free (R = H); in heterobactin A, R is probably a 2-hydroxybenzoxazolyl-carbonyl group.

30 DHB-NH-$(CH_2)_3$-CH(NHR)-CO-NH-CH_2-CO-cOHOrn

Rhodobactin (**31**) was isolated from *Rhodococcus rhodochrous* (*86*). A sequence of four Orn units derivatized in different ways is linked together. The nitrogen atoms of the N-terminal Orn are substituted with DHB groups, the N-terminal Orn is followed by two Orn moieties, for which the N^5-amino groups are transformed into urea units (NH_2CONH-), and the C-terminus is cOHOrn. The stereochemistry of the Orn units was not determined. Rhodobactin forms a 1:1 Fe^{3+}/Lig complex. Iron uptake was studied with $^{55}Fe^{3+}$.

31 DHB-NH-$(CH_2)_3$-CH(NH-DHB)-CO-(NH-CH-CO)$_2$-CO-cOHOrn
with a branch $(CH_2)_3$-NH-$CONH_2$ on the CH

Thermobifida fusca, belonging to the Actinomycetales, produces three closely related siderophores, namely, the fuscachelins (*92*). Fuscachelin B starts with the sequence DHB-Arg-Gly-Gly-Ser, which is bound to the hydroxylated N^5-amino group of Orn. Its N^2-amino group (the carboxyl group is free) is bound to the C-terminus of the sequence Gly-Gly-Arg-DHB (**32**). Fuscachelin A is considered to be the genuine metabolite, with B and C degradation products.

32 DHB-Arg-Gly-Gly-Ser-N^5-OHOrn-N^2H-Gly-Gly-Arg-N^2-DHB

In fuscachelin C the carboxyl group of Orn forms an amide, while in fuscachelin A an ester bond occurs between the carboxyl group of Orn and the hydroxy group of Ser.

2.8. Lipopeptidic Siderophores

From *Burkholderia cepacia* (formerly *Pseudomonas cepacia*) three siderophores named ornibactins (**33**) were isolated for which the structures were determined by

degradation and NMR studies (*335*, *336*) as containing 3-hydroxy fatty acid residues and putrescine that blocks the C-terminus, with acyl = R-CHOH-CH_2-CO (R = CH_3, C_3H_7, C_5H_{11}).

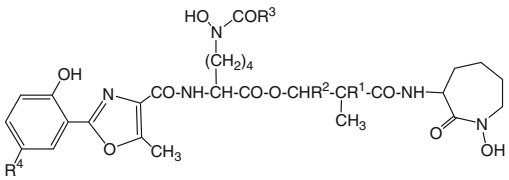
33 acylOHOrn-OHAsp-Ser-formylOHOrn-NH-$(CH_2)_4$-NH_2

The three ornibactins are accompanied by minor components, which contain an additional oxygen atom. Their structure has not been investigated. Ornibactins are the main siderophores of a series of *Burkholderia* strains accompanied in part by pyochelin (Sect. 5) and cepabactin (Sect. 6) (*235*). A further *B. cepacia* siderophore is cepaciachelin (Sect. 3.2) (*15*). The iron acquisition by the various siderophores of *B. cepacia* has been discussed in detail (*359*).

From *Nocardia* strains several closely related compounds (nocobactins, formobactin, amamistatins) were isolated that contain three typically Fe^{3+} binding sites, two hydroxamate units, and a hydroxyphenyloxazole structure (*cf.* Sect. 3.2 below). The C-terminus is *N*-hydroxy-*cyclo*-Lys bound to a long chain 3-hydroxy fatty acid, whose hydroxy group is esterified by N^6-acyl-N^6-hydroxy-Lys, the α-amino group of which is bound to 2-*o*-hydroxyphenyl-5-methyl-oxazole-4-carboxylic acid (Table 4). For the amamistatins the configuration of the cyclic lysine was determined as L, the open one as D, and that of C-3 of the fatty acid as (*S*). The involvement in the iron metabolism was not investigated.

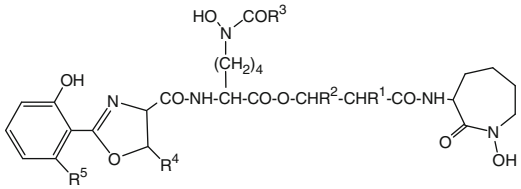
Structurally related with the nocobactin family are the mycobactins and carboxymycobactins (the latter were also referred to as exochelins, Sect. 2.5 (*128*)) from *Mycobacterium* spp. For reviews see (*85*, *331*, *369*). They have the same basic skeleton as the nocobactins, but the 4,5-double bond of the oxazole ring is saturated. A series of differently substituted representatives has been isolated (see Table 5). The major group comprises mixtures carrying saturated and unsaturated long-chain fatty acid residues as substituents of the hydroxamic acid unit formed by the N^6-amino group of lysine. For some ("J", M, and N), the fatty acid residues are located in the chain, as for the nocobactins. Representatives of the MAIS group (*Mycobacterium avium*, *M. intracellulare*, *M. scrofulaceum*) possess two long

Table 4. The nocobactin family



Compound	R^1	R^2	R^3	R^4	References
nocobactin NA	H	C_9H_{19},$C_{11}H_{23}$	CH_3	H	(*294*, *295*)
formobactin	CH_3	C_9H_{19}	H	H	(*252*)
amamistatin A	CH_3	C_7H_{15}	H	H	(*191*, *341*)
amamistatin B	CH_3	C_7H_{15}	H	OCH_3	(*191*, *341*)

Table 5. The mycobactin family (adapted from (*369*))



Mycobactin	R^1	R^2	R^3	R^4	R^5	References
A	H	CH_3	C_{13}	H	CH_3	(*332*)
F	H	CH_3	$C_{9\text{-}17}$	CH_3	H	(*332*)
H	H	CH_3	$C_{17,19}$	CH_3	CH_3	(*381*)
J	CH_3	$CH(CH_3)_2$	C_{15}	H	H	(*224*)
"J"	CH_3	b	a	CH_3	H	(*18*)
P	CH_3	C_2H_5	$C_{13\text{-}19}$	H	CH_3	(*329*)
R	CH_3	C_2H_5	C_{19}	H	H	(*332*)
S	H	CH_3	$C_{13\text{-}19}$	H	H	(*381*)
T	H	CH_3	$C_{14\text{-}21}$	H	H	(*330*)
M	CH_3	$C_{14\text{-}17}$	CH_3	CH_3	H	(*332*)
N	CH_3	$C_{14\text{-}17}$	C_2H_5	CH_3	H	(*332*)
MAIS	CH_3	b	a	H	H	(*18*)
	CH_3	b	a	CH_3	H	(*18*)
carboxy	H	CH_3	c	H	H	(*128*)
	H	CH_3	c	CH_3	H	(*128*)
	CH_3	C_2H_5	d	CH_3	H	(*199*, *292*)

a – unsaturated alkyl chain, b – saturated alkyl chain, c – saturated and unsaturated dicarboxylic acid methyl ester, d – unsaturated dicarboxylic acid

chain fatty acid residues. The stereochemistry of most chiral centers has been determined. For the Fe^{3+} complex of mycobactin P an X-ray analysis is available (*157*). For the carboxymycobactins the residues R^3 in Table 5 are saturated or unsaturated alkyl groups with terminal carboxyl groups or their methyl esters.

Transvalencin Z (*245a*) from *Nocardia transvalensis* could be a precursor or side product of mycobactin biosynthesis, possibly acquired from a vagabonding gene. It comprises the left part of the serine/salicylic acid based molecules (Table 5 $R^4 = R^5 = H$) and ends with N^6-formyl-Lys ($R^3 = H$, no *N*-hydroxy group). The stereochemistry of the two chiral centers was not determined. Transvalencin Z seems not to bind Fe^{3+}.

Iron uptake of *Mycobacterium smegmatis* involving mycobactin S was studied with $^{55}Fe^{3+}$ (*293*). Mycobactin is not given off into the surrounding medium but is located instead in the lipid envelope of the cell and is active in the trans-membrane transport of Fe^{3+} (taxi mechanism). Iron is relased at the inside of the membrane by a reductive mechanism. There is some evidence that salicylic acid is the extracellular siderophore.

Corrugatin (**34**) (Fig. 9) is the siderophore of *Pseudomonas corrugata* (*302*). It was also found as secondary siderophore of several pyoverdin producing *Pseudomonas* strains as *P. fluorescens*, occasionally in slightly modified forms such as

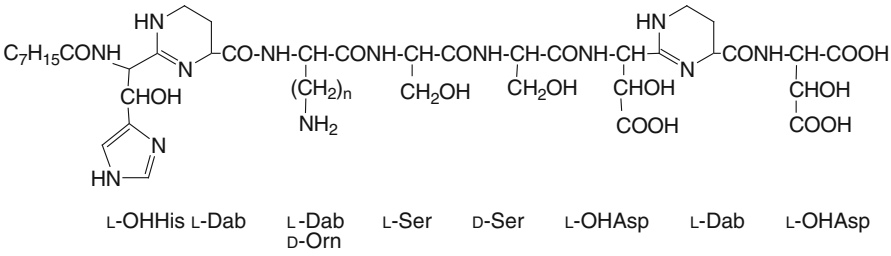


Fig. 9. Corrugatin (n = 2, L-Dab) (**34**) and ornicorrugatin (n = 3, D-Orn) (**35**)

36: RCO-OHAsp-Dab-Ser-acetylOHOrn-Ser-acetylOHOrn
37: RCO-OHAsp-Ser-Ser-Gln-acetylOHOrn-Ser-acetylOHOrn
38: RCO- acetylOHOrn-acetylOHOrn-Ser-acetylOHOrn (2 D-,1L-Orn, L-Ser)
39: RCO-OHAsp-Ser-Gln-Ser-acetylOHOrn-Dhb-Ser-cOHOrn

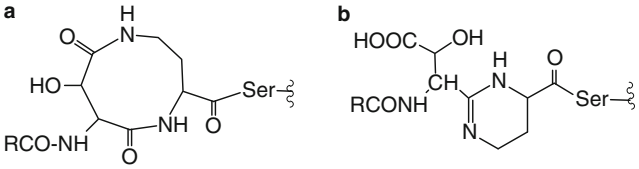


Fig. 10. Amphiphilic marine siderophores

ornicorrugatin (**35**) where one Dab is replaced by Orn (*218*), or with OHHis instead of OHAsp as the C-terminus (*S. Matthijs*, unpublished).

A group of amphiphilic siderophores was isolated from marine bacteria (*410*), the marinobactins (Fig. 10, **36**), from *Marinobacter* sp., aquachelins (Fig. 10, **37**), from *Halomonas aquamarina* (*215*, *217*), the amphibactins (Fig. 10, **38**), from *Vibrio* sp. (*216*), and the loihichelins (Fig. 10, **39**), from *Halomonas* sp. (*150*). They all comprise series of related molecules differing in the nature of the saturated or unsaturated fatty acid (for amphibactins and loihichelins also 3-hydroxy fatty acids) linked to the N-terminus (see also ochrobactins and synechobactins, Sect. 4.1). Structure elucidations were effected by spectroscopic methods and degradation studies. For the marinobactins a N-terminal nine-membered lactam ring was suggested to be formed by an amide bond between the carboxyl group of Asp and the C-4 amino group of Dab (Fig. 10, **a**). It may be suggested that rather a condensation with the amide carbonyl group had occurred (Fig. 10, **b**; *cf.* Chart 1). This would keep the α-hydroxycarboxyl grouping of OHAsp intact, which acts as a binding site for Fe^{3+} and is essential for photolytic degradation. The rather scarce structural data presented do not allow a decision to be made. The siderophores show a strong affinity to lipid membranes (*389*). The Fe^{3+} complexes of aquachelins and marinobactins suffer degradation under sunlight irradiation. For the Fe^{3+}-aquachelin complexes the formation of Fe^{2+}, of hydrophobic and of hydrophylic cleavage

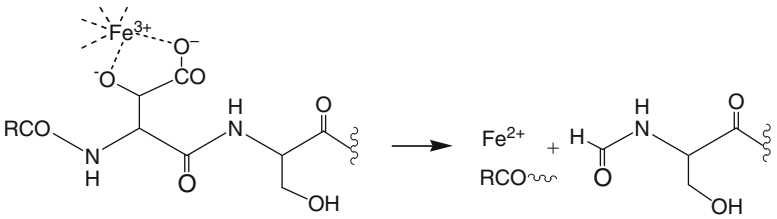


Chart 2. Light-induced degradation of Fe^{3+}-aquachelins

products was observed. For the latter a *N*-formyl-Ser terminus was suggested based on mass spectral data (Chart 2) (*12*). There is evidence that this type of photolytic degradation is common for siderophores containing α-hydroxycarboxyl ligands (*13*, *150*, *401*).

2.9. Pseudomonas mendocina Siderophores

From *Pseudomonas mendocina* five siderophores were isolated by chromatography. They are reported to have identical molecular masses of 1,152 Da (the also reported (*3a*) value of 929 Da is an error; *L. E. Hersman*, private communication) and an identical amino acid composition, which has not been revealed (*141a*). Color reactions show the presence of a hydroxamate, but not of a catecholate grouping. A gene analysis suggests a partial sequence acyl-Asp-Dab-Ser-formylOHOrn-Ser-formylOHOrn where asparagine could be OHAsp and the C-terminal ornithine cOHOrn (*9b*). In which way the five isomeric siderophores with identical molecular masses differ from each other is not clear.

3. Siderophores Based on Diamino- and Triaminoalkane Skeletons

3.1. Rhizobactin

Rhizobactin (**40**) is the siderophore of *Rhizobium meliloti* (*328*). It contains one α-hydroxycarboxylic acid and two α-amino acid units as probable binding sites for Fe^{3+}. Acid hydrolysis yields *inter alia* L-malic acid. The stereochemistry of the other two chiral centers is not known.

40 $HOOC\text{-}CH(CH_3)\text{-}NH\text{-}(CH_2)_2\text{-}NH\text{-}CH(COOH)\text{-}(CH_2)_4$
$\text{-}NH\text{-}CO\text{-}CH_2\text{-}CHOH\text{-}COOH$

3.2. *Catecholate Siderophores*

For other catecholate siderophores, see the peptide-based siderophores above (Sect. 2.7) and the citric acid derivatives below (Sect. 4.3); for a review on syntheses, see (*24*), for a general review, (*38*).

The tricatecholate siderophore protochelin (**41**) (Fig. 11) was obtained from a methanol – bacterium (*351*). Subsequently it was also found to be produced by *Azotobacter vinelandii* (*72*, *360*) together with its constituents 2,3-dihydroxybenzoic acid, azotochelin (bis-DHB lysine) (*70*) and aminochelin (mono-DHB cadaverine) (*273*). Cepaciachelin from *Burkholderia cepacia* (*15*) lacks the DHB residue from the aminochelin part of protochelin. The amino acid in all compounds is L-lysine. *Azotobacter vinelandii* shows an interesting rationale when confronted with a deficiency in iron supply. At concentrations >7 μM, 2,3-dihydroxybenzoic acid is secreted, between 3 and 7 μM, the di- and tricatecholate siderophores are produced, and at still lower concentrations, it is resorted to azotobactin D (see above Sect. 2.2) (*72*). Myxochelin A from *Angiococcus disciformis* (*197*) and *Nonomuraea pusilla* (*239a*) can be considered as a reduction product of azotochelin (lysinol instead of Lys). The absolute configuration of lysinol (*S*) was determined by synthesis. Both antipodes show about the same antitumor activity (*239a*).

Pistillarin was first isolated from *Clavariadelphus pistillaris* and from several *Ramaria* spp. (Basidiomycetes) (*334*). Recently, it was found to be produced also by the marine fungus *Penicillium bilaii* (*56*). Like siderochrome II below it is a spermidine derivative substituted only at the terminal NH_2-groups (N^1, N^{10}-di-(3,4-dihydroxy)benzoyl-spermidine). Its synthesis and that of siderochrome II was reported, their siderophore activity and their complexation with Fe^{3+} (1:1 complexes) was investigated (*102*, *299*). A derivative of pistillarin substituted at all three amino functions has not been reported yet.

When DHB is bound to serine or threonine cyclization may occur resulting in an oxazoline ring (*cf.* above anachelin, Sect. 2.3, and mycobactins, Sect. 2.8). It has been discussed whether the oxazoline nitrogen atom may act as a ligand site (see below, (*303*)). This would explain why DHB is replaced by a salicylic acid residue in some cases.

To this group of siderophores belong photobactin (**42a**) from *Photorhabdus luminescens* (Fig. 12) (*66*), derived from 1,4-diaminobutane substituted by DHB and by cyclized DHB-Thr (^{1}H-NMR data indicate that the substituents of the oxazoline ring are in *trans* positions; the absolute stereochemistry is not known),

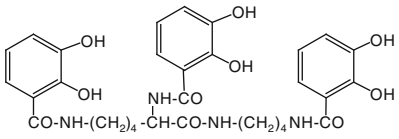
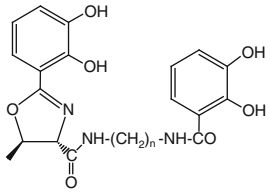
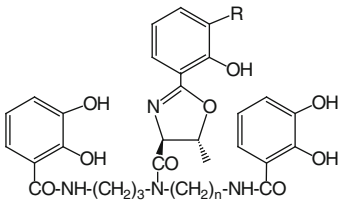


Fig. 11. Protochelin (**41**)



42a: n = 4
42b: n = 3

Fig. 12. Photobactin (**42a**), serratiochelin (**42b)**



43: n = 4, R = OH
44: n = 4, R = H
45: n = 3, R = OH

Fig. 13. Agrobactin (**43**), parabactin (**44**), fluvibactin (**45**)

and its lower homolog serratiochelin (**42b**) from *Serratia marcescens* derived from 1,3-diaminopropane. Its structure including the absolute stereochemistry (L-Thr) was confirmed by synthesis (*101*).

Spermidine derivatives are agrobactin from *Agrobacterium tumefaciens* (Fig. 13, **43**) (*268*), for which the structure was confirmed by X-ray analysis (*109*) and synthesis of the hydrolyzed form (DHB-Thr) agrobactin A (*283*), and parabactin (Fig. 13, **44**) from *Paracoccus denitrificans* (*284*). Two syntheses are reported for parabactin (*28*, *28c*, *255*) (see Sect. 8.3). The open form (parabactin A) as well as the precursors 2,3-dihydroxybenzoic acid and a compound with a free central NH group (N^1, N^{10}-di-DHB-spermidine, siderochrome II) were also found (*347*). The 1:1 Ga^{3+}/Lig complex shows Λ-*cis* configuration (*28a*). Parabactin also forms a 1:1 complex with Fe^{3+} (*347*) for which the structure was investigated by X-ray photoelectron and electron spin resonance spectroscopy. In particular, the question as to whether the oxazoline nitrogen acts as a binding site has been discussed. An experimental proof seemed not to be possible (*303*).

Iron transport was studied using the $^{55}Fe^{3+}$- and ^{3}H-complexes of parabactin (*25*). After a quick uptake of 10% of both labels there was a continuing steady uptake of $^{55}Fe^{3+}$ while the amount of ^{3}H remained constant. This could either mean that after binding to the cell surface $^{55}Fe^{3+}$ only is transferred into the cell ("taxi mechanism") or there is a fast re-export of the ligand. A decision in favor of the

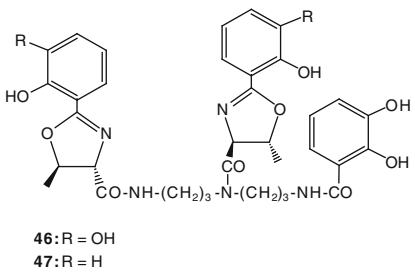


Fig. 14. Vibriobactin (**46**), vulnibactin (**47**)

taxi-mechanism could be reached by offering the Ga^{3+} complex of [^{3}H]-parabactin (Ga^{3+} cannot be released reductively in the cell and hence a re-export of the ligand is not possible). The uptake curve resembled that of ferri-[^{3}H]-parabactin: a small amount of complex is bound to the cell surface, but there is no transport of the ligand in the cell. This is in agreement with temperature studies (30 and 4°C). While the uptake of $^{55}Fe^{3+}$ decreases that of ^{3}H is not influenced.

Fluvibactin (Fig. 13, **45**) from *Vibrio fluvialis* (*391*) differs from agrobactin by replacement of spermidine by norspermidine. Also here the precursor with a free central NH group could be isolated. Vibriobactin from *Vibrio cholerae* (Fig. 14, **46**) contains two cyclized DHB-Thr substituents (*129*). Syntheses of agrobactin, fluvibactin and vibriobactin are published (*26*, *30*, *308*). In vulnibactin from *Vibrio vulnificus* (Fig. 14, **47**) (*264*) two DHB groups are replaced by salicylic acid units. The precursor with a free central NH group was also found.

3.3. Hydroxamic Acid Siderophores

Bisucaberin (**48**) from *Alteromonas haloplanktis* (*181*) is a cyclic dimer of succinyl-(*N*-hydroxycadaverin) (*348*); *cf.* the cyclic trimer proferrioxamine E (Table 6).

48 [-CO-CH_2-CH_2-CO-NH-CH_2-CH_2-CH_2-CH_2-CH_2-NOH-]$_2$

In putrebactin from *Shewanella putrefaciens* (*201*) cadaverine is replaced by putrescine (**49**, R = H). For the cyclic trimer, see proferrioxamine X_2 in Table 6. The arctic *S. gelidimarina* living in a habitat with extremely low iron supply produces a cell-associated hydroxamic acid siderophore with the mass 977 Da for $[M+H]^+$ of unknown structure (*274*).

Alcaligin from *Alcaligenes denitrificans* (*260*) and from *Bordetella* spp. (*244*) is a cyclic dimer of succinyl-N^1,3*S*-dihydroxyputrescine (**49**, R = H) confirmed by synthesis (*402*).

49 [-CO-CH_2-CH_2-CO-NH-CH_2-CHR-CH_2-CH_2-NOH-]$_2$

Table 6. Structures and nomenclature of proferrioxamines (pFO) (adapted from (*110*))[a]

H_2N-$(CH_2)_m$-NOH-CO-CH_2-CH_2-CO-NH-$(CH_2)_n$-NOH-CO-CH_2-CH_2-CO-NH-$(CH_2)_o$-NOH-CO-CH_2-CH_2-CO-NH-$(CH_2)_p$-NOH-CO-CH_2-CH_2-COOH

pFO	cyclic	m	n	o	p	N-terminus	C-terminus	Abbreviation	References
A_1	–	5	5	4	0	–	Ac	pFO_{554Ac}	(*185a*)
A_2	–	5	4	4	0	–	Ac	pFO_{544Ac}	(*185a*)
B	–	5	5	5	0	–	Ac	pFO_{555Ac}	(*30e*)
D_1	–	5	5	5	0	Ac	Ac	Ac-pFO_{555Ac}	(*185b*)
D_2	+	4	5	5	0	–	Suc	pFO_{455c}	(*185a*)
E[b]	+	5	5	5	0	–	Suc	pFO_{555c}	(*155a*, *186*)
G_1[c]	–	5	5	5	0	–	Suc	pFO_{555}	(*186a*)
G_{2a}	–	5	5	4	0	–	Suc	pFO_{554}	(*115*)
G_{2b}[c]	–	5	4	5	0	–	Suc	pFO_{545}	(*115*)
G_{2c}[c]	–	4	5	5	0	–	Suc	pFO_{455}	(*115*)
H	–	5	5	0	0	Suc	Ac	Suc-pFO_{55Ac}	(*1*)
T_1	+	5	5	5	5	–	Suc	pFO_{5555c}	(*115*)
T_2	+	4	5	5	5	–	Suc	pFO_{4555c}	(*115*)
T_3	+	3	5	5	5	–	Suc	pFO_{3555c}	(*115*)
X_1	+	4	4	5	0	–	Suc	pFO_{445c}	(*115*)
X_2	+	4	4	4	0	–	Suc	pFO_{444c}	(*115*, *398*)
X_7	+	3	5	5	0	–	Suc	pFO_{355c}	(*115*, *398*)

[a]Structures were not established for C and F (R_f values and physical constants) (*30d*), T_4-T_6, and X_8, X_9 (mass spectra) (*115*)
[b]Identical with norcardamin (*186*, *338*)
[c]Accompanied by "truncated" compounds without the terminal succinic acid unit (G_{1t}, G_{2bt}, G_{2ct}) (*115*, *398*)

Alcaligin forms at *pH* 2.0 a 1:1 and at *pH* 6.0 a 2:3 Fe-to-ligand complex. The structure (Plate 3) of the $(Fe^{3+})_2Lig_3$ complex was studied by X-ray analysis (*156*). One ligand bridges two metal ions while the remaining two are coordinated with a single Fe^{3+} each. The metal centers show Λ-configuration.

Alcaligin E from *Alcaligenes eutrophus* is described from color tests as a phenolic siderophore (*126a*). According to a recent publication (*90a*) it is identical with staphyloferrin B, a citrate siderophore (Sect. 4.2). No further information is given to resolve these discrepancies.

A group of related siderophores comprises the desferri- or deferriferrioxamines (occasionally abbreviated as desferrioxamines) or proferrioxamines. Originally they were obtained from Actinomycetes, mainly *Nocardia* and *Streptomyces* spp. (*187*) and later found to be produced also by *Erwinia* spp. (several representatives) (*e.g.* (*30a*, *113*, *115*, *180*)), *Arthrobacter simplex* (B), *Chromobacterium violaceum* (E) (*246a*), and by *Pseudomonas stutzeri* (several) (*229a*, *246*, *398*). They consist of three (or in rare cases four) mono-*N*-hydroxy-1,4-diaminobutane (putrescine), mono-*N*-hydroxy-1,5-diaminopentane (cadaverine) or (rarely) mono-*N*-hydroxy-1,3-diaminopropane units connected by succinic acid links. The hydroxylated terminus carries an acetyl or a succinyl (as in the structural formula heading Table 6)

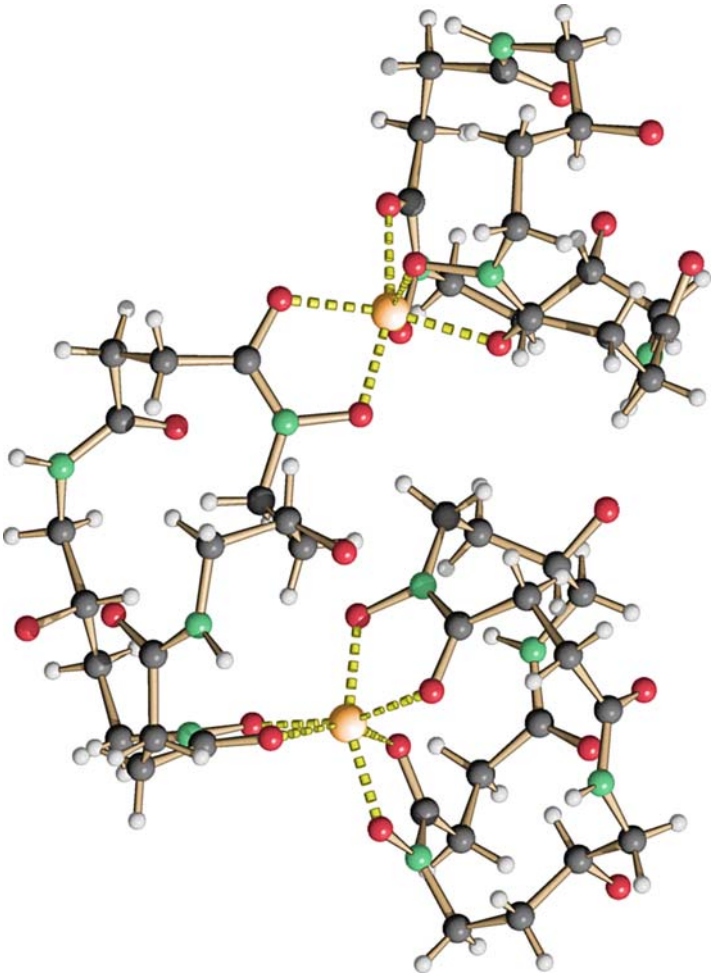


Plate 3. X-ray structure of ferri-alcaligin (ferri-**49**)

residue, and in the latter case the free carboxyl group and the free N-terminus may form a macrolactam. The terminal acid residue can also be missing (referred to as "truncated") (*115*, *398*). By feeding of suitable diamino precursors to the culture medium unnatural analogs can be obtained (*111*, *194*, *227*). At *pH* values above 6.5 $(Fe^{3+})_2Lig_3$ complexes prevail, in more acidic media Fe^{3+}Lig is formed (*194*). The crystals of the Fe^{3+}Lig complexes of ferrioxamine D_1 and E are racemic mixtures of Λ-*cis* and Δ-*cis* coordination isomers (*154*, *366a*). The outer membrane receptor protein of *Erwinia amylovora* was structurally determined (*180*). Siderophore activity was demonstrated for ^{55}Fe-labeled ferrioxamine E (*30a*). For the mass spectrometric analysis, see (*112a*).

Originally the various natural representatives had been designated by capital letters, but later a nomenclature system was proposed (*110*). In short, the indices and modifications as listed in Table 6 (p = 0 means that the entire fourth diaminoalkane-succinyl unit is missing) are grouped around the acronym pFO. The system is essentially self-explanatory; for details and possible extensions see the original publication.

4. Citrate Siderophores

For a review, see (*39*). Some citrate siderophores are accompanied by cyclic imide structures formed by the loss of water from the central carboxyl group and a lateral amide NH (Chart 3). They are usually designated by an A following the name of the siderophore. Free citric acid can be a true siderophore, *e.g.* for *Bradyrhizobium* spp. (*205*), *Pseudomonas aeruginosa* (*213*), and *Mycobacterium smegmatis* (*228a*). The mode of the uptake differs. *Bradyrhizobium* and *Pseudomonas* incorporate ferric citrate but *Pseudomonas* shows also a citrate mediated Fe^{2+} uptake, while in the case of *Mycobacterium* no citrate enters the cell. Ferric citrate is a complex system depending on the *pH* of the solution and the relative concentration of the two constituents (*333a*, *333b*). In an acidic milieu equimolar concentrations form $[FeCit]^{-}$, at about *pH* 4 polymerization starts resulting at *pH* 8–9 in an insoluble complex with an iron hydroxide core and citrate ions bound to the surface. With a citrate excess species like $[FeCit_2]^{5-}$ are discussed.

It should be mentioned that the central carbon atom of citric acid becomes chiral when the two peripheral carboxy groups are substituted differently (examples will be found below). For enzyme reactions it is a prochirality center. This has been shown for vibrioferrin (**58**) and staphyloferrin B (**59**).

4.1. Siderophores with Two Hydroxamic Acid Units

In siderophores of this series, 1,3-diaminopropane, 1,5-diaminopentane, or lysine (by its α-amino group) is connected to the outer two carboxyl groups of citric acid.

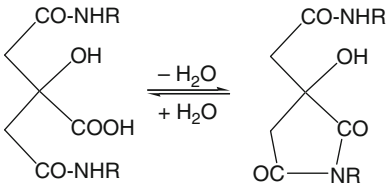


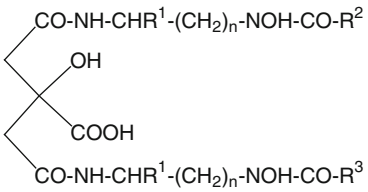
Chart 3. Cyclization of citrate siderophores to amidic structures

These spacers, in turn, are acylated and derivatized by a *N*-hydroxy group thus forming hydroxamic acids. For a synthesis concept see (*404*).

Schizokinen (Fig. 15, **50**) was first isolated from *Bacillus megaterium* (*53*), subsequently from *Ralstonia solanacearum* (*43*), *Rhizobium leguminosarum* (*339*), and several species of the cyanobacterium *Anabena* (*e.g.* (*326*)). It was named after its cell division promoting effect observed with *Bacillus* cultures (*200*). Its structure was elucidated by degradation and spectral data and confirmed by synthesis (*43*, *202*, *237*, *248*). For a compilation of details on structural data the review (*39*) should be consulted. Both natural and synthetic schizokinen is accompanied by the cyclized schizokinen A (*43*, *202*, *237*, *248*). Schizokinen forms a 1:1 complex with Fe^{3+}, but at the central hydroxy group acetylated schizokinen yields $(Fe^{3+})_2Lig_3$. This proves that the central unit is one of the binding sites (*285*). Also *N*-deoxyschizokinen from *Bacillus megaterium* lacking one hydroxamic acid unit still binds Fe^{3+} (*158*). Whether it acts as a siderophore is not known.

The schizokinen-mediated Fe^{3+} transport in *Bacillus megaterium* was studied by double labelling with ^{59}Fe and ^{3}H (*8*). At 37°C, uptake of ^{59}Fe and of ^{3}H are parallel during the first 30 sec, then that of ^{59}Fe continues until it levels off after 2 min, while that of [^{3}H]-schizokinen drops to a low constant level. At 0°C, uptake of both labels reaches this low level which is obviously due to the binding of the ferrisiderophore to the cell surface. At 37°C, transport into the cell, release of iron, and re-export of the ligand follow. Apparently a shuttle mechanism takes place, *cf.* the experimental results obtained with parabactin (Sect. 3.2) indicative of a taxi mechanism.

Arthrobactin (Fig. 15, **51**) was obtained from *Arthrobacter* spp. and originally described as the growth factor of *A. terregens*, the "terregens factor" (*51*). Its structure was elucidated (*207*) and confirmed by synthesis (*202*). Also the structure



50: R^1 = H, R^2 = R^3= CH_3, n = 2
51: R^1 = H, R^2 = R^3 = CH_3, n = 4
52: R^1 = H, R^2 = R^3 = (*E*)-CH=CH-$(CH_2)_4$-CH_3 , n = 2
53: R^1 = COOH, R^2 = R^3 = CH_3, n = 4
54: R^1 = COOH, R^2 = R^3 = (*E*)-CH=CH-C_6H_5 , n = 4
55: R^1 = COOH, $R^2$and R^3 alkyl or alkenyl groups, n = 4
56: R^1 = H, R^2 = CH_3, R^3 = (*E*)-CH=CH-$(CH_2)_6$-CH_3 , n = 2
57: R^1 = H, R^2 = CH_3, R^3 = alkyl groups, n = 2

Fig. 15. Citrate siderophores with two hydroxamic acid units

of acinetoferrin from *Acinetobacter haemolyticus* was established (Fig. 16, **52**) (*265*) and confirmed by synthesis (*375*). It shows strong interaction with lipid membranes like the marine liposiderophores above (*211*) (Sect. 2.8).

Aerobactin (Fig. 15, **53**) was first isolated from *Aerobacter* (*Enterobacter*) *aerogenes* (*126*), *Enterobacter cloacae* (*368*) and subsequently from various enterobacteria such as *Escherichia* (*376*), *Salmonella* (*225*), *Shigella* (*277*), *Yersinia* (*340*), but also from *Erwinia carotovora* (*163*), *Pseudomonas* sp. (*52*) and *Vibrio* spp. (*141*, *266*). Aerobactin is an important virulence factor for enterobacteria (*75*). Aerobactin contains L-lysine. A synthesis is described (*222*). The bright orange Fe^{3+} complex was investigated in detail (predominant Λ configuration in solution, stability constant, redox potential) (*138*). Fe^{3+} transport was studied by double labelling (^{59}Fe and ^{3}H) (*8*). The results corresponded to those obtained with schizokinen. Aerobactin binds to the same receptor as the bacteriocin cloacin DF13 and thus alleviates the growth inhibiting effect of the latter (*368*).

Nannochelin C (Fig. 15, **54**) from the myxobacterium *Nannocystis exedens* contains two L-Lys and two (*E*)-cinnamic acid units. The reported mono- and di-methyl esters (nannochelin B and A) may be artifacts from the work-up (*198*). A synthesis is described (*29*) (see Sect. 8.4). The ochrobactins (Fig. 15, **55**) isolated from the sea-shore bacterium *Ochrobactrum* sp. (*214*) with the spacer L-lysine are membrane active due to the fatty acid residues (saturated C_8 and (2*E*)-unsaturated C_8 and C_{10}); *cf.* lipopeptidic siderophores in Sect. 2.8.

Rhizobactin 1021 (Fig. 15, **56**) (for rhizobactin, see diaminoalkane-based siderophores, Sect. 3.1) from *Rhizobium meliloti* (*281*), contains an acetyl and an (*E*)-decenoyl group. Its Fe^{3+} complex in aqueous solution is Λ-configured and forms an equilibrium between a monomeric and a dimeric form that can be separated by chromatography. A synthesis is described (*404*).

Synechobactins (Fig. 15, **57**) from the cyanobacterium *Synechococcus* (*165*), contain an acetyl and C_{12}-, C_{10}-, and C_8-saturated acid residues and thus belong to the amphiphilic marine siderophores (*cf.* Sect. 2.8). Both rhizobactin 1021 and the synechobactins are substituted unsymmetrically. Hence, for each, the central C-atom of citric acid is chiral, but its stereochemistry has not been determined.

Awaitins are synthetic homologs of siderophores (A: **53**, n = 3; B: **50**, n = 3; C: **53**, n = 2) "awaited" to be found in nature, so far without success (*405*).

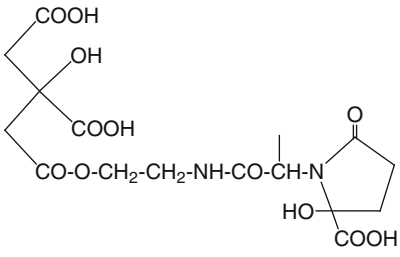


Fig. 16. Vibrioferrin (cyclic form) (**58**)

4.2. *Siderophores with 2-Oxoglutaric Acid Units*

N-Alkylated 2-oxoglutaric acid derivatives cyclize at neutral *pH* values to two epimeric 5-carboxy-5-hydroxy-2-oxopyrolidine structures (Chart 4). In this way, α-hydroxycarboxylic acid groupings are formed that can act as ligand sites for Fe^{3+}.

Vibrioferrin (**58**, Fig. 16) was isolated from *Vibrio parahaemolyticus*. The stereochemistry of the central citric acid C-atom is *R*, that of the alanine part is *S* as shown by stereospecific synthesis (*411*). Iron uptake was studied with $^{55}Fe^{3+}$ proving that vibrioferrin acts as a siderophore despite the fact that it has only five ligand sites, the two α-hydroxy acids and the free citric acid carboxyl group. Possibly a solvent molecule satisfies the eighth octahedral position (*393*, *411*). Vibrioferrin is also formed by *Marinobacter* spp. It is a week Fe^{3+} chelator (complexing constant 10^{24}). Its Fe^{3+} complex is very susceptible to photodegradation by oxidative decarboxylation of the cyclized 2-oxoglutaric acid unit yielding a succinimide ring. This species cannot bind Fe^{3+}. The concomitantly formed Fe^{2+} (*cf.* Chart 2) is reoxidized to fairly soluble Fe^{3+} hydroxo complexes, which are readily taken up by the bacteria (*410*).

Staphyloferrin B (**59**, Fig. 17) is produced together with staphyloferrin A (see below Sect. 4.4) by *Staphylococcus hyicus* and other staphylococci (*94*, *131*), by *Ralstonia eutropha* (*250*) (= *Cupriavidus metallidurans* (*90a*)). Comparison of its CD spectrum with those of model compounds suggests the (*S*)-configuration of the central citric acid C-atom. Mass spectral investigations show a 1:1 Fe^{3+}-to-ligand ratio, and NMR studies of the Ga^{3+} complex confirm the participation of the two α-hydroxy- and of the α-amino acid functions in complex formation. Uptake studies with $^{55}Fe^{3+}$ showed that staphyloferrin B acts as a siderophore, but it is less efficient than staphyloferrin A.

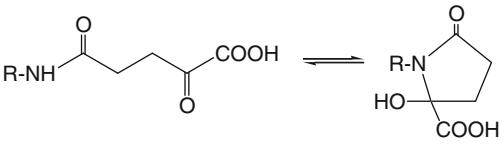


Chart 4. Cyclization of 2-oxoglutaric acid substituents

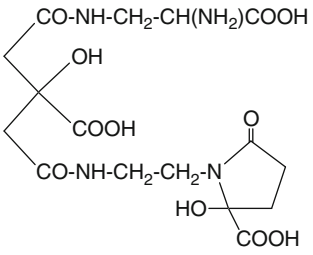


Fig. 17. Staphyloferrin B (cyclic form) (**59**)

Achromobactin (**60**, Fig. 18) is produced by *Erwinia chrysanthemi* in addition to chrysobactin (see above under the catecholate siderophores, Sect. 2.7). It has two chiral centers, a L-Dab unit and the central citric acid C-atom (not determined) (*249*). Recently, achromobactin was also found to be produced by *Pseudomonas syringae* (*30b*), a very versatile bacterial species (see pyoverdin, Sect. 2.1, and yersiniabactin, Sect. 5).

4.3. Siderophores with Two Catecholate Units

In petrobactin, spermidine residues are bound to citric acid substituted with 3,4-dihydroxybenzoyl (*27*), and not 2,3-dihydroxybenzoyl units (Fig. 19, **61**), as assumed originally (*14*). One or both of the substituents can carry a sulfonic acid group in the 2-position of the aromatic ring (Fig. 19, **62** and **63**) (*142*, *149*); *cf.* also (*40*). Petrobactin was originally obtained from *Marinobacter hydrocarbonoclasticus* (*14*) and subsequently from *Bacillus anthracis* (*195*, *382*), *B. cereus* and *B. thuringiensis* (*195a*), its sulfonated derivatives from *Marinobacter* spp. It is probably identical with the incompletely characterized anthrachelin (*123*).

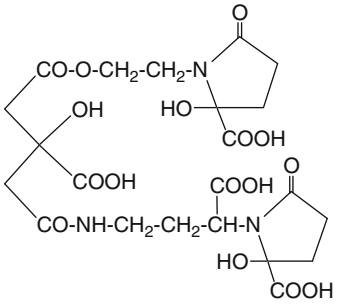
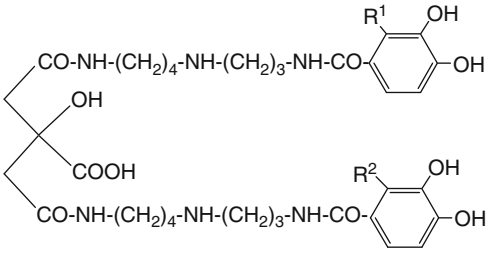


Fig. 18. Achromobactin (cyclic form) (**60**)



61: $R^1 = R^2 = H$
62: $R^1 = H$, $R^2 = SO_3H$
63: $R^1 = R^2 = SO_3H$

Fig. 19. Petrobactin (**61**), petrobactin monosulfonic acid (**62**), petrobactin disulfonic acid (**63**)

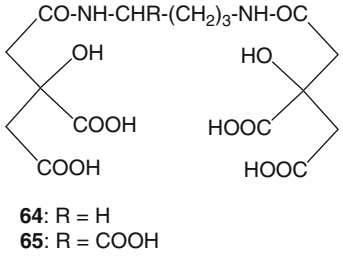


Fig. 20. Rhizoferrin (**64**), staphyloferrin A (**65**)

4.4. Siderophores with Two Citric Acid Units

(*S*,*S*)-(*enantio*)-Rhizoferrin (Fig. 20, **64**) was obtained from *Ralstonia pickettii* (*251*). It is the optical antipode of the fungal (*R*,*R*)-rhizoferrin first isolated from *Rhizopus microsporus* (*93*) and subsequently found to be a common siderophore of Zygomycetes (*358*). It is accompanied by two dehydration products, which are due to the formation of one or two imide rings (*cf.* Chart 3). UV spectral studies revealed that rhizoferrin forms a 1:1 Fe^{3+}-to-ligand complex despite the fact that it has only two α-hydroxy acid binding sites (*95*). NMR studies of the Ga^{3+} complex proved the twofold symmetry of the complex and showed that only the carboxyl groups, but not the hydroxy groups are deprotonated between *pH* 5.5 and 9.0. The Fe^{3+} complex is chiral and shows Λ-configuration (*58*). Uptake studies suggest a shuttle mechanism (*61*). While *Ralstonia* accepts both antipodes with equal rates *Rhizopus* shows a clear preference for its native (*R*,*R*)-enantiomer (*251*).

Staphyloferrin A (Fig. 20, **65**) is a second siderophore of *Staphylococcus* spp. (*226*). D-Ornithine connects the two citric acid parts. Due to the unsymmetrical link the central C-atoms of the citric acid units are chiral, but their stereochemistry has not been determined. Another consequence of the asymmetric structure is that two mono- and one di-dehydration products are observed. Staphyloferrin A forms a 1:1 Fe^{3+}-to-ligand complex, which is preferentially Λ-configured. For steric considerations only *cis*-(*SR*′) or *cis*-(*RS*′) arrangements can be considered. Uptake experiments with ^{55}Fe showed that it is a true siderophore (*193*).

4.5. Legiobactin

Legionella pneumophila produces a siderophore named legiobactin, which shows no catecholate or hydroxamate reactions (*206*). Enzymatic studies suggest a citrate structure in agreement with the data obtained by mass spectrometry (molecular mass *ca*. 350 Da) and NMR (three carbonyl and ten aliphatic C atoms). It is not clear yet as to whether legiobactin is essential for the iron acquisition in the aqueous habitat of the bacterium or during lung infection (*2*, *65*).

5. Pyochelin and Related Structures

This group comprises condensation products of salicylic acid with cysteine giving a thiazoline ring. For a review, see (*310*). Some structurally related compounds will also be mentioned here. Salicylic acid isolated from *Burkholderia* (*Pseudomonas*) *cepacia* was named azurochelin (*333*). It was found to act as a siderophore, *e.g.* for *Pseudomonas fluorescens* (*230*) and *P. syringae* (*178*); see also *Mycobacterium smegmatis* (Sect. 2.8). For details on the siderophore activity of salicylic acid, see (*359*).

The structure of pyochelin (for a detailed bibliography, see (*37*)), a secondary siderophore of *Pseudomonas aeruginosa* and of *Burkholderia cepacia* was established (*73*) as 2-(2-*o*-hydroxyphenyl-2-thiazolin-4-yl)-3-methylthiazolidine-4-carboxylic acid. It consists of a mixture of two easily interconvertible stereoisomers (pyochelin I and II) differing in the configuration of C-2″. They can be separated by chromatography, but in methanolic solution (not in DMSO) the equilibrium (*ca.* 3:1) is restored quickly. For a discussion of the mechanism of isomerization, see (*37*, *317*).

The relative and absolute stereochemistry (4′*R*,2″*R*,4″*R*) of pyochelin I (Fig. 21, **66**) were established by an X-ray analysis of its Fe^{3+} complex (*316*). Fe^{3+} is associated with the phenolate and the carboxylate oxygen ions and with the two nitrogen atoms. Two of these units are bridged by an acetate ion and a water molecule satisfying the remaining two ligand loci of Fe^{3+} (Plate 4). However, by titration a (Fe^{3+})/pyochelin ratio of 1:2 has been determined at *pH* 2.5 (*370*). This may be due to a partial protonation of the complexing sites. From *Burkholderia cepacia*, a mixed complex was obtained comprising Fe^{3+}/pyochelin/cepabactin 1:1:1 (see Sect. 6 below) (*188*). An X-ray analysis has been performed of ferri-pyochelin bound to its outer membrane receptor (*67a*). Pyochelin II has the configuration (4′*R*,2″*S*,4″*R*). It does not complex Fe^{3+} (*140*).

Several syntheses resulting in mixtures of stereoisomers (C-4′ and C-2″) have been developed (*6*, *301*, *397*) (Sect. 8.5). *Pseudomonas fluorescens* CHA0 produces *enantio*-pyochelin (*394*). The two optical antipodes are not accepted reciprocally by the two *Pseudomonas* species.

Pyochelin is a non-ribosomal condensation product of salicylic acid with two molecules of cysteine (*289*). Intermediates with one cysteine unit are aeruginoic acid (Fig. 21, **67**) first isolated from *Pseudomonas aeruginosa* (*390*), and (+)-(*S*)-4,5-dihydroaeruginoic acid, from *Pseudomonas fluorescens* (*57*). Detailed studies (*274a*) suggest that *N*-hydroxybenzoyl-L-cysteine bound to the synthetase

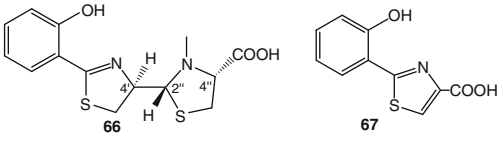


Fig. 21. Pyochelin I (**66**), aeruginoic acid (**67**)

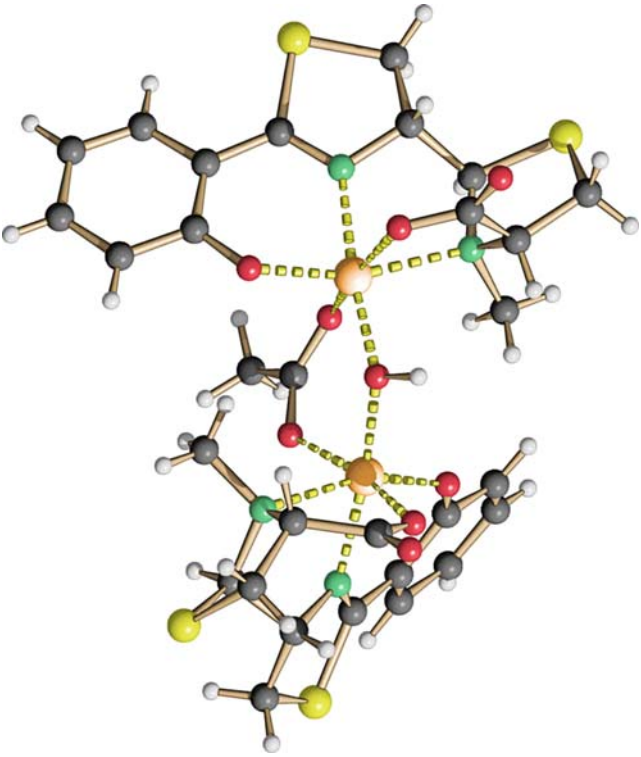


Plate 4. X-ray structure of ferri-pyochelin I (ferri-**66**)

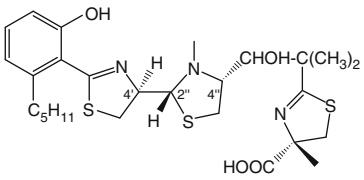


Fig. 22. Micacocidin (**68**)

racemizes, that bound dihydroaeruginoic acid is still a racemate, and that in the further steps only the 4′(*R*) isomer is used.

Micacocidin (Fig. 22, **68**) from *Pseudomonas* sp. complexes Fe^{3+} and other metal ions (*189*, *190*). Whether it acts as a siderophore has not been investigated. A stereospecific synthesis was elaborated (*161*, *161a*), but the same isomerization problems at C-4′ and C-2″ were encountered as had been observed with pyochelin (see Note 14 in (*161*)).

Yersiniabactin (Fig. 23, **69**) was obtained from *Yersinia* spp., and is produced also by *Pseudomonas syringae* (*49*) and *Escherichia coli* (*178*). Its structure was elucidated independently by two groups and given the names yersiniabactin (*96*)

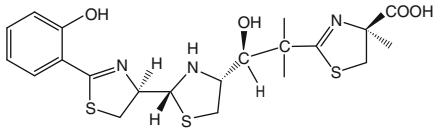


Fig. 23. Yersiniabactin (**69**)

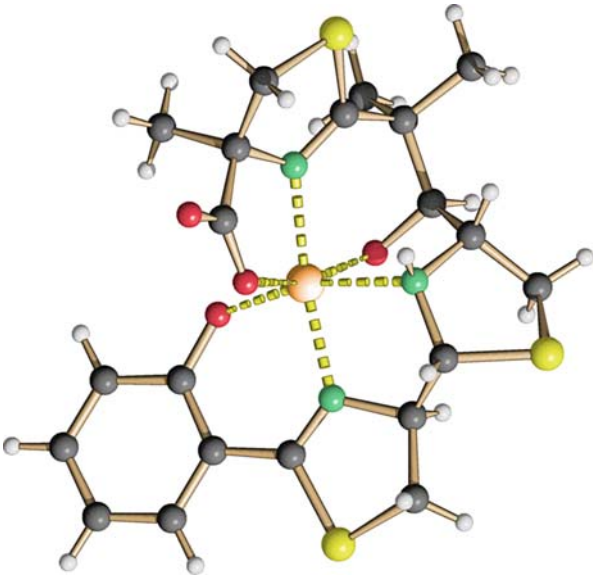


Plate 5. X-ray structure of ferri-yersiniabactin (ferri-**69**)

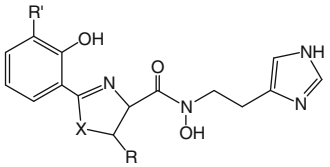
and yersiniophore (*64*). The configurations of the four chiral centers were not determined, but epimerization probably at C-10 (corresponding to C-2″ of pyochelin) was indicated. A recent X-ray analysis (Plate 5) of the Fe^{3+} complex (*238*) established the absolute stereochemistry [N-2 (*R*), C-9 (*R*), C-10 (*R*) as for pyochelin, C-12 (*R*), C-13 (*S*), C-19 (*S*)], with Δ-configuration.

Anguibactin (Fig. 24, **70**) from *Vibrio anguillarum* (*171*) contains DHB condensed with Cys (stereochemistry not determined). It is accompanied by a biosynthetic by-product (*311*) without the histamine part as its methyl ester.

6. Miscellaneous Siderophores

Desferri-ferrithiocin from *Streptomyces antibioticus* (Fig. 25, **71**) (*4*, *254*) is structurally related to the pyochelin group. It is (*S*)-configured and forms a $Fe^{3+}Lig_2$ complex (*131a*).

Cepabactin (Fig. 25, **72**) from *Burkholderia cepacia* (*232*) forms a $(Fe^{3+})Lig_3$ complex (*386*) and a mixed Fe^{3+} complex with pyochelin (Sect. 5).



70: X = S, R = H, R' = OH
78: X = O, R = CH_3, R' = OH
79: X = O, R = CH_3, R' = H

Fig. 24. Anguibactin (**70**), pre-acinetobactin (**78**), pre-pseudomonine (**79**)

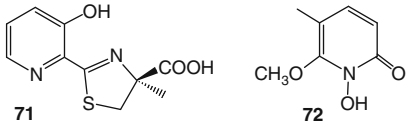


Fig. 25. Desferri-ferrithiocin (**71**), cepabactin (**72**)

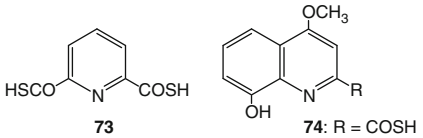


Fig. 26. Pyridine-di(monothiocarboxylic acid) (**73**), thioquinaldic (**74**), quinaldic acid (**75**)

Pyridine-2,6-di(monothiocarboxylic acid) (Fig. 26, **73**) [for a review, see (*36*), *cf*. also (*37*)] was obtained from *Pseudomonas putida* (*262*) and later from *Pseudomonas stutzeri* (*203*). It forms a brown Fe^{3+} complex and a blue Fe^{2+} complex (both $FeLig_2$) (*143*), which may be accompanied by complexes carrying two additional cyanide ions (*145*). An X-ray analysis (Plate 6) of the Fe^{3+} complex of **73** shows a distorted octahedral symmetry (*143*). There is evidence that a sulfenic acid residue (-CO-SOH) is the biosynthetic link between -COOH and -COSH (*144*).

From iron-deficient cultures of *Pseudomonas fluorescens*, 8-hydroxy-4-methoxy-monothioquinaldic acid (thioquinolobactin) together with the corresponding quinaldic acid (quinolobactin) (Fig. 26, **74** and **75**), could be isolated (*258*). Quinolobactin can act as an alternative siderophore of *Pseudomonas fluorescens* (*245*), although it is the hydrolysis product of the thioacid (*220*). Its synthesis and complex formation as $(Fe^{3+})Lig_2$ was described (*98*).

Pseudomonine (Fig. 27, **76**) is produced by *Pseudomonas fluorescens* strains (*7*, *228*) and by *P. entomophila*, where it can act as a secondary siderophore (*209*). The substituents on C-4 and C-5 of the isoxazolinone ring are in *trans* positions (*311*). The complex formation has not been studied. *In vitro* enzyme-catalyzed synthesis studies (*311*, *388*) showed that initially the intermediate pre-pseudomonine (Fig. 24, **79**) is formed, which non-enzymatically rearranges to pseudomonine.

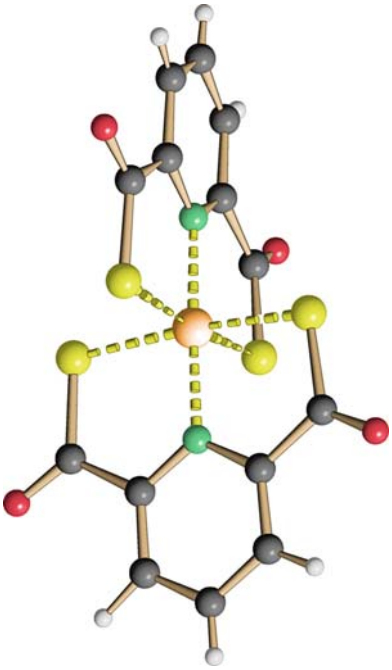
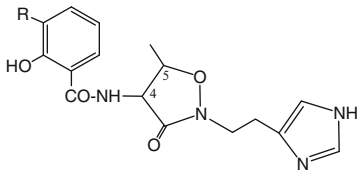


Plate 6. X-ray structure of the Fe^{3+}-complex of **73**



76: R = H
77: R = OH

Fig. 27. Pseudomonine (**76**), acinetobactin (**77**)

An analogous set of studies demonstrated that acinetobactin from *Acinetobacter baumannii* (*392*) has actually the structure **77** shown in Fig. 27 and that the one originally proposed (Fig. 24, **78**) is that of pre-acinetobactin. In contrast, the thiazoline ring of anguibactin (Fig. 24, **70**) (see above Sect. 5) is stable. Acinetobactin forms a 1:1 complex with Fe^{3+}.

Domoic acid (Fig. 28, **80**) (*263*) is a neuro-phycotoxin responsible for the mortality of wildlife and for amnesic shellfish poisoning (ASP) of humans during algal bloom. Domoic acid was first isolated from the red alga *Chondria armata* ("domoi" in Japanese), and it is produced also by diatoms, such as *Pseudo-nitzschia* spp. For the latter, evidence has been presented that it is involved in iron acquisition (*307*).

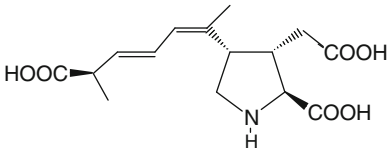


Fig. 28. Domoic acid (**80**)

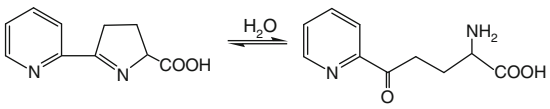


Chart 5. Proferrorosamin A (**81**)

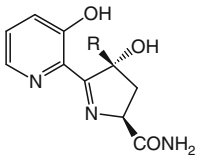


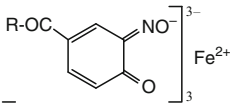
Fig. 29. Siderochelin A (R = CH_3) (**82**), B (C-3 epimer) (**83**) and C (R = C_2H_5) (**84**)

The smallest hydroxamate siderophore is *N*-methyl-*N*-thioformylhydroxylamine, CH_3-N(OH)-CHS, named thioformin (*100*) or fluopsin (*325*). The synthesis was described (CH_3-N(OH)-CHO + P_2S_5 or CH_3-N(OH)-H + HCSSK) (*100*, *166a*). It forms a purple $Fe^{3+}Lig_3$ complex. *Pseudomonas mildenbergii* produces *N*-methyl-*N*-phenylacetylhydroxylamine (CH_3-N(OH)-CO-CH_2-C_6H_5) (*159*), which also forms a purple Fe^{3+} complex.

7. Fe^{2+} Binding Ligands

Pseudomonas roseus fluorescens (*288*), *Pseudomonas* GH (*324*) and *Erwinia rhapontici* (*113*) produce pro-ferrorosamine A (**81**), also named pyrimine, which forms a red (Fe^{2+})Lig_3 complex. Under acidic conditions, an open form of pro-ferrorosamine A prevails, which cannot bind Fe^{2+} (Chart 5). Pro-ferrorosamine B is probably an artifact produced by condensation of pro-ferrorosamine A with CHO-COOH. Pro-ferrorosamine A is essential for iron uptake by *Pseudomonas* (*367*) and for the pathogenicity of *Erwinia* (*114*).

Structurally closely related is the *Nocardia* metabolite, siderochelin, for which the structure and relative and absolute stereochemistry were all established by X-ray crystallography (*208*, *267*). It is a mixture of two epimers A and B (Fig. 29, **82** and **83**). Siderochelin C, with an ethyl residue (Fig. 29, **84**), was obtained from a different actinomycete, tentatively identified as *Streptoalloteichus* sp. (*239*).



85: R = *p*-CH_2=CH-C_6H_4-O-
86: 2 R = *p*-CH_2=CH-C_6H_4-O-, 1 R = *p*-CHOH=CH-C_6H_4-O-
87: 2 R = *p*-CH_2=CH-C_6H_4-O-, 1 R = *p*-HOOC-CH=CH-C_6H_4-C-O-
88: R = NH_2

Fig. 30. Ferroverdins

The green pigments produced by *Streptomyces* spp. chelating Fe^{2+} with *o*-nitrosophenolate residues are occasionally referred to as siderophores, but whether they are really involved in iron metabolism has not been investigated. Ferroverdin A (*11*) forms a (Fe^{2+})Lig_3 complex (*55*), with the ligand being *p*-vinylphenyl-3-nitroso-4-hydroxybenzoate (Fig. 30, **85**). In ferroverdin B and C, one of the three ligands is substituted at the vinyl group (Fig. 30, **86** and **87**) (*346*, *361*). From *Streptomyces murayamaensis*, a precursor of ferroverdin was obtained (Fig. 30, **88**) (*69*).

For a further chelator of Fe^{2+}, see pyridine-2,6-di(monothiocarboxylic acid) above (Sect. 6).

8. Selected Syntheses

In this section the syntheses of several typical siderophores will be presented in a summarized form pointing out interesting features.

8.1. Anachelin H (10)

The challenge lay in the stereochemically correct synthesis of the polyketide part of the molecule. Starting from L-serine (**89**) (Chart 6) by C_2-elongation steps, reduction of the obtained keto functions including adequate protection and deprotection, and introduction of the salicylic acid residue the four stereoisomeric 3,5-diols (**90**) were obtained. Comparison of the ^{1}H-NMR data with those of anachelin (**10**) showed that the isomer with (3*R*,5*S*,6*S*) configuration was the correct starting material.

The chromophore part was prepared from Boc-protected *N*, *N*-dimethyl-L-DOPA (**91**), reduction to the diamine **92** and tellurium-mediated oxidative ring closure (**93**). The free amino group of **94** was coupled with protected L-Ser and L-Thr-D-Ser (**95**) and then the two constituent parts were connected and deprotected yielding **10** (*121*).

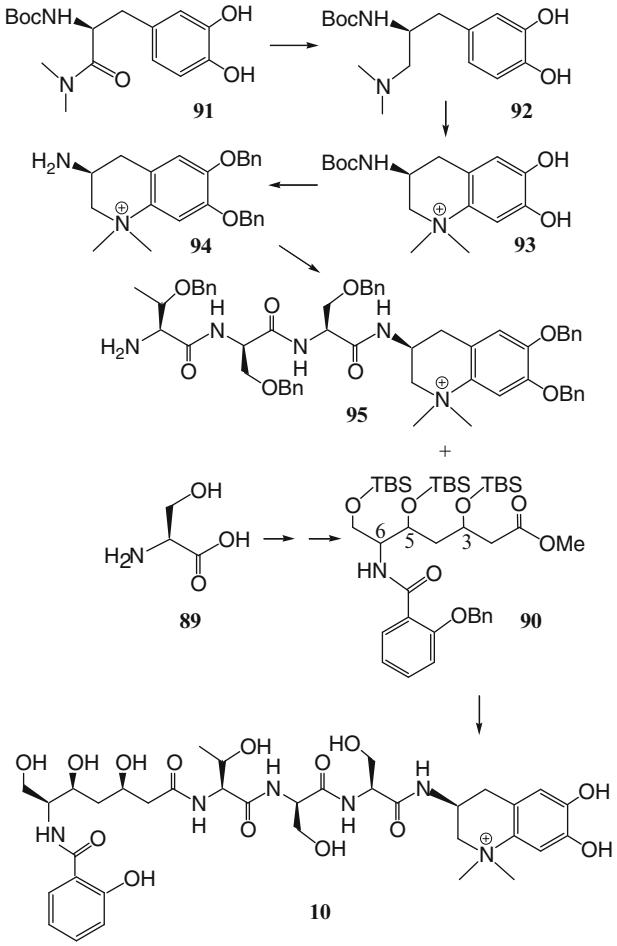


Chart 6. Synthesis scheme of anachelin H (**10**)

8.2. Alterobactin (26)

Several building blocks were prepared separately (Chart 7). Methyl *trans*-cinnamate gave by *Sharpless* enantiocontrolled dihydroxylation a diol from which by a series of stereo- and regioselective transformations (**96**) and Ru-catalyzed oxidation for transformation of the phenyl into a carboxyl group accompanied by adequate protection (**97**) and deprotection steps the protected OHAsp derivative **98** was obtained.

The protected (*S*)-4,8-diamino-3-oxooctanoic acid **99** was reduced with $NaBH_4$, the resulting mixture of diastereomers was separated and the (3*R*,4*S*)-product was derivatized with benzylated DHB (**100**). Then derivatized D-Ser-Gly was added and the serine OH-group was esterified with the protected OHAsp (**101**). The Gly carboxyl group was finally set free.

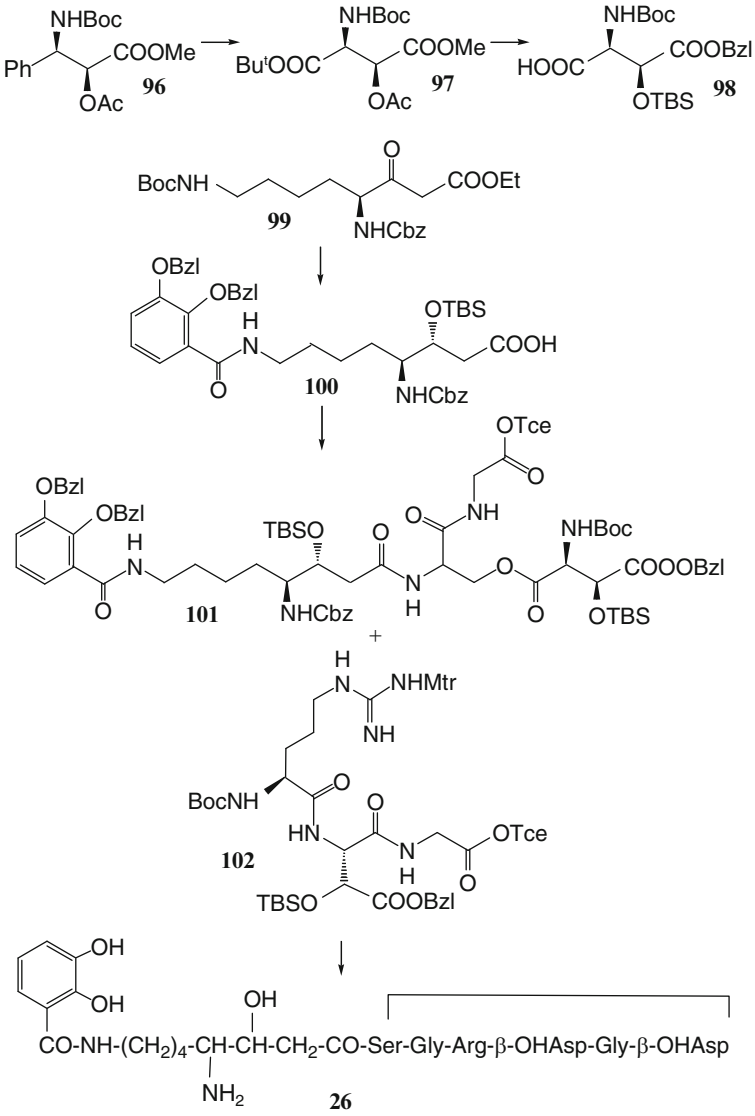


Chart 7. Synthesis scheme of alterobactin (**26**)

The synthesis of the remaining part of the molecule started from a condensation of protected Gly with the OHAsp derivative **98**, and subsequently with protected Arg (**102**). In the resulting protected tripeptide the Boc group from the Arg residue was removed. Connection of the two building blocks between Gly and Arg was followed by ring closure between Ser and Gly. Deprotection yielded finally alterobactin (**26**) (*83*).

8.3. *Parabactin (44)*

Here the critical step is the formation of the oxazoline ring. Both the stereochemistry of the two chiral centers and its acid lability had to be considered. Two approaches have been published. They can be modified for other members of this class.

The terminal NH_2-groups of N^5-benzylspermidine (Chart 8) were acylated with 2,3-dimethoxybenzyol chloride and the benzyl group was removed by hydrogenolysis (*28b*). N^1, N^{10}-bis(2,3-dimethoxy)benzoylspermidine (**103**) was then reacted with protected L-threonine (**104**). The Boc group was removed with CF_3COOH and the methoxy groups were cleaved with BF_3 (**105**). Subsequent reaction with 2-hydroxybenzimidoethyl ether (**106**) gave parabactin (**44**) (*28*, *28c*).

In the second synthesis (Chart 9) of **44** the carboxyl group of benzoyl-protected salicylic acid was activated by transformation into the 1,2-thiazolidine-2-thione derivative **107** and reacted with D-threonine. The methyl ester was debenzoylated reductively (**108**). Treatment with $SOCl_2$ resulted in cyclization accompanied by stereoinversion of C_β of threonine. The resulting *cis*-oxazoline derivative **109** was epimerized at C_α with C_2H_5ONa. Subsequent hydrolysis of the ester function gave the *trans*-carboxylic acid **110** which was reacted with N^1, N^{10}-bis(benzyloxycarbonyl)spermidine by treatment with phenylbis-(2-thioxo-1,3-thiazolidine-3-yl) phosphinoxide (**111**). The remaining steps leading to **44** (removal of the N-protecting

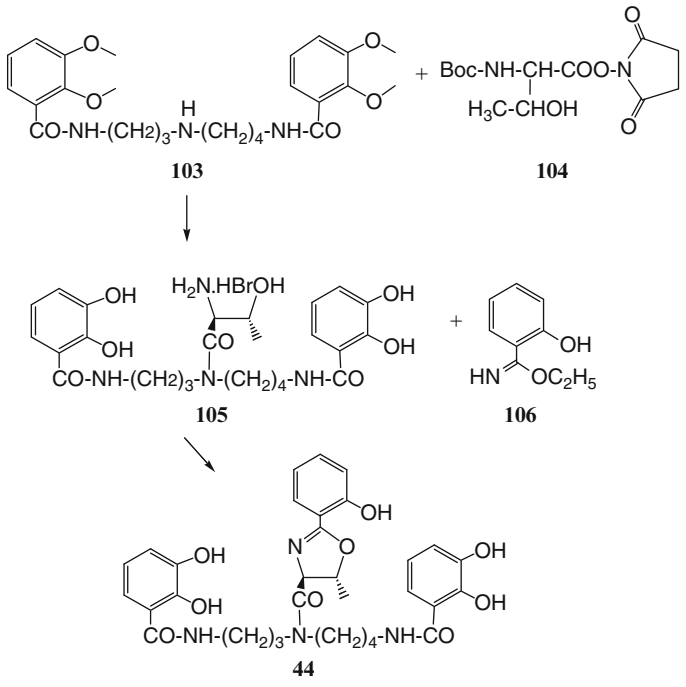


Chart 8. Synthesis I of parabactin (**44**)

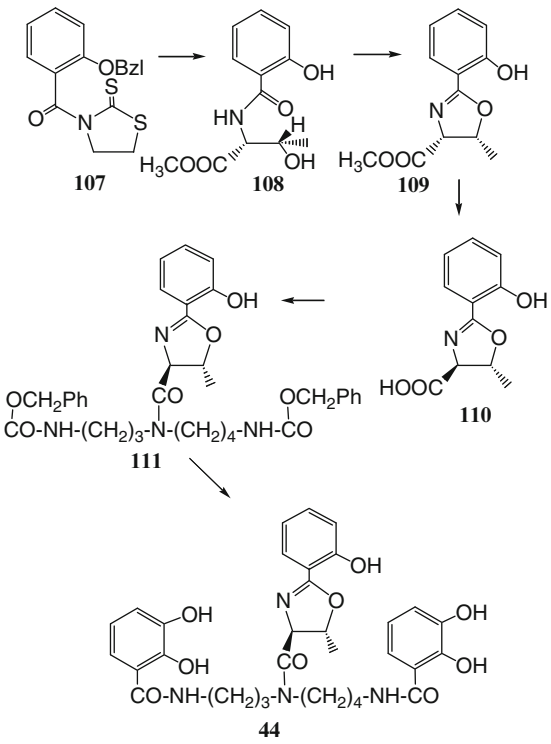


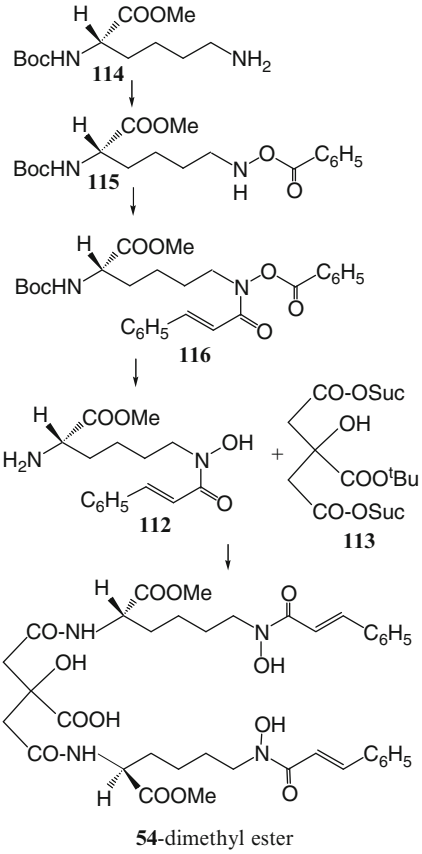
Chart 9. Synthesis II of parabactin (**44**)

groups, reaction with 2,3-diacetoxybenzyl chloride and cleavage of the acetoxyl groups) were standard operations (*255*).

In a recent modification of the second synthesis (*308*) effected for fluvibactin (**45**) an *o*-xylene protection group was proposed (reaction of 2,3-dihydroxybenzoic acid methyl ester with 1,2-di(bromomethyl)benzene) which could be removed later by hydrogenolysis. The formation of the oxazoline ring from protected DHB-L-threonine methyl ester was achieved with Mo(VI) catalysts (*e.g.* $(NH_4)_2MoO_4$) without affecting the chiral centers. Derivatization of the primary amino groups of norspermidine with the protected DHB methyl ester was catalyzed by $Sb(OC_2H_5)_3$.

8.4. Nannochelin A

For the condensation with the properly derivatized lysine part (**112**) 3′-*tert*-butyl-1,5-di-*N*-hydroxysuccinimidyl citrate (**113**) was used (Chart 10). It was prepared from 1,5-dimethyl citrate by reaction with *tert*-butyl acetate, alkaline hydrolysis of the methyl ester and coupling with *N*-hydroxysuccinimide by DCCI (*237*).



54-dimethyl ester

Chart 10. Synthesis of nannochelin A (**54**-dimethyl ester)

For the synthesis of the lysine part (**112**) N^2-Boc-L-lysine methyl ester (**114**) was treated with benzoylperoxide/Na_2CO_3 (**115**) and subsequently with *trans*-cinnamoyl chloride yielding **116**. The hydroxamate ester was deprotected with NH_3/CH_3OH at −23°C and the Boc group was removed with CF_3COOH. Condensation with the citric acid 3-*tert*-butyl ester was effected with $(C_2H_5)_3N$. After cleavage of the ester with CF_3COOH nannochelin A (**54**-dimethyl ester) was obtained (*29*). The difficulties in the synthesis lay in the various functional and protecting groups, which had to be introduced and removed in a deliberate sequence.

8.5. Pyochelin

The problem encountered with all published syntheses (*6*, *301*, *397*) is the non-stereospecific formation of C-4′ and the facile conversion of C-2″. The common approach (Chart 11) consists in the reaction of 2-hydroxybenzonitrile (**117**) with

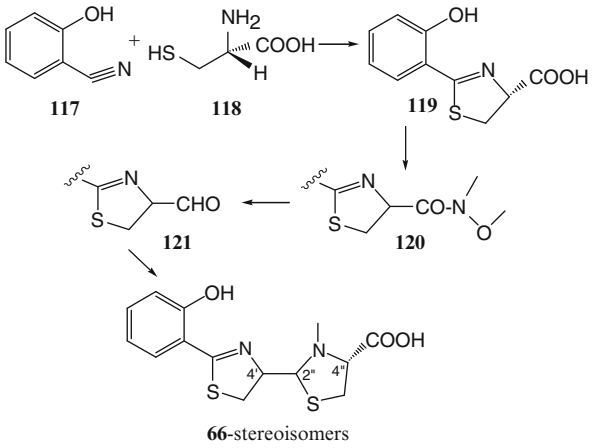


Chart 11. Synthesis of pyochelin stereoisomer mixture

L-cysteine (**118**) giving dihydroaeruginoic acid (**119**), reduction of the carboxyl group to the aldehyde **121** and condensation of the latter with L-*N*-methyl-cysteine. Details will be given for the procedure worked out by *Zamri* and *Abdallah* (*397*). The first condensation step was effected in a phosphate buffer (*pH* 6.4) to minimize epimerization at C-4′. Then the carboxyl group was reacted with *N*,*O*-dimethyl-hydroxylamine (**120**) using diethylcyanophosphonate as condensation agent. Reduction with $LiAlH_4$ yielded the aldehyde **121**, which then was treated with L-*N*-methyl-cysteine. A mixture of the four stereoisomers of (**66**), (4′*R*,2″*S*,4″*R*), (4′*S*,2″*S*,4″*R*), (4′*R*,2″*R*,4″*R*), (4′*S*,2″*R*,4″*R*) in a ratio of 2:1:2:5 was obtained.

9. Epilog

The history of siderophores actually began towards the end of the nineteenth century when laboratories engaged in bacteriological research observed that certain bacterial cultures showed a green fluorescence, and when in 1891 the first attempts were reported to isolate the fluorescent pigment (later namend pyoverdin, Sect. 2.1) produced by *Bacterium fluorescens liquefaciens* (*Pseudomonas fluorescens*), although it was not before 1978 that *J.-M. Meyer* demonstrated its being involved in the iron transport into the bacterial cell (*37*). Pyoverdins were among the centers of interest during the last decades, and other preferred topics were the fungal siderophores (Sect. 2.6), and more recently the marine lipopeptides (Sect. 2.8).

This review is mainly concerned with structural aspects of siderophores and their iron transport, intended to give a status report of what has been achieved up to late-2009. But the fields of interest in siderophores are much wider, spreading into

– genetics (identification of the genes responsible for the synthesis of the siderophores and their receptors (*e.g.* (*403*, *409*)),

- medicine (siderophores as virulence factors (*e.g.* (*75*)), but serving also as carriers for antibiotics in a Trojan Horse strategy (*e.g.* (*35a*)),
- agriculture (starving phytopathogenic bacteria by binding iron (*e.g.* (*187b*, *406*)),
- environmental problems (binding heavy metal ions (*e.g.* (*90a*)), degrading detrimental compounds (*e.g.* (*205a*)), mobilizing uranium and *trans*-uranium elements in contanimated soils (*e.g.* (*242a*)),

just to mention some areas. The diversity of scientific journals to be found in the References Section gives an idea of where information on siderophores can be hidden.

Structural work may take its time. Examples are *Pseudomonas mendocina* (Sect. 2.9) where the first structural data were reported in 2000 and the next pertinent publication appeared in 2008, or *Legionella pneumophila* (Sect. 4.5) whose legiobactin was first characterized in 2000, further details followed in 2007 and 2009, with loose ends in both cases. Only partially characterized siderophores are mentioned wherever data were available in order to stimulate further work. This would be worthwhile: siderophore research is a fascinating branch of natural products chemistry promising sometimes surprising results (*e.g.* (*311*, *388*)).

Acknowledgement Many thanks are due to Dr. *J. Neudörfl* for preparing the Plates with siderophore X-ray structures. Data bases for the X-ray structures: Plate 1: FEPSBC 10; 3: TEQKQV; 4: YELJOP; 5: VENPAC; 6: CUHGUH.

Appendix

Table 7. Pyoverdins Isolated from *Pseudomonas* spp.

P.	Name	Peptide chain[a,b,c,d]	Mass[e]	References[f]
(a) Complete or fairly complete structures				
Pyoverdins with a C-terminal cOHOrn				
		6 amino acids		
f	Ps (= B10[h])	εLys-OHAsp-Ala-aThr-Ala-cOHOrn	989	(*352–354*)
f	Py 9AW[n]	Ser-Lys-OHHis-aThr-Ser-cOHOrn	1043	(*42*)
ap	Py 4a[l] (= Py SB83)	Ala-Lys-Thr-Ser-AcOHOrn-cOHOrn	1046	(*47*)
p	iPy BTP1	Asp-Ala-Asp-AcOHOrn-Ser-cOHOrn	1047	(*168*)
		7 amino acids		
f	Py PL7	Ser-AcOHOrn-Ala-Gly-aThr-Ala-cOHOrn	1046	(*16*)
f	Py BTP2	Ser-Val-OHAsp-Gly-Thr-Ser-cOHOrn	1049	(*270*)
p	Py G4R	Asp-Orn-(OHAsp-Dab)-Gly-Ser-cOHOrn[i]	1073	(*33*, *309*)
	Py 2908	Ser-Orn-OHAsp-Ser-Ser-Ser-cOHOrn	1088	(*373*)
ae	Py T II[g] (=27853)	Ser-FoOHOrn-Orn-Gly-aThr-Ser-cOHOrn[bb]	1091	(*350*)
f	Py PL8	Lys-AcOHOrn-Ala-Gly-aThr-Ser-cOHOrn	1103	(*16*)

Table 7. *(continued)*

P.	Name	Peptide chain[a,b,c,d]	Mass[e]	References[f]
p	Py 11370	Asp−εLys-OHAsp-Ser-Ala-Ser-cOHOrn	1106	(*48*)
p	iPy 90-33	Asp-Lys-Thr-OHAsp-Thr-aThr-cOHOrn	1164	(*345*)
		8 amino acids		
p	Py 90-51	Asp-εLys-OHAsp-Ser-Gly-aThr-Lys-cOHOrn	1234	(*343*)
		9 amino acids		
c, *au*	Py Pau[u]	Ser-AcOHOrn-Gly-aThr-Thr-Gln-Gly-Ser-cOHOrn	1277	(*21*)
f	Py 2392 (= A6[h])	Lys-AcOHOrn-Gly-aThr-Thr-Gln-Gly-Ser-cOHOrn	1318	(*23*)
p	Ps 589A[o]	Asp−εLys-OHAsp-Ser-Thr-Ala-Glu-Ser-cOHOrn	1336	(*279*)
p	Py 2461 (=L1[h], WCS358[h])	Asp-εLys-OHAsp-Ser-aThr-Ala-Thr-Lys-cOHOrn[cc]	1349	(*365*)
ap	Py 3b[t]	Asp-(AcOHOrn-Dab)-Thr-Ala-Thr-Thr-Gln-cOHOrn	1358	(*349*)
		10 amino acids		
f	Py 2798 (=W[aa])	(Ser-Dab)-Gly-Ser-OHAsp-Ala-Gly-Ala-Gly-cOHOrn	1187	(*78*)
f	Py 17400	Ala-Lys-Gly-Gly-OHAsp-(Gln-Dab)-Ser-Ala-cOHOrn[i]	1299	(*77*)
p	Py 1,2	Ser-Thr-Ser-Orn-OHAsp-(Gln-Dab)-Ser-aThr-cOHOrn	1405	(*130*)
f	Py 1.3	Ala-Lys-Gly-Gly-OHAsp-(Gln-Dab)-Gly-Ser-cOHOrn	1285	(*125*)
t	Py 2192	Ser-Lys-Ser-Ser-Thr-Ser-AcOHOrn-Thr-Ser-cOHOrn	1424	(*78*)
p	iPy 90-44	Asp-Lys-AcOHOrn-Thr-Ser-Ser-Gly-Ser-Ser-cOHOrn[s]	1408	(*344*)
		11 amino acids		
f	Py 51W	Ala-Lys-Gly-Gly-OHAsp-Gln-Ser-Ala-Gly-aThr-OHOrn	1375	(*371*)

[a]In part (a) D-amino acids are underlined; a broken line indicates either that the stereochemistry of the amino acid has not been determined or that a specific amino acid occurs both in the D- and the L-form, but a localization of the the two enantiomers has not been effected. In part (b) D-amino acids are indicated only when data are available from the literature

[b]Abbreviations: *P, Pseudomonas*; *ae, aeruginosa*; *ap, aptata*; *as*, *asplenii*; *au*, *aureofaciens*; *c*, *costantinii*; *ci*, *cichoriae*; *en, entomophila*; *f, fluorescens*; *li*, *libanensis*; *m*, *marginalis*; *mo*, *monteilii*; *p, putida*; *pa, palleroniana*; *r*, *rhodesiae*; *s*, *syringae*; *t*, *tolaasii*; Ps, pseudobactin; Py, pyoverdin; iPy, isopyoverdin; amino acids: 3-letter code - in addition: OHAsp, *threo*-β-hydroxy-Asp; OHHis, *threo*-β-hydroxy-His; OHOrn, N^5-hydroxy-Orn; Ac(Fo,Bu)OHOrn, N^5-acetyl (formyl, (R)-β-hydroxy-butyryl) OHOrn; cOHOrn, *cyclo*-OHOrn (3-amino-1-hydroxy-piperidone-2); aThr, *allo*-Thr

[c]Amino acids are bound to the chromophore or to the preceding amino acid by their α-amino group or in the case of Lys occasionally by its ε-amino group (indicated as εLys)

Table 7. *(continued)*

P.	Name	Peptide chain[a,b,c,d]	Mass[e]	References[f]
		12 amino acids		
f	Py GM	Ala-Lys-Gly-Gly-OHAsp-Gln-Ser-Ala-Ala-Ala-Ala-cOHOrn	1430	(*242*)
	Py 1547	Ser-Lys-Ala-AcOHOrn-Thr-Ala-Gly-Gln-Ala-Ser-Ser-OHOrn	1547	(*304*)
Pyoverdins with a C-terminal cyclo-tetra- or tripeptide				
		cyclo-tetrapeptide		
f	Py G173	Ser-Ala-AcOHOrn-(Orn-Asp-AcOHOrn-Ser)	1175	(*363*)
	Py 96-312	Ser-Ser-FoOHOrn-(Lys-FoOHOrn-Lys-Ser)	1190	(*315*)
	Py 96.188	Ser-Lys-FoOHOrn-(Lys-FoOHOrn-Glu-Ser)	1232	(*379*)
ae	Py C-E (= PAO1[h], ATCC 15692, Pa)	Ser-Arg-Ser-FoOHOrn-(Lys-FoOHOrn-Thr-Thr)	1333	(*35*, *81*)
	Py 95-275 (= BTP7[h])	Ser-Ser-FoOHOrn-Ser-Ser-(Lys-FoOHOrn-Lys-Ser)	1364	(*342*)
f	Py 12	Ser-Lys-Gly-FoOHOrn-Ser-Ser-Gly-(Lys-FoOHOrn-Glu-Ser)	1520	(*124*)
		cyclo-tripeptide		
f	Py 13525[m]	Ser-Lys-Gly-FoOHOrn-(Lys-FoOHOrn-Ser)	1160	(*146*)
pa	Py 96-318	Ser-Orn-FoOHOrn-Ser-Ser-(Lys-FoOHOrn-Ser)	1263	(*315*)
f	Py 18-1	Ser-Lys-Gly-FoOHOrn-Ser-Ser-Gly-(Lys-FoOHOrn-Ser)	1391	(*3*)
Pyoverdins with a C-terminal cyclodepsipeptide or a free carboxyl group				
		6 amino acids		
a	PS 6.10	Ala-Orn-OHAsp-Dab-AcOHOrn-Lys	1091	(*46*)
		7 amino acids		
ae	Py R′	(Ser-Dab)-FoOHOrn-Gln-FoOHOrn-Gly	1046	(*305*)

[d]Parentheses indicate either a cycle formed by an amide or ester bond between the carboxyl group of the C-terminal amino acid and a side chain functionality of another amino acid or the condensation product of the NH_2 groups of Dab with the amide carbonyl group of the preceding amino acid giving a tetrahydropyrimidine ring (see Chart 1)

[e]Nominal molecular mass for a Py or iPy chromophore with a succinic acid side chain; the exact mass is about 0.5 Da higher

[f]References to complete structure elucidations. For further details see (*37*)

[g]Probably identical with the pyoverdin of *Pseudomonas aeruginosa* ATCC 9027 (*212*)

[h]The structure published originally had to be corrected or amended; literature references to the originally proposed structure may be found in (*37*)

[i]Accompanied by the not cyclized Dab form (M + 18)

[j]Accompanied by a non-cyclic pyoverdin with the same amino acid sequence

[k]For this pyoverdin an ε-amino Lys linkage was claimed but not substantiated. It is probably identical with the pyoverdin from *P. putida* 9AW where a α-amino Lys linkage was established

[l]*P. aptata* is a pathovar of *P. syringae*. The same pyoverdin was found produced by *P. fluorescens* SB83 (*20*). The identification of *P. aptata* may, therefore, be questioned (*cf.* also (*179*))

Table 7. *(continued)*

P.	Name	Peptide chain[a,b,c,d]	Mass[e]	References[f]
ci	PaB	εLys-OHAsp-Thr-(Thr-Gly-OHAsp-Ser)	1093	(*50*)
s	Py 19310	εLys-OHAsp-Thr-(Thr-Ser-OHAsp-Ser)[j]	1123	(*179*)
ae	Py R (=Pa6)	(Ser-Dab)-FoOHOrn-Gln-Gln-FoOHOrn-Gly	1173	(*127*)
		8 amino acids		
p	Ps A214 (= Ps 39167)	Ser-AcOHOrn-Ala-Gly-(Ser-Ala-OHAsp-Thr)[j]	1134	(*365*)
f	Py P19 (= Ps 7 SR1[h], Ps A 225)	Ser-AcOHOrn-Ala-Gly-(Ser-Ser-OHAsp- Thr)[j]	1150	(*372*)
ch	Py D-TR133	Asp-FoOHOrn-Lys-(Thr-Ala-Ala-FoOHOrn-Ala)[j,x]	1230	(*17*)
f	Py I-III	Asn-FoOHOrn-Lys-(Thr-Ala-Ala-FoOHOrn-Lys)	1286	(*287*)
f	CHAO	Asp-FoOHOrn-Lys-(Thr-Ala-Ala-FoOHOrn-Lys)	1287	(*387*)
		9 amino acids		
p	Py C	Asp-BuOHOrn-Dab-Thr-Gly-Ser-Ser-OHAsp-Thr	1370	(*319*)
p	Py BTP16	Asp-BuOHOrn-Dab-Thr-Gly-Ser-Ser-OHAsp-Thr [v]	1370	(*271*)
		10 amino acids		
as	Py fuscovaginae	εLys-OHAsp-Ala-(Thr-Dab-Gly-Gly-Thr-(OHAsp-Dab))	1316	(*49a*, *231*)
(b) Partial or tentative structures				
Pyoverdins with a C-terminal cOHOrn				
p	Thai	(Ser-Dab)-Thr-Ser-AcOHOrn-cOHOrn	1016	(*306*)
f	Py 244[k]	Ser-εLys-OHHis-aThr-Ser-cOHOrn	1043	(*132–134*)
p	Py 12633[o]	Asp-Lys-OHAsp-Ser-Thr-Ala-Glu-Ser-cOHOrn	1336	(*80*)
Pyoverdins with a C-terminal cyclo-tetra- or tripeptide				
		cyclo-tetrapeptide		
f	D47	Ser-Orn-FoOHOrn-(Lys-FoOHOrn-Glu-Ser)	1218	(*119*)
r	L25	Ser-Lys-FoOHOrn-Ser-Ser-Gly-(Lys-FoOHOrn-Ser-Ser)	1421	(*119*)

[m]The same pyoverdin was isolated from *P. chlororaphis* ATCC 9446 (*146*) and CNR15 (*162*). The reported isolation from *P. putida* KT2440 (*297*) is the result of a mix-up of strains (*J.-M. Meyer*, private communication)

[n]Probably identical also with that from *P. fluorescens* 244

[o]The Py 589A is probably identical with the pyoverdin Py Pp 12633

[p]Either the preliminary structural work or the identification of the strains may be questioned since screening of a large number of *P. aeruginosa* strains revealed the existence of only three siderovars characterized by the production of the pyoverdins Py C-E, Py R and Py Pa TII (*234*) plus probably of a mutant of Py R (R′ (*305*)). Py Pa 15152 was shown to be identical with Pa D above (*20*)

[q]The structural proposals are tentative; Orn/Asn and Lys/Gln have the same mass, Lys may be incorporated in the peptide chain by its α- or its ε-amino group

Table 7. *(continued)*

P.	Name	Peptide chain[a,b,c,d]	Mass[e]	References[f]
		cyclo-tripeptide		
m	G 76	Ser-Ser-FoOHOrn-Ser-Ser-(Lys-FoOHOrn-Ser)	1236	(*119*)
	DSM 50106	Ser-Lys-Gly-FoOHOrn-Ser-Ser-Gly-(Orn- FoOHOrn-Ser)	1377	(*119*)
Pyoverdins where only limited mass spectral data are available[q]				
p	Py GS43	Lys-OHAsp-Ser-Ser-Ser-cOHOrn	1007	(*231*)
li	Py 96.195	Ala-Orn-OHAsp-Ser-Orn-Ser-cOHOrn	1091	(*231*)
	Py G 85	Ser-Lys-OHAsp-Ser-Orn-Ser-cOHOrn	1121	(*231*)
	Py G 76	Ser-Ser-FoOHOrn-Ser-Ser-Lys-(FoOHOrn-Ser)	1236	(*231*)
	Py HR6	Asp-ε-Lys-OHAsp-Ser-Ser-Thr-Thr-Thr-cOHOrn	1238	(*231*)
	LBSA1	Asp-Arg-AcOHOrn-Lys-Ser-Asp-cOHOrn	1260	(*231*)
mo	iPy Lille 1	Asp-Lys-AcOHOrn-Ala-Ser-Ser-Gly-Ser-cOHOrn	1291	(*231*)
f	Py G153	Ser-Lys-Ala-Ser-Ser- AcOHOrn-Ser-Ser-cOHOrn	1293	(*231*)
en	L48	Ala-Asn-Dab-OHHis-Gly-Gly-Ala-Thr-Ser-cOHOrn	1298	(*219*)
p	Py G172	Ala-Lys-Dab-OHAsp-Thr-Gly- OHAsp-Gly-Thr-Thr - H_2O	1335	(*231*)
f	Pf0-1	Ala-AcOHOrn-Orn-Ser-Ser-Ser-Arg-OHAsp-Thr	1381	(*231*)
p	90-136/ G 168	Ser-Lys-Ser-Ser-Thr-Thr-AcOHOrn-Ser-Ser-cOHOrn	1424	(*231*)
	IB3	Ser-Ala-Thr-Gln-Orn-AcOHOrn-Thr-Thr-Ala-Ser-Thr-Ala-Ala-cOHOrn	1764	(*231*)
Various pyoverdins with incomplete structural data				
ae	Py UNK[p]	Ser-Thr-Ser-Gly-OHOrn-OHOrn		(*107*)
ae	Pa 15152[p]	2 Arg, 2 Orn, 3 Ser, 3 Thr		(*107*)
p	Py Pm	OHAsp, Lys, OHOrn, 2 Ser, 3 Thr		(*212a*)
s	Py Ps	Lys, OHOrn, 3 Ser, 3 Thr		(*362*)
s	Py PSS[z]	2 OHAsp, Lys, 2 Ser, 2 Thr		(*68*)
	P. mildenbergii	Glu, Lys, Ser, Thr[w]		(*259*)

[r]The reported amino acid composition cannot be correct. The minimum molecular mass calculated from it is about 120 u higher than the molecular mass determined by mass spectrometry. Also the amino acids acting as ligands for Fe^{3+} are missing

[s]2 D-Ser, 2 L-Ser

[t]Contains 2 Thr and one aThr. The amino acid analysis of the corresponding ferribactin gave D-Ala, L-Asp, L-Dab, D- and L-Glu, L-Orn, D-aThr, L-Thr and D-Tyr

[u]The same pyoverdin was isolated from *P. tolaasii* NCBBP 2192 (*P. constantinii*); the fact that the strain designated as *P. aureofaciens* does not produce phenazines casts doubts on the correct identification (*364*)

[v]1 Thr, 1 aThr

[w]Ratios of 1:1:2:4 and 1:2:3:5 are reported for the pyoverdins from two strains of *P. mildenbergii*; for the second one a blocked N-terminus was demonstrated

[x]1 D-Ala, 2L-Ala; the pyoverdin D-TR 133 is accompanied by a small amount of a pyoverdin where the second Ala is replaced by Gly

Table 7. *(continued)*

P.	Name	Peptide chain[a,b,c,d]	Mass[e]	References[f]
p	Py A1	Asx, Glx, 3 Gly, His, Lys, 4 Ser, Thr, Val[r]		(*32*)
f	BTP9[y]	2 Lys, 2 FoOHOrn, 5 Ser		(*269*)
p	BTP14[aa]	Asx, Dab, Glx, Gly, Orn, 2 Ser, Thr, aThr		(*269*)

[y]Probably identical with the pyoverdins of BTP7 and BTP16 (private communication Dr. *M. Ongena*, Liège)
[z]Probably identical with the pyoverdin Py 19310
[aa]Identical with pyoverdin W mentioned in (*79*) (private communication Dr. *J.-M. Meyer*, Strasbourg)
[bb]Accompanied by a variety with one AcOHOrn (*187a*)
[cc]Accompanied by a small amount of a pyoverdin where Ala is replaced by Gly

Notes Added in Proof

Section 2.5

Coelichelin from *Streptomyces coelicolor* comprises D-N^5-formyl-N^5-hydroxy-Orn-D-aThr bound to N^5 of L-N^5-hydroxy-Orn whose N^2 is acylated by D-N^5-formyl-N^5-hydroxy-Orn (*412*).

Section 2.6

Erythrochelin from *Saccharopolyspora erythraea* is a coprogen-type siderophore (Table 2) with Ac^1 = **i** and Ac^2 = D-Ser-D-N^2, N^5-diacetyl-N^5-hydroxy-Orn (*413*).

Section 2.7

The transport system of *Bacillus subtilis* accommodates the Fe^{3+} complexes of enterobactin (Δ-configured), *enantio*-D-enterobactin and of corynebactin (bacillibactin) (both Λ). Since only Λ complexes can be bound to the receptor a configurational change from Δ to Λ is induced. Only the natural ferri-L-siderophores can be degraded enzymatically (*399*, *408*).

From *Nocardia tenerifensis* the heterobactin JBIR-16 was obtained (**30**, R = DHB). The stereochemistry of the two Orn residues was not established. By mass spectrometry a 1:1 Fe^{3+}/Lig ratio was determined for the red complex (*407*).

References

1. Adapa S, Huber P, Keller-Schierlein W (1982) Stoffwechselprodukte von Mikroorganismen. 216. Mitteilung. Isolierung, Strukturaufklärung und Synthese von Ferrioxamin H. Helv Chim Acta **65**: 1818

1a. Adolphs M, Taraz K, Budzikiewicz H (1996) Catecholate Siderophores from *Chryseomonas luteola*. Z Naturforsch **51c**: 281
2. Allard KA, Dao J, Sanjeevaiah P, McCoy-Simandle K, Chatfield CH, Crumrine DS, Castignetti D, Cianciotto NP (2009) Purification of Legiobactin and the Importance of this Siderophore in Lung Infection by *Legionella pneumophila*. Infect Immun **77**: 2887
3. Amann C, Taraz K, Budzikiewicz H, Meyer JM (2000) The Siderophores of *Pseudomonas fluorescens* 18.1 and the Importance of Cyclopeptidic Substructures for the Recognition at the Cell Surface. Z Naturforsch **55c**: 671
3a. Ams DA, Maurice PA, Hersman LE, Forsythe JH (2002) Siderophore Production by an Aerobic *Pseudomonas mendocina* Bacterium in the Presence of Kaolinite. Chem Geol **188**: 161
4. Anderegg G, Räber M (1990) Metal Complex Formation of a New Siderophore Desferrithiocin and of Three Related Ligands. J Chem Soc Chem Commun 1194
5. Anke H, Kinn J, Bergquist KE, Sterner O (1991) Production of Siderophores by Strains of the Genus *Trichoderma*. Isolation and Characterization of the New Lipophilic Coprogen Derivative, Palmitoylcoprogen. Biol Metals **4**: 176
6. Ankenbauer RG, Toyokuni T, Staley A, Rinehard KL Jr, Cox CD (1988) Synthesis and Biological Activity of Pyochelin, a Siderophore of *Pseudomonas aeruginosa*. J Bacteriol **170**: 5344
7. Anthoni U, Christophersen C, Nielsen PH, Gram L, Petersen BO (1995) Pseudomonine, an Isoxazolidone with Siderophoric Activity from *Pseudomonas fluorescens* AH2 Isolated from a Lake Victorian Nile Perch. J Nat Prod **58**: 1786
8. Arceneau JEL, Davis WB, Downer DN, Haydon AH, Byers BR (1973) Fate of Labeled Hydroxamates during Iron Transport from Hydroxamate-Iron Chelates. J Bacteriol **115**: 919
8a. Arnow LE (1937) Colorimetric Determination of the Components of 3,4-Dihydroxyphenylalanine-Tyrosine Mixtures. J Biol Chem **118**: 531
9. Atkin CL, Neilands JB (1968) Rhodotorulic Acid, a Diketopiperazine Dihydroxamic Acid with Growth-Factor Activity. I. Isolation and Characterization. Biochemistry **7**: 3734
9a. Atkin CL, Neilands JB, Phaff HJ (1970) Rhodotorulic Acid from Species of *Leucosporidium*, *Rhodosporidium*, *Rhodotorula*, *Sporidiobolus*, and *Sporobolomyces*, and a New Alanine-containing Ferrichrome from *Cryptococcus melibiosum*. J Bacteriol **103**: 722
9b. Awaya JD, DuBois JL (2008) Identification, Isolation, and Analysis of a Gene Cluster Involved in the Iron Acquisition by *Pseudomonas mendocina* ymp. Biometals **21**: 353
10. Bachhawat AK, Ghosh S (1987) Iron Transport in *Azospirillum brasiliense*: Role of the Siderophore Spirilobactin. J Gen Microbiol **133**: 1759
11. Ballio A, Bertholdt H, Carilli A, Chain EB FRS, Di Vittorio V, Tonolo A, Vero-Barcellona L (1963) Studies on Ferroverdin, a Green Iron-containing Pigment Produced by a *Streptomyces* Wak. Species. Proc Royal Soc London; Ser B; Biol Sci **158**: 43
12. Barbeau K, Rue EL, Bruland KW, Butler A (2001) Photochemical Cycling of Iron in the Surface Ocean Mediated by Microbial Iron(III)-Binding Ligands. Nature **413**: 409
13. Barbeau K, Rue EL, Trick CG, Bruland KW, Butler A (2003) Photochemical Reactivity of Siderophores Produced by Marine Heterotrophic Bacteria and Cyanobacteria Based on Characteristic Fe(III) Binding Groups. Limnol Oceanogr **48**: 1069
14. Barbeau K, Zhang G, Live DH, Butler A (2002) Petrobactin, a Photoreactive Siderophore Produced by the Oil-Degrading Marine Bacterium *Marinobacter hydrocarbonoclasticus*. J Am Chem Soc **124**: 378
15. Barelmann I, Meyer JM, Taraz K, Budzikiewicz H (1996) Cepaciachelin, a New Catecholate Siderophore from *Burkholderia* (*Pseudomonas*) *cepacia*. Z Naturforsch **51c**: 627
16. Barelmann I, Taraz K, Budzikiewicz H, Geoffroy V, Meyer JM (2002) The Structures of the Pyoverdins from Two *Pseudomonas fluorescens* Strains Accepted Mutually by their Respective Producers. Z Naturforsch **57c**: 9
17. Barelmann I, Uría Fernández D, Budzikiewicz H, Meyer JM (2003) The Pyoverdine from *Pseudomonas chlororaphis* D-TR133 Showing Mutual Acceptance with the Pyoverdine from *Pseudomonas fluorescens* CHA0. BioMetals **16**: 263

18. Barklay R, Ewing DF, Ratledge C (1985) Isolation, Identification, and Structural Analysis of the Mycobactins of *Mycobacterium avium*, *Mycobacterium intracellulare*, *Mycobacterium scrofulaceum*, and *Mycobacterium paratuberculosis*. J Bacteriol **164**: 896
19. Barry SM, Challis GL (2009) Recent Advances in Siderophore Biosynthesis. Curr Opin Chem Biol **13**: 205
20. Beiderbeck H (1997) Untersuchung der Pyoverdine aus *Pseudomonas aeruginosa* ATCC 15152, *Pseudomonas fluorescens* CFBP 2392 und *Pseudomonas putida* 2461. Diplomarbeit, Universität zu Köln, and unpublished results
21. Beiderbeck H, Risse D, Budzikiewicz H, Taraz K (1999) A New Pyoverdin from *Pseudomonas aureofaciens*. Z Naturforsch **54c**: 1
22. Beiderbeck H, Taraz K, Budzikiewicz H, Walsby AE (2000) Anachelin, the Siderophore of the Cyanobacterium *Anabena cylindrica* CCAP 1403/2A. Z Naturforsch **55c**: 681
23. Beiderbeck H, Taraz K, Meyer JM (1999) Revised Structures of the Pyoverdins from *Pseudomonas putida* CFBP 2461 and from *Pseudomonas fluorescens* CFBP 2392. BioMetals **12**: 331-338
24. Bergeron RJ (1987) Synthesis and Properties of Polyamine Catecholamide Chelators. In: Winkelmann G, van der Helm D, Neilands JB (eds) Iron Transport in Microbes, Plants and Animals. VCH: Weinheim, p 285
25. Bergeron RJ, Dionis JB, Elliot GT, Kline SJ (1985) Mechanism and Stereospecificity of the Parabactin-mediated Iron-Transport System in *Paracoccus denitrificans*. J Biol Chem **260**: 7936
26. Bergeron RJ, Garlich JR, McManis JS (1985) Total Synthesis of Vibriobactin. Tetrahedron **41**: 507
27. Bergeron RJ, Huang G, Smith RE, Bharti N, McManis JS, Butler A (2003) Total Synthesis and Structure Revision of Petrobactin. Tetrahedron **59**: 2007
28. Bergeron RJ, Kline SJ (1982) Short Synthesis of Parabactin. J Am Chem Soc **104**: 4489
28a. Bergeron RJ, Kline SJ (1984) 300-MHz ^{1}H NMR Study of Parabactin and its Ga(III) Chelate. J Am Chem Soc **106**: 3089
28b. Bergeron RJ, Kline SJ, Stolowich NJ, McGovern KA, Burton PS (1981) Flexible Synthesis of Polyamine Catecholamides. J Org Chem **46**: 4524
28c. Bergeron RJ, McManis JS, Dionis JB, Garlich JR (1985) An Efficient Total Synthesis of Agrobactin and its Ga(III) Chelate. J Org Chem **50**: 2780
29. Bergeron RJ, Phanstiel O iv (1992) The Total Synthesis of Nannochelin, a Novel Cinnamoyl Hydroxamate-containing Siderophore. J Org Chem **57**: 7140
30. Bergeron RJ, Xin MG, Weimar WR, Smith RE, Wiegand J (2001) Significance of Asymmetric Sites in Choosing Siderophores as Deferration Agents. J Med Chem **44**: 2469
30a. Berner I, Konetschny-Rapp S, Jung G, Winkelmann G (1988) Characterization of Ferrioxamine E as the Principal Siderophore of *Erwinia herbicola* (*Enterobacter agglomerans*). Biol Metals **1**: 51
30b. Berti AD, Thomas MG (2009) Analysis of Achromobactin Biosynthesis by *Pseudomonas syringae* pv. *syringae* B728a. J Bacteriol **191**: 4594
30c. Bertrand S, Larcher G, Landreau A, Richomme P, Duval O, Bouchara JP (2009) Hydroxamate Siderophores of *Scedosporium apiospermum*. Biometals **22**: 1019
30d. Bickel H, Bosshardt R, Gäumann E, Reusser P, Vischer E, Voser W, Wettstein A, Zähner H (1960) Stoffwechselprodukte von Actinomyceten. 26. Mitteilung. Über die Isolierung und Charakterisierung der Ferrioxamine A–F, neuer Wuchsstoffe der Sideramingruppe. Helv Chim Acta **43**: 2118
30e. Bickel H, Hall GE, Keller-Schierlein W, Prelog V, Vischer E, Wettstein A (1960) Stoffwechselprodukte von Actinomyceten. 27. Mitteilung. Über die Konstitution von Ferrioxamin B. Helv Chim Acta **43**: 2129
31. Bister B, Bischoff D, Nicholson GJ, Valdebenito M, Schneider K, Winkelmann G, Hantke K, Süssmuth RD (2004) The Structure of Salmochelins: C-Glucosylated Enterobactins of *Salmonella enterica*. BioMetals **17**: 471

32. Boopathi E, Rao KS (1999) A Siderophore from *Pseudomonas putida* Type A1: Structural and Biological Characterization. Biochim Biophys Acta **1435**: 30

33. Boukhalfa H, Reilly SD, Michalczyk R, Iyer S, Neu P (2006) Iron (III) Coordination Properties of a Pyoverdin Siderophore Produced by *Pseudomonas putida* ATCC 33015. Inorg Chem **45**: 5607

34. Braun V, Pramanik A, Gwinner T, Köberle M, Bohn E (2009) Sideromycins: Tools and Antibiotics. Biometals **22**: 3

35. Briskot G, Taraz K, Budzikiewicz H (1989) Pyoverdin-Type Siderophores from *Pseudomonas aeruginosa*. Liebigs Ann Chem 375

35a. Budzikiewicz H (2001) Siderophore-Antibiotic Conjugates used as Trojan Horses against *Pseudomonas aeruginosa*. Curr Top Med Chem **1**: 73

36. Budzikiewicz H (2003) Heteroaromatic Monothiocarboxylic Acids from *Pseudomonas* spp. Biodegradation **14**: 65

37. Budzikiewicz H (2004) Siderophores of the Pseudomonadaceae *sensu stricto* (Fluorescent and Non-fluorescent *Pseudomonas* spp.). Progr Chem Org Nat Prod **87**: 81

38. Budzikiewicz H (2004) Bacterial Catecholate Siderophores. Mini-Rev Org Chem **1**: 163

39. Budzikiewicz H (2005) Bacterial Citrate Siderophores. Mini-Rev Org Chem **3**: 119

40. Budzikiewicz H (2006) Bacterial Aromatic Sulfonates – a *Bucherer* Reaction in Nature? Mini-Rev Org Chem **3**: 93

41. Budzikiewicz H, Bössenkamp A, Taraz K, Pandey A, Meyer JM (1997) Corynebactin, a Cyclic Catecholate Siderophore from *Corynebacterium glutamicum* ATCC 14067 (*Brevibacterium* sp. DSM 20411). Z Naturforsch **52c**: 551

42. Budzikiewicz H, Kilz S, Taraz K, Meyer JM (1997) Identical Pyoverdines from *Pseudomonas fluorescens* 9AW and from *Pseudomonas putida* 9BW. Z Naturforsch **52c**: 721

43. Budzikiewicz H, Münzinger M, Taraz K, Meyer JM (1997) Schizokinen, the Siderophore of the Plant Deleterious Bacterium *Ralstonia* (*Pseudomonas*) *solanacearum* ATCC 11969. Z Naturforsch **52c**: 496

44. Budzikiewicz H, Schäfer M, Meyer JM (2007) Siderotyping of Fluorescent Pseudomonads – Problems in the Determination of Molecular Masses by Mass Spectrometry. Mini-Rev Org Chem **4**: 246

45. Budzikiewicz H, Schäfer M, Uría Fernández D, Matthijs S, Cornelis P. (2007) Characterization of the Chromophores of Pyoverdins and Related Siderophores by Electrospray Tandem Mass Spectrometry. BioMetals **20**: 135

46. Budzikiewicz H, Schäfer M, Uría Fernández D, Meyer JM (2006) Structure Proposal for a New Pyoverdin from *Pseudomonas* sp. PS 6.10. Z Naturforsch C **61c**: 815

47. Budzikiewicz H, Schröder H, Taraz K (1992) Zur Biogenese der *Pseudomonas*-Siderophore: Der Nachweis analoger Strukturen eines Pyoverdin-Desferriferribactin-Paares. Z Naturforsch **47c**: 26

48. Budzikiewicz H, Uría Fernández D, Fuchs R, Michalke R, Taraz K, Ruangviriyachai C (1999) Pyoverdins with a Lys ε-Amino Link in the Peptide Chain? Z Naturforsch **54c**: 1021

49. Bultreys A, Gheysen I, de Hoffmann E (2006) Yersiniabactin Production by *Pseudomonas syringae* and *Escherichia coli*, and Description of a Second Yersiniabactin Locus Evolutionary Group. Appl Environ Microbiol **72**: 3814

49a. Bultreys A, Gheysen I, Wathelet B, Maraite H, de Hoffman E (2003) High-Performance Liquid Chromatography Analyses of Pyoverdin Siderophores Differentiate among Phytopathogenic Fluorescent *Pseudomonas* Species. Appl Environ Microbiol **69**: 1143 and unpublished material

50. Bultreys A, Gheysen I, Wathelet B, Schäfer M, Budzikiewicz H (2004) The Pyoverdins of *Pseudomonas syringae* and *Pseudomonas cichorii*. Z Naturforsch **59c**: 613

51. Burton MO, Sowden FJ, Lochhead AG (1954) The Isolation and Nature of the "Terregens Factor". Can J Biochem Physiol **32**: 400 (Chem Abstr **48**, 10839d, 1954).

52. Buyer JS, de Lorenzo V, Neilands JB (1991) Production of the Siderophore Aerobactin by a Halophilic Pseudomonad. Appl Environ Microbiology **57**: 2246

53. Byers BR, Powell MV, Lankford CE (1967) Iron-Chelating Hydroxamic Acid (Schizokinen) Active in Initiation of Cell Division in *Bacillus megaterium*. J Bacteriol **93**: 286
54. Calugay RJ, Takeyama H, Mukoyama D, Fukuda Y, Suzuki T, Kanoh K, Matsunaga T (2006) Catechol Siderophore Excretion by Magnetotactic Bacterium *Magnetospirillum magneticum* AMB-1. J Biosci Bioeng **101**: 445
55. Candeloro S, Gardenić D, Taylor N, Thompson B, Viswamitra M, Hodgkin DC (1969) Structure of Ferroverdin. Nature **224**: 589
56. Capon RJ, Steward M, Ratnayake R, Lacey E, Gill JH (2007) Citromycetins and Bilains A-C: new Aromatic Polyketides and Diketopiperazines from Australian Marine-derived and Terrestrial *Penicillium* spp. J Nat Prod **70**: 1746
57. Carmi R, Carmeli S, Levy E, Gough FJ (1994) (+)-(*S*)-Dihydroaeruginoic Acid, an Inhibitor of *Septoria tritici* and other Phytopathogenic Fungi and Bacteria, Produced by *Pseudomonas fluorescens*. J Nat Prod **57**: 1200
58. Carrano CJ, Drechsel H, Kaiser D, Jung G, Matzanke B, Winkelmann G, Rochel N, Albrecht-Gary AM (1996) Coordination Chemistry of the Carboxylate Type Siderophore Rhizoferrin: the Iron(III) Complex and its Metal Analogs. Inorg Chem **35**: 6429
59. Carrano CJ, Jordan M, Drechsl H, Schmid DG, Winkelmann G (2001) Heterobactins: a New Class of Siderophores from *Rhodococcus erythropolis* IGTS8 Containing both Hydroxamate and Catecholate Donor Groups. BioMetals **14**: 119
60. Carrano CJ, Raymond KN (1978) Coordination Chemistry of Microbial Iron Transport Compounds. 10. Characterization of the Complexes of Rhodotorulic Acid, a Dihydroxamate Siderophore. J Am Chem Soc **100**: 5371
61. Carrano CJ, Thieken A, Winkelmann G (1996) Specificity and Mechanism of Rhizoferrin-Mediated Metal Ion Uptake. BioMetals **9**: 185
61a. Carson KC, Glenn AR, Dilworth MJ (1994) Specificity of Siderophore-mediated Transport of Iron in Rhizobia. Arch Microbiol **161**: 333
62. Chakraborty RN, Patel HN, Desai SB (1990) Isolation and Partial Characterization of Catechol-Type Siderophore from *Pseudomonas stutzeri*. Curr Microbiol **20**: 283
63. Challis GL (2005) A Widely Distributed Bacterial Pathway for Siderophore Biosynthesis Independent of Nonribosomal Peptide Synthetases. ChemBioChem **6**: 601
64. Chambers CE, McIntyre DD, Mouck M, Sokol PA (1996) Physical and Structural Characterization of Yersiniophore, a Siderophore Produced by Clinical Isolates of *Yersinia enterocolitica*. BioMetals **9**: 157
65. Cianciotto NP (2007) Iron Acquisition by *Legionella pneumophila*. Biometals **20**: 323
66. Ciche TA, Blackburn M, Carney JR, Ensign JB (2003) Photobactin: a Catechol Siderophore Produced by *Photorhabdus luminescens*, an Entomopathogen Mutually Associated with *Heterorhabditis bacteriophora* NC1 Nematodes. Appl Environ Microbiol **69**: 4706
67. Cobessi D, Celia H, Folschweiller N, Schalk IJ, Abdallah MA, Pattus F (2005) The Crystal Structure of the Outer Pyoverdine Membrane Receptor FpvA from *Pseudomonas aeruginosa* at 3.6 Å Resolution. J Mol Biol **347**: 121
67a. Cobessi D, Celia H, Pattus F (2005) Crystal Structure at High Resolution of Ferric-Pyochelin and its Membrane Receptor FptA from *Pseudomonas aeruginosa.* J Mol Biol **352**: 893
68. Cody YS, Gross DC (1987) Characterization of Pyoverdin$_{pss}$, the Fluorescent Siderophore Produced by *Pseudomonas syringae* pv. *syringae*. Appl Environ Microbiol **53**: 928
69. Cone MC, Melville CR, Carney JR, Gore MP, Gould, SJ (1995) 4-Hydroxy-3-nitrosobenzamide and its Ferrous Chelate from *Streptomyces murayamaensis*. Tetrahedron **51**: 3095
70. Corbin JL, Bulen WA (1969) The Isolation and Identification of 2,3-Dihydroxybenzoic Acid and 2-*N*,6-*N*-di(2,3-dihydroxybenzoyl)-L-lysine Formed by Iron-deficient *Azozobacter vinelandii*. Biochemistry **8**: 757
71. Corey EJ, Bhattacharyya S (1977) Total Synthesis of Enterobactin, a Macrocyclic Iron Transporting Agent of Bacteria. Tetrahedron Lett 3919
72. Cornish AS, Page WJ (1995) Production of the Triacetocholate (*sic*!) Siderophore Protochelin by *Azotobacter vinelandii*. BioMetals **8**: 332

73. Cox CD, Rinehart KL Jr, Moore ML, Cook, JC Jr (1981) Pyochelin: Novel Structure of an Iron-chelating Growth Promotor for *Pseudomonas aeruginosa*. Proc Natl Acad Sci USA **78**: 4256

74. De M, Basu M, Chakrabartty PK (2003) Increased Synthesis of Dihydroxybenzoic Acid in the Presence of Aluminum by *Rhizobium* MO1. Acta Microbiol Polon **52**: 195

75. De Lorenzo V, Martinez JL (1988) Aerobactin Production as a Virulence Factor: a Reevaluation. Eur J Clin Microbiol Infect Dis **7**: 621

76. Demange P, Bateman A, Dell A, Abdallah MA (1988) Structure of Azotobactin D, a Siderophore of *Azotobacter vinelandii* Strain D (CCM 289). Biochemistry **27**: 2745

77. Demange P, Bateman A, MacLeod JK, Dell A, Abdallah MA (1990) Bacterial Siderophores: Unusual 3,4,5,6-Tetrahydropyrimidine-Based Amino Acids in Pyoverdins from *Pseudomonas fluorescens*. Tetrahedron Lett **31**: 7611

78. Demange P, Bateman A, Mertz C, Dell A, Piémont Y, Abdallah MA (1990) Bacterial Siderophores: Structure of Pyoverdins Pt, Siderophores of *Pseudomonas tolaasii* NCPPB 2192, and Pyoverdins Pf, Siderophores of *Pseudomonas fluorescens* CCM 2798. Identification of an Unusual Natural Amino Acid. Biochemistry **29**: 11041

79. Demange P, Wendenbaum S, Bateman A, Dell A, Meyer JM, Abdallah MA (1986) Bacterial Siderophores: Structure of Pyoverdins and Related Compounds. In: Swinburne TR (ed) Iron, Siderophores, and Plant Diseases. Plenum, New York, p 131

80. Demange P, Wendenbaum S, Linget C, Bateman A, MacLeod J, Dell A, Albrecht AM, Abdallah MA (1989) *Pseudomonas* Siderophores: Structure and Physicochemical Properties of Pyoverdins and Related Peptides. Second Forum on Peptides **174**: 95

81. Demange P, Wendenbaum S, Linget C, Mertz C, Cung MT, Dell A, Abdallah MA (1990) Bacterial Siderophores: Structure and NMR Assignment of Pyoverdins Pa, Siderophores of *Pseudomonas aeruginosa* ATCC 15692. Biol Metals **3**: 155

82. Deml G, Voges K, Jung G, Winkelmann G (1984) Tetraglycylferrichrome – the First Heptapeptide Ferrichrome. FEBS **173**: 53

83. Deng J, Hamada Y, Shioiri T (1995) Total Synthesis of Alterobactin A, a Super Siderophore from an Open-Ocean Bacterium. J Am Chem Soc **117**: 7824

84. Dertz EA, Xu J, Stintzi A, Raymond KN (2006) Bacillibactin-mediated Iron Transport in *Bacillus subtilis*. J Am Chem Soc **128**: 22

85. de Voss JJ, Rutter K, Schroeder BG, Barry CE III (1999) Iron Acquisition and Metabolism by Mycobacteria. J Bacteriol **181**: 4443

86. Dhungana S, Michalczyk R, Boukhalfa H, Lack JG, Koppisch AT, Fairlee JM, Johnson MT, Ruggiero CE, John SG, Cox MM, Browder CC, Forsythe JH, Vanderberg LA, Neu MP, Hersman LE (2007) Purification and Characterization of Rhodobactin: a Mixed Ligand Siderophore from *Rhodococcus rhodochrous* Strain OFS. Biometals **20**: 853

87. Dhungana S, Miller MJ, Dong L, Ratledge C, Crumbliss AL (2003) Iron Chelation Properties of an Extracellular Siderophore Exochelin MN. J Am Chem Soc **125**: 7654

88. Diekmann H (1967) Stoffwechselprodukte von Mikroorganismen. 56. Mitteilung. Fusigen – ein neues Sideramin aus Pilzen. Arch Mikrobiol **58**: 1

89. Diekmann H (1970) Stoffwechselprodukte von Mikroorganismen. 81. Mitteilung. Vorkommen und Strukturen von Coprogen B und Dimerumsäure. Arch Microbiol **73**: 65

90. Diekmann H, Krezdorn E (1975) Stoffwechselprodukte von Mikroorganismen. 150. Mitteilung. Ferricrocin, Triacetylfusigen und andere Sideramine aus Pilzen der Gattung *Aspergillus*, Gruppe *Fumigatus*. Arch Microbiol **106**: 191

90a. Diels L, Van Roy S, Taghavi S, Van Houdt R (2009) From Industrial Sites to Environmental Applications with *Cupriavidus metallidurans*. Antonie van Leeuwenhoek **96**: 247

91. Dilworth MJ, Carson KC, Giles RGF, Byrne LT, Glenn AR (1998) *Rhizobium leguminosarum* bv. *viciae* Produces a Novel Cyclic Trihydroxamate Siderophore, Vicibactin. Microbiology **144**: 781

92. Dimise EJ, Widboom PF, Bruner SD (2008) Structure Elucidation and Biosynthesis of Fuscachelins, Peptide Siderophores from the Moderate Thermophile *Thermobifida fusca*. Proc Natl Acad Sci USA **105**: 15311

93. Drechsel H, Metzger J, Freund S, Jung G, Boelaert JR, Winkelmann G (1991) Rhizoferrin – a Novel Siderophore from the Fungus *Rhizopus microsporus* var. *rhizopodiformis*. Biol Metals **4**: 238

94. Drechsel H, Freund S, Nicholson G, Haag H, Jung O, Zähner H, Jung G. (1993) Purification and Chemical Characterization of Staphyloferrin B, a Hydrophilic Siderophore from Staphylococci. BioMetals **6**: 185

95. Drechsel H, Jung G, Winkelmann G (1992) Stereochemical Characterization of Rhizoferrin and Identification of its Dehydration Products. BioMetals **5**: 141

96. Drechsel H, Stephan H, Lotz R, Haag H, Zähner H, Hantke K, Jung G (1995) Structure Elucidation of Yersiniabactin, a Siderophore from Highly Virulent *Yersinia* Strains. Liebigs Ann Chem 1727

97. Drechsel H, Winkelmann G (1997) Iron Chelation and Siderophores. In: Winkelmann G, Carrano CJ (eds) Transition Metals in Microbial Metabolism. Harwood Academic Publishers, Amsterdam, p 1

98. du Moulinet d'Hardemare A, Serratrice G, Pierre JL (2004) Synthesis and Iron-binding Properties of Quinolobactin, a Siderophore from a Pyoverdine-deficient *Pseudomonas fluorescens*. BioMetals **17**: 691

99. Ecker DJ, Lancaster JR Jr., Emery T (1982) Siderophore Iron Transport Followed by Electron Paramagnetic Resonance Spectroscopy. J Biol Chem **257**: 8623

100. Egawa Y, Umino K, Ito Y, Okuda T. (1971) Antibiotic YC 73 of *Pseudomonas* Origin. II. Structure and Synthsis of Thioformin and its Cupric Complex (YC 73). J Antibiot **24**: 124

101. Ehlert G, Taraz K, Budzikiewicz H (1994) Serratiochelin, a New Catecholate Siderophore from *Serratia marcescens*. Z Naturforsch **49c**: 11

102. El Hage Chahine JM, Bauer AM, Baraldo K, Lion C, Ramiandrasoa F, Kunesch G. (2001) Kinetics and Thermodynamics of Complex Formation between Fe^{III} and Two Synthetic Chelators of the Dicatecholspermidine Family. Eur J Inorg Chem 2287

103. Emery T (1971) Role of Ferrichrome as a Ferric Ionophore in *Ustilago sphaerogena*. Biochemistry **10**: 1483

103a. Emery T (1976) Fungal Ornthine Esterases: Relationship to Iron Transport. Biochemistry **15**: 2723

104. Emery T. (1980) Malonichrome, a New Iron Chelate from *Fusarium roseum*. Biochim Biophys Acta **629**: 382

105. Emery T (1987) Reductive Mechanisms of Iron Assimilation. In: Winkelmann G, van der Helm D, Neilands JB (eds) Iron Transport in Microbes, Plants and Animals. VCH, Weinheim, p 235

106. Emery T, Neilands JB (1961) Structure of the Ferrichrome Compounds. J Am Chem Soc **83**: 1626

107. Eng-Wilmot DL, Kerley EL, Perryman DD, Brown C, Noah WH, McDyer D, Gore M, Mergo PJ, Cockburn BA (1990) Pyoverdin Type Siderophores from Various Strains of *Pseudomonas aeruginosa*. Reported at the International Symposium on Iron Transport and Metabolism II, 20.–22. June 1990, Austin TX, USA

108. Eng-Wilmot DL, Rahman A, Mendenhall JV, Grayson SL, van der Helm D (1984) Molecular Structure of Ferric Neurosporin, a Minor Siderophore-like Compound Containing N^{δ}-hydroxy-D-ornithine. J Am Chem Soc **106**: 1285

109. Eng-Wilmot DL, van der Helm D (1980) Molecular and Crystal Structure of the Linear Tricatechol Siderophore, Agrobactin. J Am Chem Soc **102**: 7719

110. Feistner GJ (1995) Suggestion for a New, Semirational Nomenclature for the Free Chelators of Ferrioxamines. BioMetals **8**: 193

111. Feistner GJ (1995) Proferrioxamine Synthesis in *Erwinia amylovora* in Response to Precursor or Hydroxylysine Feeding: Metabolic Profiling with Liquid Chromatography-Electrospray Mass Spectrometry. BioMetals **8**: 318

112. Feistner G, Beaman BL (1987) Characterization of 2,3-Dihydroxybenzoic Acid from *Nocardia asteroides* GUH-2. J Bacteriology **169**: 3982

112a. Feistner GJ, Hsieh LL (1995) On the Collision-activated Fragmentation of Proferrioxamines: Evidence for a Succinimide-mediated Mechanism. J Am Soc Mass Spectrom **6**: 836
113. Feistner GJ, Korth H, Ko H, Pulverer G, Budzikiewicz H (1983) Ferrorosamine A from *Erwinia rhapontici*. Curr Microbiol **8**: 239
114. Feistner GJ, Mavridis A, Rudolph K (1997) Proferrorosamines and Phytopathogenicity in *Erwinia* spp. BioMetals **10**: 1
115. Feistner GJ, Stahl DC, Gabrik AH (1993) Proferrioxamine Siderophores of *Erwinia amylovora*. A Capillary Liquid Chromatographic/Electrospray Tandem Mass Spectrometric Study. Org Mass Spectrom **28**: 163
115a. Fekete FA, Lanzi RA, Beaulieu JB, Longcope DC, Sulya AW, Hayes RN, Mabbott GA (1989) Isolation and Preliminary Characterization of Hydroxamic Acids Formed by Nitrogen-fixing *Azotobacter chroococcum* B-8. Appl Envir Microbiol **55**: 298
116. Filsak G, Taraz K, Budzikiewicz H. (1994) Untersuchungen zur Struktur und Derivatisierung von Kondensationsprodukten der 2,4-Diaminobuttersäure mit anderen Aminosäuren. Z Naturforsch **49c**: 18
117. Frederick CB, Bentley MD, Shive W (1981) Structure of Triornicin, a New Siderophore. Biochemistry **20**: 2436
118. Frederick CB, Bentley MD, Shive W (1982) The Structure of the Fungal Siderophore, Isotriornicin. Biochem Biophys Res Commun **105**: 133
119. Fuchs R (2000) Massenspektrometrische Untersuchung cyclischer Pyoverdine: Strukturaufklärung und Siderotyping. Dissertation; Universität zu Köln.
120. Fukasawa K, Goto M, Sasaki K, Hirata Y, Sato S (1972) Structure of the Yellow-Green Fluorescent Peptide Produced by Iron-deficient *Azotobacter vinelandii* Strain O. Tetrahedron **28**: 5359
121. Gademann K, Bethuel Y, Locher HH, Hubschwerlen C (2007) Biomimetic Total Synthesis and Antimicrobial Evaluation of Anachelin H. J Org Chem **72**: 8361
122. Gademann K, Budzikiewicz H (2004) The Peptide Alkaloid Anachelin: NMR Spectroscopic Evidence for a β-Turn Formation in Aqueous Solution. Chimia **58**: 212
123. Garner BL, Arceneaux JEL, Byers BR (2004) Temperature Control of a 3,4-dihydroxybenzoate (Protocatechuate)-based Siderophore in *Bacillus anthracis*. Curr Microbiol **49**: 89
124. Geisen K, Taraz K, Budzikiewicz H (1992) Neue Siderophore des Pyoverdin-Typs aus *Pseudomonas fluorescens*. Monatsh Chem **123**: 151
125. Georgias H, Taraz K, Budzikiewicz H, Geoffroy V, Meyer JM (1999) The Structure of the Pyoverdin from *Pseudomonas fluorescens* 1.3. Structural and Biological Relationship of Pyoverdins from Different Strains. Z Naturforsch **54c**: 301
126. Gibson F, Magrath DI (1969) The Isolation and Characterization of a Hydroxamic Acid (Aerobactin) Formed by *Aerobacter aerogenes* 62-I. Biochim Biophys Acta **192**: 175
126a. Gilis A, Khan MA, Cornelis P, Meyer JM, Mergeay M, van der Lelie D (1996) Siderophore-mediated Iron Uptake in *Alcaligenes eutrophus* CH34 and Identification of *aleB* Encoding the Ferric Iron-Alcaligin E Receptor. J Bacteriol **178**: 5499
127. Gipp S, Hahn J, Taraz K, Budzikiewicz H (1991) Zwei Pyoverdine aus *Pseudomonas aeruginosa* R. Z Naturforsch **46c**: 534
128. Gobin J, Moore CH, Reeve JR Jr, Wong DK, Gibson BW, Horwitz MA (1995) Iron Acquisition by *Mycobacterium tuberculosis*: Isolation and Characterization of a Family of Iron-binding Exochelins. Proc Natl Acad Sci USA **92**: 5189
128a. Greenwald J, Nader M, Celia H, Gruffaz C, Geoffroy V, Meyer JM, Schalk IJ, Pattus F (2009) FpvA Bound to Non-cognate Pyoverdines: Molecular Basis of Siderophore Recognition by an Iron Transporter. Mol Microbiol **72**: 1246
129. Griffiths GL, Sigel SP, Payne SM, Neilands JB (1984) Vibriobactin, a Siderophore from *Vibrio cholerae*. J Biol Chem **10**: 383
130. Gwose I, Taraz K (1992) Pyoverdine aus *Pseudomonas putida*. Z Naturforsch **47c**: 487
131. Haag H, Fiedler HP, Meiwes J, Drechsel H, Jung G, Zähner H (1994). Isolation and Biological Characterization of Staphyloferrin B, a Compound with Siderophore Activity from Staphylococci. FEMS Microbiol Lett **115**: 125

131a. Hahn FE, McMurry TJ, Hugi A, Raymond KN (1990) Coordination Chemistry of Microbial Iron Transport. 42. Structural and Spectroscopic Characterization of Diastereomeric Cr(III) and Co(III) Complexes of Desferriferrithiocin. J Am Chem Soc **112**: 1854
132. Hancock DK (1991) Isolation and Structure of a Unique Pyoverdine-type Siderophore Containing L-*threo*-β-Hydroxyhistidine. Ph.D Thesis, University of Maryland
133. Hancock DK, Coxon B, Wang SY, White VE, Reeder DJ, Bellama JM (1993) L-*threo*-β-Hydroxyhistidine, an Unprecedented Iron (III) Ion-Binding Amino Acid in a Pyoverdine-Type Siderophore from *Pseudomonas fluorescens* 244. J Chem Soc Chem Commun 468
134. Hancock DK, Reeder DJ (1993) Analysis and Configuration Assignment of the Amino Acids in a Pyoverdine-Type Siderophore by Reversed-Phase High-Performance Liquid Chromatography. J Chromatogr **646**: 335
135. Hantke K, Nicholson G. Rabsch W, Winkelmann G (2003) Salmochelins, Siderophores of *Salmonella enterica* and Uropathogenic *Escherichia coli* Strains, are Recognized by the Outer Membrane Receptor Iron. Proc Natl Acad Sci USA **100**: 3677
136. Harada K, Tomita K, Fujii K, Masuda K, Mikami Y, Yazawa K, Komaki H (2004) Isolation and Structural Characterization of Siderophores, Madurastatins, Produced by a Pathogenic *Actinomadura madurae*. J Antibiot **57**: 125
137. Harrington, JM, Crumbliss AL (2009) The Redox Hypothesis in the Siderophore-mediated Iron Uptake. Biometals **22**: 679
138. Harris WR, Carrano CJ, Raymond KN (1979) Coordination Chemistry of Microbial Iron Transport Compounds. 16. Isolation, Characterization, and Formation Constants of Ferric Aerobactin. J Am Chem Soc **101**: 2722
139. Haselwandter K, Dobernigg B, Beck W, Jung G, Cansier A, Winkelmann G (1992) Isolation and Identification of Hydroxamate Siderophores of Ericoid Mycorrhizal Fungi. BioMetals **5**: 51
140. Hayen H, Volmer DA (2006) Different Iron-chelating Properties of Pyochelin Diastereoisomers Revealed by LC/MS. Anal Bioanal Chem **385**: 606
141. Haygood MG, Holt PD, Butler A (1993) Aerobactin Production by a Planctonic Marine *Vibrio* sp. Limnol Oceanogr **38**: 1091
141a. Hersman LE, Huang A, Maurice PA, Forsythe JH (2000) Siderophore Production and Iron Reduction by *Pseudomonas mendocina* in Response to Iron Deprivation. Geomicrobiology J **17**: 261
142. Hickford SHJ, Küpper FC, Zhang G, Carrano CJ, Blunt JW, Butler A (2004) Petrobactine Sulfonate, a New Siderophore Produced by the Marine Bacterium *Marinobacter hydrocarbonoclasticus*. J Nat Prod **67**: 1897
143. Hildebrand U, Lex J, Taraz K, Winkler S, Ockels W, Budzikiewicz H (1984) Untersuchungen zum Redox-System Bis(pyridin-2,6-dicarbothioato)-ferrat(II)/ferrat(III). Z Naturforsch **39b**: 1607
144. Hildebrand U, Taraz K, Budzikiewicz H (1986) 6-(Hydroxythio)carbonylpyridin-2-carbonsäure und Pyridin-2-carbonsäure-6-monothiocarbonsäure als biosynthetische Zwischenstufen bei der Bildung von Pyridin-2,6-di(monothiocarbonsäure) aus Pyridin-2,6-dicarbonsäure. Z Naturforsch **41c**: 691
145. Hildebrand U, Taraz K, Budzikiewicz H, Korth H, Pulverer G. (1985) Dicyano-bis(pyridin-2,6-dicarbothioato)-ferrat (II)/ferrat (III), ein weiteres eisenhaltiges Redoxsystem aus der Kulturlösung eines *Pseudomonas*-Stammes. Z Naturforsch **40c**: 201
145a. Hoegy F, Celia H, Mislin GL Vicent M, Gallay J, Schalk IJ (2005) Binding of Iron-free Siderophore, a Common Feature of Siderophore Outer Membrane Transporters of *Escherichia coli* and *Pseudomonas aeruginosa*. J Biol Chem **280**: 20222
146. Hohlneicher U, Hartmann R, Taraz K, Budzikiewicz H (1995) Pyoverdin, Ferribactin, Azotobactin – a new Triad of Siderophores from *Pseudomonas chlororaphis* ATTC 9446 and its Relation to *Pseudomonas fluorescens* ATCC 13525. Z Naturforsch **50c**: 337
147. Holinsworth B, Martin JD (2009) Siderophore Production by Marine-derived Fungi. Biometals **22**: 625

148. Holt PD, Reid RR, Lewis BL, Luther GW III, Butler A (2005) Iron(III) Coordination Chemistry of Alterobactin A: a Siderophore from the Marine Bacterium *Alteromonas luteoviolacea*. Inorg Chem **44**: 7671
149. Homann VV, Edwards KJ, Webb EA, Butler A (2009) Siderophores of *Marinobacter aquaeolei*: Petrobactin and its Sulfonated Derivatives. Biometals **22**: 565
150. Homann VV, Sandy M, Tincu JA, Templeton AS, Tebo BM, Butler A (2009) Loihichelins A-F, a Suite of Amphiphilic Siderophores Produced by the Marine Bacterium *Halomonas* LOB-5. J Nat Prod **72**: 884
151. Hopkinson BM, Morel FMM (2009) The Role of Siderophores in Iron Acquisition by Photosynthetic Marine Microorganisms. Biometals **22**: 659
152. Hossein MB, Eng-Wilmot DL, Loghry RA, van der Helm D (1980) Circular Dichroism, Crystal Sructure, and Absolute Configuration of the Siderophore Ferric *N*,*N*′,*N*″-Triacetylfusarinine, $FeC_{39}H_{57}N_6O_{15}$. J Am Chem Soc **102**: 5766
153. Hossein MB, Jalal MAF, Benson BA, Barnes CL, van der Helm D (1987) Structure and Conformation of Two Coprogen-type Siderophores: Neocoprogen I and Neocoprogen II. J Am Chem Soc **109**: 4948
154. Hossein MB, Jalal MAF, van der Helm D (1986) The Structure of Ferrioxamine D1-Ethanol-Water (1/2/1) Acta Cryst C **42**: 1305
155. Hossain MB, Jalal MAF, van der Helm D (1997) 6-L-Alanineferrirubin, a Ferrichrome-type from the Fungus *Aspergillus ochraceous*. Acta Cryst C **53**: 716
155a. Hossein MB, van der Helm D, Poling M (1983) The Structure of Deferriferrioxamine E (Norcardamin), a Cyclic Trihydroamate. Acta Cryst B **39**: 258
156. Hou Z, Sunderland CJ, Nishio T, Raymond KN (1996) Preorganization of Ferric Alcaligin, Fe_2L_3. The First Structure of a Ferric Dihydroxamate Siderophore. J Am Chem Soc **118**: 5148
157. Hough E, Rodgers D (1974) The Crystal Structure of Ferrimycobactin P, a Growth Factor for the *Mycobacteria*. Biochem Biophys Res Commun **57**: 73
157a. Howard DH (1999) Acquisition, Transport, and Storage of Iron by Pathogenic Fungi. Clin Microbiol Rev **12**: 394
157b. Howard DH, Rafie R, Tiwari A, Faull KF (2000) Hydroxamate Siderophores of *Histoplasma capsulatum*. Infect Immun **68**: 2338
158. Hu X, Boyer GL (1995) Isolation and Characterization of the Siderophore *N*-Deoxyschizokinen from *Bacillus megaterium* ATCC 19213. BioMetals **8**: 357
159. Hulcher FH (1982) Isolation and Characterization of a New Hydroxamic Acid from *Pseudomonas mildenbergii*. Biochemistry **21**: 4491
160. Huschka HG, Jalal MAF, van der Helm D, Winkelmann G (1986) Molecular Recognition of Siderophores in Fungi: Role of Iron-surrounding *N*-Acyl Residues and the Peptide Backbone During Membrane Transport in *Neurospora crassa*. J Bacteriol **167**: 1020
160a. Huschka H, Naegeli HU, Leuenberger-Ryf H, Keller-Schierlein W, Winkelmann G (1985) Evidence for a Common Siderophore Transport System but Different Siderophore Receptors in *Neurospora crassa*. J Bacteriol **162**: 715
161. Ino A, Hasegawa Y, Murabayashi A (1998) Total Synthesis of the Antimycoplasma Antibiotic Micacocidin. Tetrahedron Lett **39**: 3509
161a. Ino A, Hasegwa Y, Murabayashi A (1999) Synthetic Studies of Thiazoline- and Thiazolidine-Containing Natural Products. 2. Total Synthesis of Antimycoplasma Antibiotic Micacocidin. Tetrahedron **55**: 10283
162. Inoue H, Takimura O, Kawaguchi K, Nitoda T, Fuse H, Murakami K, Yamaoka Y (2003) Tin-Carbon Cleavage of Organotin Compounds by Pyoverdine from *Pseudomonas chlororaphis*. Appl Environ Microbiol **69**: 878
163. Ishimaru CA, Loper JE (1992) High-Affinity Iron Uptake Systems Present in *Erwinia carotovora* subsp. *carotovora* Include the Hydroxamate Siderophore Aerobactin. J Bacteriol **174**: 2993
164. Ito T, Neilands JB (1958) Products of "Low-iron Fermentation" with *Bacillus subtilis*: Isolation, Characterization and Synthesis of 2,3-Dihydroxybenzoylglycine. J Am Chem Soc **80**: 4645

165. Ito Y, Butler A (2005) Structure of Synechobactins, New Siderophores of the Marine Cyanobacterium *Synechococcus* sp. PCC 7002. Limnol Oceanogr **50**: 1918
166. Ito Y, Ishida, K, Okada S, Murakami M (2004) The Absolute Stereochemistry of Anachelins, Siderophores from the Cyanobacterium *Anabena cylindrica*. Tetrahedron **60**: 9075
166a. Ito Y, Umino K, Sekiguchi T, Miyagishima T, Egawa Y (1971) Antibiotic YC 73 of *Pseudomonas* Origin. III. Synthesis of Thioformin Analogues. J Antibiot **24**: 131
167. Itou Y, Okada S, Murakami M (2001) Two Structural Isomeric Siderophores from the Freshwater Cyanobacterium *Anabena cylindrica* (NIES-19). Tetrahedron **57**: 9093
168. Jacques P, Ongena M, Gwose I, Seinsche D, Schröder H, Delphosse P, Thonart P, Taraz K, Budzikiewicz H (1995). Structure and Characterization of Isopyoverdin from *Pseudomonas putida* BTP1 and its Relation to the Biogenetic Pathway Leading to Pyoverdins. Z Naturforsch **50c**: 622
169. Jalal MAF, Galles JL, van der Helm D (1985) Structure of Des(diserylglycyl)ferrirhodin, DDF, a Novel Siderophore from *Aspergillus ochraceous*. J Org Chem **50**: 5642
170. Jalal MAF, Hossain MB, van der Helm D, Barnes CL (1988) Structure of Ferrichrome-type Siderophores with Dissimilar N^{δ}-acyl Groups: Asperchrome B_1, B_2, B_3, D_1, D_2 and D_3. Biol Metals **1**: 77
171. Jalal MAF, Hossain MB, van der Helm D, Sanders-Loehr J, Actis LA, Crosa JH (1989) Structure of Anguibactin, a Unique Plasmid-related Siderophore from Fish-pathogen *Vibrio anguillarum*. J Am Chem Soc **111**: 292
172. Jalal MAF, Love SK, van der Helm D (1986) Siderophore Mediated Iron(III) Uptake in *Gliocladium virens*. 1. Properties of *cis*-Fusarinine, *trans*-Fusarinine, Dimerum Acid, and their Ferric Complexes. J Inorg Biochem **28**: 417
173. Jalal MAF, Love SK, van der Helm D (1988) N^{α}-Dimethylcoprogens. Three Novel Trihydroxamate Siderophores from Pathogenic Fungi. Biol Metals **1**: 4
174. Jalal MAF, Mocharla R, Barnes CL, Hossain MB, Powell DR, Eng-Wilmot DL, Grayson SL, Benson BA, van der Helm D (1984) Extracellular Siderophores from *Aspergillus ochraceous*. J Bacteriol **158**: 683
175. Jalal MAF, Mocharla R, van der Helm D (1984) Separation of Ferrichromes and Other Hydroxamate Siderophores of Fungal Origin by Reversed-phase Chromatography. J Chromatogr **301**: 247
176. Jalal MAF, van der Helm D (1989) Siderophores of Highly Phytopathogenic *Alternaria longipes*. Structures of Hydroxycoprogens. Biol Metals **2**: 11
177. Jalal MAF, van der Helm D (1991) Isolation and Spectroscopic Identification of Fungal Siderophores. In: Winkelmann G (ed) Handbook of Microbial Iron Chelates. CRC, Boca Raton, FL, p 235
178. Jones AM, Lindow SE, Wildermuth MC (2007) Salicylic Acid, Yersiniabactin, and Pyoverdin Production by the Model Phytopathogen *Pseudomonas syringae* pv. tomato DC3000: Synthesis, Regulation, and Impact on Tomato and *Arabidopsis* Host Plants. J Bacteriol **189**: 6773
179. Jülich M, Taraz K, Budzikiewicz H, Geoffroy V, Meyer JM, Gardan L (2001) The Structure of the Pyoverdin Isolated from *Pseudomonas syringae* Pathovars. Z Naturforsch **56c**: 687
180. Kachadourian R, Dellagi A, Laurent J, Bricard L, Kunesch G, Expert D (1996) Desferrioxamine-dependent Iron Transport in *Erwinia amylovora* CFBP1430: Cloning of the Gene Encoding the Ferrioxamine Receptor FoxR. BioMetals **9**: 143
181. Kameyama T, Takahashi A, Kurasawa S, Ishizuka M, Okami Y, Takeuchi T, Umezawa H (1987) Bisucaberin, a New Siderophore, Sensitizing Tumor Cells to Macrophage-mediated Cytolysis. I. Taxonomy of the Producing Organism, Isolation and Biological Properties. J Antibiotics **40**: 1664
182. Kamnev AA (1998) Reductive Solubilization of Fe(III) by Certain Products of Plant and Microbial Metabolism as a Possible Alternative to Siderophore Secretion. Dokl Biophys **358-360**, 48 (translation from Dokl Akad Nauk **359**: 691).
183. Kanoh K, Kamino K, Leleo G, Adachi K, Shizuri Y (2003) Pseudoalterobactin A and B, New Sidrophores Excreted by Marine Bacterium *Pseudoalteromonas* sp. KP20-4. J Antibiotics **56**: 871

184. Keller-Schierlein W, Deér A (1963) Stoffwechselprodukte von Mikroorganismen. 44. Mitteilung. Zur Konstitution von Ferrichrysin und Ferricrocin. Helv Chim Acta **46**: 1907
184a. Keller-Schierlein W, Diekmann H (1970) Stoffwechselprodukte von Mikroorganismen. 85. Mitteilung. Zur Konstitution des Coprogens. Helv Chim Acta **53**: 2035
185. Keller-Schierlein W, Hagmann L, Zähner H, Huhn W (1988) Stoffwechselprodukte von Mikroorganismen. 250. Mitteilung. Maduraferrin, ein neuartiger Siderophor aus *Actinomadura madurae*. Helv Chim Acta **71**: 1528
185a. Keller-Schierlein W, Mertens P, Prelog V, Walser A (1965) Stoffwechselprodukte von Mikroorganismen. 49. Mitteilung. Die Ferrioxamine A_1, A_2 und D_2. Helv Chim Acta **48**: 710
185b. Keller-Schierlein W, Prelog V (1961) Stoffwechselprodukte von Actinomyceten. 29. Mitteilung. Die Konstitution des Ferrioxamins D_1. Helv Chim Acta **44**: 709
186. Keller-Schierlein W, Prelog V (1961) Stoffwechselprodukte von Actinomyceten. 30. Mitteilung. Über das Ferrioxamin E; ein Beitrag zur Konstitution des Nocardamins. Helv Chim Acta **44**: 1981
186a. Keller-Schierlein W, Prelog V (1961) Stoffwechselprodukte von Actinomyceten. 34. Mitteilung. Ferrioxamin G. Helv Chim Acta **45**: 590
187. Keller-Schierlein W, Prelog V, Zähner H (1964) Siderochrome (Natürliche Eisen(III)-trihydroxamat-Komplexe). Progr Chem Org Nat Prod **22**: 279
187a. Kilz S, Lenz C, Fuchs R, Budzikiewicz H (1999) A Fast Screening Method for the Identification of Siderophores from Fluorescent *Pseudomonas* spp. by Liquid Chromatography/Electrospray Mass Specrtrometry. J Mass Spectrom **34**: 281
187b. Kloepper JW, Leong J, Teintze M, Schroth MN (1980) *Pseudomonas* Siderophores: A Mechanism Explaining Disease-Suppressive Soils. Curr Microbiol **4**: 317
188. Klumpp C, Burger A, Mislin GL, Abdallah MA (2005) From a Total Synthesis of Cepabactin and its 3:1 Ferric Complex to the Isolation of a 1:1:1 Mixed Complex between Iron (III), Cepabactin and Pyochelin. Bioorg Med Chem Lett **15**: 1721
189. Kobayashi S, Hidaka S, Kawamura Y, Ozaki M, Hayase Y (1998) Micacocidin A, B and C, Novel Antimycoplasma Agents from *Pseudomonas* sp. I. Taxonomy, Fermentation, Isolation, Physico-chemical Properties and Biological Activities. J Antibiotics **51**: 323
190. Kobayashi S, Nakai H, Ikenishi Y, Sun WY, Ozaki M, Hayase Y, Takeda R (1998) Micacocidin A, B and C, Novel Antimycoplasma Agents from *Pseudomonas* sp. II. Structure Elucidation. J Antibiotics **51**: 328
191. Kokubo S, Suenaga K, Shinohara C, Tsuji T, Uemura D (2000) Structures of Amamistatins A and B, Novel Growth Inhibitors of Human Tumor Cell Lines from *Nocardia asteroides*. Tetrahedron **56**: 6435
192. Konetschny-Rapp S, Huschka HG, Winkelmann G, Jung G (1988) High-performance Liquid Chromatography of Siderophores from Fungi. Biol Metals **1**: 9
193. Konetschny-Rapp S, Jung G, Meiwes J, Zähner H (1900) Staphyloferrin A: a Structurally New Siderophore from Staphylococci. Eur J Biochem **191**: 65
194. Konetschny-Rapp S, Jung G, Raymond KN, Meiwes J, Zähner H (1992) Solution Thermodynamics of the Ferric Complexes of New Desferrioxamine Siderophores by Directed Fermentation. J Am Chem Soc **114**: 2224
195. Koppisch AT, Browder CC, Moe AL, Shelley JT, Kinkel BA, Hersman LE, Iyer S, Ruggiero CE (2005) Petrobactin is the Primary Siderophore Synthesized by *Bacillus anthracis* str. *Sterne* under Conditions of Iron Starvation. BioMetals **18**: 577
195a. Koppisch AT, Dhungana S, Hill KK, Boukhalfa H, Heine HS, Colip LA, Romero RB, Shou Y, Ticknor LO, Marrone BL, Hersman LE, Iyer S, Riggiero CE (2008) Petrobactin is Produced by Both Pathogenic and Non-pathogenic Isolates of the *Bacillus cereus* Group of Bacteria. Biometals **21**: 581
196. Korth H (1970) Über das Vorkommen von 2,3-Dihydroxybenzoesäure und ihrer Aminosäurederivate in Kulturmedien von *Klebsiella oxytoca*. Arch Microbiol **70**: 297
197. Kunze B, Bedorf N, Kohl W, Höfle G, Reichenbach H (1989) Myxochelin A, a New Iron-Chelating Compound from *Angiococcus disciformis* (Myxobacterales). Production, Isolation, Physicochemical and Biological Properties. J Antibiotics **42**: 14

198. Kunze B, Trowitzsch-Kienast W, Höfle G, Reichenbach H (1992) Nannochelins A, B and C, New Iron Chelating Compounds from *Nannocystis exedens* (Myxobacteria). Production, Isolation, Physico-chemical and Biological Properties. J Antibiotics **45**: 147
199. Lane SJ, Marshall PS, Upton RJ, Ratledge C, Ewing M (1995) Novel Extracellular Mycobactins, the Carboxymycobactins from *Mycobacterium avium*. Tetrahedron Lett **36**: 4129
200. Lankford CE, Walker JR, Reeves JB, Nabbut NH, Byers BR, Jones RJ (1966) Inoculum-Dependent Division Lag of *Bacillus* Cultures and its Relation to an Endogenous Factor(s) ("Schizokinen"). J Bacteriol **91**: 1070
201. Ledyard KM, Butler A (1997) Structure of Putrebactin, a New Dihydroxamate Siderophore Produced by *Shewanella putrefaciens*. J Biol Inorg Chem **2**: 93
202. Lee BH, Miller MJ (1983) Natural Ferric Ionophores: Total Synthesis of Schizokinen, Schizokinen A, and Arthrobactin. J Org Chem **48**: 24
203. Lee CH, Lewis TA, Paszczynski A, Crawford RL (1999) Identification of an Extracellular Catalyst of Carbon Tetrachloride Dehalogenation from *Pseudomonas stutzeri* Strain KC as Pyridine-2,6-bis(thiocarboxylate). Biochem Biophys Res Commun **261**: 562
204. Leong SA, Winkelmann G (1998) Molecular Biology of Iron Transport in Fungi. In: Sigel A, Sigel H (eds) Metal Ions in Biological Systems. Marcel Dekker, New York, 147
205. Lesueur D, Diem HG, Meyer JM (1993) Iron Requirement and Siderophore Production in *Bradyrhizobium* Strains Isolated from *Acacia mangium*. J Appl Bacteriol **74**: 675
205a. Lewis TA, Crawford RL (1995) Transformation of Carbon Tetrachloride via Sulfur and Oxygen Substitution by *Pseudomonas* sp. Strain KC. J Bacteriol **177**: 2204
206. Liles MR, Scheel TA, Cianciotto NP (2000) Discovery of a Nonclassical Siderophore, Legiobactin, Produced by Strains of *Legionella pneumophila*. J Bacteriol **182**: 749
207. Linke WD, Crueger A, Diekmann H (1972) Stoffwechselprodukte von Mitroorganismen. 106. Mitteilung. Zur Konstitution des Terregens-Faktors. Arch Mikrobiol **85**: 44
208. Liu WC, Fisher SM, Wells JS Jr, Ricca CS, Principe PA, Trejo WH, Bonner DP, Gougoutos JZ, Toeplitz BK, Sykes RB (1981) Siderochelin, a New Ferrous-ion Chelating Agent Produced by *Nocardia*. J Antibiot **34**: 791
209. Llinás L, Neilands JB (1976) The Structure of Two Alanine Containing Ferrichromes: Sequence Determination by Proton Magnetic Resonance. Biophys Struct Mechanism **2**: 105
210. Loomis LD, Raymond KN (1991) Solution Equilibria of Enterobactin and Metal-enterobactin Complexes. Inorg Chem **30**: 906
211. Luo M, Fadeev EA, Groves JT (2005) Membrane Dynamics of the Amphiphilic Siderophore, Acinetoferrin. J Am Chem Soc **127**: 1726
212. MacDonald JC, Bishop GG (1984) Spectral Properties of a Mixture of Fluorescent Pigments Produced by *Pseudomonas aeruginosa*. Biochim Biophys Acta **800**: 11
212a. Maksimova NP, Blazhevich OV, Lysak VV, Fomichev YuK (1994) Characteristics of fluorescent pigment pyoverdin P_m produced by *Pseudomonas putida* bacteria. *Microbiology* **63**: 587 (Russian original:Mikrobiologia **63**: 1038)
213. Marshall B, Stintzi A, Gilmour C, Meyer JM, Poole K (2009) Citrate-mediated Iron-uptake in *Pseudomonas aeruginosa*: Involvement of the Citrate-inducible FecA Receptor and the FeoB Ferrous Iron Transporter. Microbiology **155**: 305
214. Martin JD, Ito Y, Homann VV, Haygood MG, Butler A (2006) Structure and Membrane Affinity of New Amphiphilic Siderophores Produced by *Ochrobactrum* sp. SP18. J Biol Inorg Chem **11**: 633
215. Martinez JS, Butler A (2007) Marine Amphiphilic Siderophores: Marinobactin Structure, Uptake, and Microbial Partitioning. J Inorg Biochem **101**: 1692
216. Martinez JS, Carter-Franklin JN, Mann EL, Martin JD, Haygood MG, Butler A (2003) Structure and Membrane Affinity of a Suite of Amphiphilic Siderophores Produced by a Marine Bacterium. Proc Natl Acad Sci USA **100**: 3754
217. Martinez JS, Zhang GP, Holt PD, Jung HT, Carrano CJ, Haygood MG, Butler A (2000) Self-assembling Amphiphilic Siderophores from Marine Bacteria. Science **287**: 1245
218. Matthijs S, Budzikiewicz H, Schäfer M, Wathelet B, Cornelis P (2008) Ornicorrugatin, a New Siderophore from *Pseudomonas fluorescens* AF76. Z Naturforsch **63c**: 8

219. Matthijs S, Laus G, Meyer JM, Abbaspour-Tehrani K, Schäfer M, Budzikiewicz H, Cornelis P (2009) Siderophore-mediated Iron Acquisition in the Entomopathogenic Bacterium *Pseudomonas entomophila* L48 and its Close Relative *Pseudomonas putida* KT2440. Biometals **22**: 951

220. Matthijs S, Tehrani KA, Laus G, Jackson RW, Cooper RM, Cornelis P (2007) Thioquinolobactin, a *Pseudomonas* Siderophore with Antifungal and anti-*Pythium* Activity. Environ Microbiol **9**: 425

221. Maurer B, Müller A, Keller-Schierlein W, Zähner H (1968) Stoffwechselprodukte von Mikroorganismen. 61. Ferribactin, ein Siderochrom aus *Pseudomonas fluorescens* Migula. Arch Microbiol **60**: 326

222. Maurer PJ, Miller MJ (1982) Microbial Iron Chelators: Total Synthesis of Aerobactin and its Constituent Amino Acid, N^6-Acetyl-N^6-hydroxylysine. J Am Chem Soc **104**: 3096

223. May JJ, Wendrich TM, Mahariel MA (2001) The *dhb* Operon of *Bacillus subtilis* Encodes the Biosynthetic Template for the Catecholic Siderophore 2,3-Dihydroxybenzoate-glycine-threonine Trimeric Ester Bacillibactin. J Biol Chem **276**: 7209

224. McCullough WG, Merkal RS (1982) Structure of Mycobactin J. Curr Microbiol **7**: 337

225. McDougall S, Neilands JB (1984) Plasmid- and Chromosome-coded Aerobactin Synthesis in Enteric Bacteria: Insertion Sequences Flank Operon in Plasmid-mediated Systems. J Bacteriol **159**: 300

226. Meiwes J, Fiedler HP, Haag H, Zähner H, Konetschny-Rapp S, Jung G (1990) Isolation and Characterization of Staphyloferrin A, a Compound with Siderophore Activity from *Staphylococcus hyicus* DSM 20459. FEMS Microbiol Lett **67**: 201

227. Meiwes J, Fiedler HP, Zähner H, Konetschny-Rapp S, Jung G (1990) Production of Desferrioxamine E and New Analogues by Directed Fermentation and Feeding Fermentation. Appl Microbiol Biotechnol **32**: 505

228. Mercado-Blanco J, van der Drift KMGM, Olsson PE, Thomas-Oates JE, van Loon LC, Bakker PAHM (2001) Analysis of the *pmsCEAB* Gene Cluster Involved in Biosynthesis of Salicylic Acid and the Siderophore Pseudomonine in the Biocontrol Strain *Pseudomonas fluorescens* WCS374. J Bacteriol **183**: 1909

228a. Messenger AJM, Ratledge C (1982) Iron Transport in *Mycobacterium smegmatis*: Uptake of Iron from Ferric Citrate. J Bacteriol **149**: 131

229. Meyer JM (2000) Pyoverdines: Pigments, Siderophores and Potential Taxonomic Markers of Fluorescent *Pseudomonas* Species. Arch Microbiol **174**: 135

229a. Meyer JM, Abdallah MA (1980) The Siderochromes of Non-fluorescent Pseudomonads: Production of Norcardamine by *Pseudomonas stutzeri*. J Gen Microbiol **118**: 125

230. Meyer JM, Azelvandre P, Georges C (1992). Iron Metabolism in *Pseudomonas*: Salicylic Acid, a Siderophore of *Pseudomonas fluorescens* CHAO. BioFactors **4**: 23

231. Meyer JM, Gruffaz C, Raharinosy V, Bezverbnaya I, Schäfer M, Budzikiewicz, H (2008) Siderotyping of Fluorescent *Pseudomonas*: Molecular Mass Determination by Mass Spectrometry as a Powerful Pyoverdine Siderotyping Method. Biometals **21**: 259

232. Meyer JF, Hohnadel D, Hallé F (1989) Cepabactin from *Pseudomonas cepacia*, a New Type of Siderophore. J Gen Microbiol **135**: 1479

233. Meyer JM, Stintzi A, Coulanges V, Shivaji S, Voss JA, Taraz K, Budzikiewicz H (1998) Siderotyping of Fluorescent Pseudomonads: Characterization of Pyoverdines of *Pseudomonas fluorescens* and *Pseudomonas putida* Strains from Antarctica. Microbiology **144**: 3119

234. Meyer JM, Stintzi A, De Vos D, Cornelis P, Tappe R, Taraz K, Budzikiewicz H (1997) Use of Siderophores to Type Pseudomonads: the Three *Pseudomonas aeruginosa* Pyoverdine Systems. Microbiology **143**: 35

235. Meyer JM, Van VT, Stintzi A, Berge O, Winkelmann G (1995) Ornibactin Production and Transport Properties in Strains of *Burkholderia vietnamensis* and *Burkholderia cepacia* (formerly *Pseudomonas cepacia*). BioMetals **8**: 309

236. Michalke R, Taraz K, and Budzikiewicz H (1996) Azoverdin – an Isopyoverdin. Z Naturforsch **51c**: 772

237. Milewska MJ, Chimiak A, Glowacki Z (1987) Synthesis of Shizokinen, Homoschizokinen, its Imide and the Detection of Imide with ^{13}C-N.M.R.-Spectroscopy. J Prakt Chem **329**: 447
238. Miller MC, Parkin S, Fetherston JD, Perry RD, DeMoll E (2006) Crystal Structure of Ferric-yersiniabactin, a Virulence Factor of *Yersinia pestis*. J Inorg Biochem **100**: 1495
239. Mitscher LA, Högberg T, Drake SD, Burgstahler AW, Jackson M, Lee B, Sheldon RI, Gracey HE, Kohl W, Theriault RJ (1984) Isolation and Structural Determination of Siderochelin C, a Fermentation Product of an Unusual *Actinomycetes* sp. J Antibiotics **37**:1260
239a. Miyanaga S, Obata T, Onaka H, Fujita T, Saito N, Sakurai H, Saiki I, Furumai T, Igarashi Y (2006) Absolute Configuration and Antitumor Activity of Myxochelin A Produced by *Nonomuraea pusilla* TP-A0861. J Antibiotics **59**: 698
240. Modi M, Shah KS, Modi VV (1985) Isolation and Characterization of Catechol-like Siderophore from Cowpea *Rhizobium* RA-1. Arch Microbiol **141**: 156
241. Mohn G, Koehl P, Budzikiewicz H, Lefèvre JF (1994) Solution Structure of Pyoverdin GM-II. Biochemistry **33**: 2843
242. Mohn G, Taraz K, Budzikiewicz H (1990) New Pyoverdin-Type Siderophores from *Pseudomonas fluorescens*. Z Naturforsch **45b**: 1437
242a. Moll H, Glorius M, Bernhard G, Johnsson A, Pedersen K, Schäfer M, Budzikiewicz H (2008) Characterization of Pyoverdins Secreted by a Subsurface Strain of *Pseudomonas fluorescens* and their Interactions with Uranium(VI). Geomicrobiol J **25**: 157
243. Moore RE, Emery T (1976) N^{α}-Acetylfusarinines: Isolation, Characterization, and Properties. Biochemistry **15**: 2719
244. Moore CH, Foster LA, Gerbig DG Jr, Dyer DW, Gibson BW (1995) Identification of Alcaligin as the Siderophore Produced by *Bordetella pertussis* and *B. bronchiseptica*. J Bacteriol **177**: 1116
245. Mossialos D, Meyer JM, Budzikiewicz H, Wolf U, Koedam N, Baysse C, Anjaiah V, Cornelis P (2000) Quinolobactin, a New Siderophore of *Pseudomonas fluorescens* ATCC 17400, the Production of which is Repressed by the Cognate Pyoverdine. Appl Environ Microbiol **66**: 487
245a. Mukai A, Fukai T, Matsumoto Y, Ishikawa J, Hoshino Y, Yazawa K, Harada K, Mikami Y (2006) Transvalencin Z, a New Antimicrobial Compound with Salicylic Acid Residue from *Nocardia transvalensis* IFM 10065. J Antibiotics **59**: 366
246. Mulet M, Gomila M, Gruffaz C, Meyer JM, Palleroni NJ, Lalucat J, García-Valdéz E (2008) Phylogenetic Analysis and Siderotyping as Useful Tools in the Taxonomy of *Pseudomonas stutzeri*: Description of a Novel Genovar. Int J System Evol Microbiol **58**: 2309
246a. Müller A, Zähner H (1968) Stoffwechselprodukte von Mikroorganismen. 65. Mitteilung. Ferrioxamine aus *Eubacteriales*. Arch Microbiol **62**: 257
247. Müller SI, Valdebenito M, Hantke K (2009) Salmochelin, the Long-overlooked Catecholate Siderophore of *Salmonella*. Biometals **22**: 691
248. Mullis KB, Pollack JR, Neilands JB (1971) Structure of Schizokinen, an Iron Transport Compound from *Bacillus megaterium*. Biochemistry **10**: 4894
249. Münzinger M, Budzikiewicz H, Expert D, Enard C, Meyer JM (2000) Achromobactin, a New Citrate Siderophore of *Erwinia chrysanthemi*. Z Naturforsch **55c**: 328
250. Münzinger M, Taraz K, Budzikiewicz H (1999) Staphyloferrin B, a Citrate Siderophore from *Ralstonia eutropha*. Z Naturforsch **54c**: 867
251. Münzinger M, Taraz K, Budzikiewicz H, Drechsel H, Heymann P, Winkelmann G, Meyer JM (1999). S,S-Rhizoferrin (*enantio*-rhizoferrin) a Siderophore of *Ralstonia* (*Pseudomonas*) *pickettii* DSM 6297 – the Optical Antipode of R,R-Rhizoferrin Isolated from Fungi. BioMetals **12**: 189
252. Murakami Y, Kato S, Nakajima M, Matsuoka M, Kawai H, Shin-Ya K, Seto H (1996) Formobactin, a Novel Free Radical Scavenging and Neuron Cell Protecting Substance from *Nocardia* sp. J Antibiotics **49**: 839
253. Naegli HU, Keller-Schierlein W (1978) Stoffwechselprodukte von Mikroorganismen. 174. Mitteilung. Eine neue Synthese des Ferrichroms; *enantio*-Ferrichrom. Helv Chim Acta **61**: 2088

254. Naegeli HU, Zähner H (1980) Stoffwechselprodukte von Mikroorganismen. 193. Mitteilung. Ferrithiocin. Helv Chim Acta **63**: 1400
255. Nagao Y, Miyasaka T, Hagiwara Y, Fujita E 1984 Total Synthesis of Parabactin, a Spermidine Siderophore. J Chem Soc Perkin Trans I 183
255a. Neilands JB (1981) Microbial Iron Compounds. Ann Rev Biochem **50**: 715
256. Neilands JB, Ericson TJ, Rastetter WH (1981) Stereospecifity of the Ferric Enterobactin Receptor of *Escherichia coli* K-12. J Biol Chem **256**: 3831
257. Nemoto A, Hoshino Y, Yazawa K, Ando A, Mikami Y, Komaki H, Tanaka Y, Gräfe U (2002) Asterobactin, a New Siderophore Group Antibiotic from *Nocardia asteroides*. J Antibiotics **55**: 593
258. Neuenhaus W, Budzikiewicz H, Korth H, Pulverer G (1980) 8-Hydroxy-4-methoxymonothiochinaldinsäure – eine weitere Thiosäure aus *Pseudomonas*. Z Naturforsch **35b**: 1569
259. Newkirk JD, Hulcher FH (1969) Isolation and Properties of a Fluorescent Pigment from *Pseudomonas mildenbergii*. Arch Biochem Biophys **134**: 395
260. Nishio T, Tanaka N, Hiratake J, Katsube Y, Ishida Y, Oda J (1988) Isolation and Structure of the Novel Dihydroxamate Siderophore Alcaligin. J Am Chem Soc **110**: 8733
261. O'Brian IG, Gibson F (1970) The Structure of Enterochelin and Related 2,3-Dihydroxy-N-benzoylserine Conjugates from *Escherichia coli*. Biochem Biophys Acta **215**: 393
262. Ockels W, Römer A, Budzikiewicz H, Korth H, Pulverer G (1978) An Fe(II) Complex of Pyridine-2,6-di(monothiocarboxylic acid) – a Novel Bacterial Metabolic Product. Tetrahedron Lett 3341
263. Ohfune Y, Tomita M (1982) Total Synthesis of (−)-Domoic acid. A Revision of the Original Structure. J Am Chem Soc **104**: 3511
264. Okujo N, Saito M, Yamamoto S, Yoshida T, Miyoshi S, Shinoda S (1994) Structure of Vulnibactin, a New Polyamine-containing Siderophore from *Vibrio vulnificus*. BioMetals **7**: 109
265. Okujo N, Sakakibara Y, Yoshida T, Yamamoto S. (1994) Structure of Acinetoferrin, a New Citrate-based Dihydroxamate Siderophore from *Acinetobacter haemolyticus*. BioMetals **7**: 170
266. Okujo N, Yamamoto S (1994) Identification of the Siderophores from *Vibrio hollisae* and *Vibrio mimicus* as Aerobactin. FEMS Microbial Lett **118**: 187
267. Okuyama D, Nakamura H, Naganawa H, Takita T, Umezawa H, Iitaka, Y (1982) Isolation, Racemization and Absolute Configuration of Siderochelin A. J Antibiotics **35**: 1240
268. Ong SA, Peterson T, Neilands JB (1979) Agrobactin, a Siderophore from *Agrobacterium tumefaciens*. J Biol Chem **25**: 1860
269. Ongena M, Jacques P, Delfosse P, Thonart P (2002) Unusual Traits of the Pyoverdin-Mediated Iron Acquisition System in *Pseudomonas putida* Strain BTP1. BioMetals **15**: 1
270. Ongena M, Jacques P, Thonart P, Gwose I, Uría Fernández D, Schäfer M, Budzikiewicz H (2001) The Pyoverdin of *Pseudomonas fluorescens* BTP2, a Novel Structural Type. Tetrahedron Lett **42**: 5849
271. Ongena M, Jacques P, van Vyncht G, Charlier P, de Pauw E, Thonart P, Budzikiewicz H (1998) Structural Analysis of Two Pyoverdins by Electrospray and FAB Mass Spectrometry. J Mass Spectrom Soc Jpn **46**: 53
272. Page WJ, Collinson SK, Demange P, Dell A, Abdallah MA (1991) *Azotobacter vinelandii* Strains of Disparate Origin Produce Azotobactin Siderophores with Identical Structures. Biol Metals **4**: 217
273. Page WJ, von Tigerstrom M (1988) Aminochelin, a Catecholamine Siderophore Produced by *Azotobacter vinelandii*. J Gen Microbiol **134**: 453
274. Pakchung AAH, Soe CZ, Codd R (2008) Studies of Iron-uptake Mechanisms in Two Bacterial Species of the *Shewanella* Genus Adapted to Middle-range (*Shewanella putrefaciens*) or Antarctic (*Shewanella gelidimarina*) Temperatures. Chem Biodivers **5**: 2113
274a. Patel HM, Tao J, Walsh CT (2003) Epimerization of an L-Cysteinyl to a D-Cysteinyl Residue during Thiazoline Ring Formation in Siderophore Chain Elongation by Pyochelin Synthetase from *Pseudomonas aeruginosa*. Biochem **42**: 10514

275. Patel HN, Chakraborty RN, Desai SB (1988) Isolation and Partial Characterization of Phenolate Siderophore from *Rhizobium leguminosarum* IARI 102. FEMS Microbiol Lett **56**: 131.
276. Pattus F, Abdallah MA (2000) Siderophores and Iron-transport in Microorganisms. J Chin Chem Soc **47**: 1
277. Payne SM, Niesel DW, Peixotto SS, Lawlor KM (1983) Expression of Hydroxamate and Phenolate Siderophores by *Shigella flexneri*. J Bacteriol **155**: 949
278. Persmark M, Expert D, Neilands JB (1989) Isolation, Characterization, and Synthesis of Chrysobactin, a Compound with Siderophore Activity from *Erwinia chrysanthemi*. J Biol Chem **264**: 3187
279. Persmark M, Frejd T, Mattiasson B (1990) Purification, Characterization, and Structure of Pseudobactin 589A, a Siderophore from a Plant Growth Promoting *Pseudomonas*. Biochemistry **29**: 7348
280. Persmark M, Neilands JB (1992) Iron(III) Complexes of Chrysobactin, the Siderophore of *Erwinia chrysanthemi*. BioMetals **5**: 29
281. Persmark M, Pittman P, Buyer JS, Schwyn B, Gill PR Jr, Neilands JB (1993) Isolation and Structure of Rhizobactin 1021, a Siderophore from the Alfalfa Symbiont *Rhizobium meliloti* 1021. J Am Chem Soc **115**: 3950
282. Peters WJ, Warren RAJ (1968) Itoic Acid Synthesis in *Bacillus subtilis*. J Bacteriol **95**: 360
283. Peterson T, Falk KE, Leong SA, Klein MP, Neilands JB (1980). Structure and Behavior of Spermidine Siderophores. J Am Chem Soc **102**: 7715
284. Peterson T, Neilands JB (1979) Revised Structure of a Catecholamide Spermidine Siderophore from *Paracoccus denitrificans*. Tetrahedron Lett 4805
285. Plowman JE, Loehr TM, Goldman SJ, Sanders-Loehr J (1984) Structure and Siderophore Activity of Ferric Schizokinen. J Inorg Biochem **20**: 183
286. Pollak JR, Neilands JB (1970) Enterobactin, an Iron Transport Compound from *Salmonella typhimurium*. Biochem Biophys Res Commun **38**: 989
287. Poppe K, Taraz K, Budzikiewicz H (1987) Pyoverdine Type Siderophores from *Pseudomonas fluorescens*. Tetrahedron **43**: 2261
288. Pouteau-Thouvenot M, Gaudemer A, Barbier M (1968). Structure chimique de la proferrorosamine. Bull Soc Chim Biol **50**: 222
289. Quadri LEN, Keating TA, Patel HM, Walsh CT (1999) Assembly of *Pseudomonas aeruginosa* Nonribosomal Peptide Siderophore Pyochelin: in vitro Reconstitution of Aryl-4, 2-bisthiazoline Synthetase Activity from PchD, PchE, and PChF. Biochemistry **38**: 14941
290. Rabsch W, Paul P, Reissbrodt R (1986) DHBA (2,3-Dihydroxybenzoesäure)-Ausscheidung durch einen enterobactinnegativen multiresistenten *Salmonella typhimurium*-Wildstamm. J Basic Microbiol **26**: 113
290a. Rabsch W, Paul P, Reissbrodt R (1987) A New Hydroxamate Siderophore for Iron Supply of *Salmonella*. Acta Microbiol Hungar **34**: 85
291. Ratledge C (1964) Relationship between the Products of Aromatic Biosynthesis in *Mycobacterium smegmatis* and *Aerobacter aerogenes*. Nature **203**: 428
292. Ratledge C, Ewing M (1996) The Occurrence of Carboxymycobactin, the Siderophore of Pathogenic Mycobacteria, as a Second Extracellular Siderophore in *Mycobacterium smegmatis*. Microbiology **142**: 2207
293. Ratledge C, Marshall BJ (1972) Iron Transport in *Mycobacterium smegmatis*: the Role of Mycobactin. Biochim Biophys Acta **279**: 58
294. Ratledge C, Patel PV (1976) The Isolation, Properties and Taxonomic Relevance of Lipid-soluble, Iron-binding Compounds (the Nocobactins) from *Nocardia*. J Gen Microbiology **93**: 141
295. Ratledge C, Snow GA (1974) Isolation and Structure of Nocobactin NA, a Lipid-soluble Iron-binding Compound from *Nocardia asteroides*. Biochem J **139**: 407
296. Raymond KN, Carrano CJ (1979) Coordination Chemistry and Microbial Iron Transport. Acc Chem Res **12**: 183

297. Regenhardt D, Heuer H, Heim S, Fernández DU, Strömpl C, Moore ERB, Timmis KN (2002) Pedigree and Taxonomic Credentials of *Pseudomonas putida* Strain KT2440. Environ Microbiol **4**: 912
298. Reid RT, Live DH, Faulkner DJ, Butler A (1993) A Siderophore from a Marine Bacterium with an Exceptional Ferric Ion Affinity Constant. Nature **366**: 455
299. Reissbrodt R, Ramiandrasoa F, Bricard L, Kunesch G (1997) Siderophore Activity of Chemically Synthesized Dihydroxybenzoyl Derivatives of Spermidines and Cystamide. BioMetals **10**: 95
300. Renshaw JC, Robson GD, Trinci APJ, Wiebe MG, Livens FR, Collison D, Taylor RJ (2002) Fungal Siderophores: Structures, Functions and Application. Mycol Res **106**: 1123
301. Rinehart KL, Staley AL, Wilson SR, Ankenbauer RG, Cox CD (1995) Stereochemical Assignment of the Pyochelins. J Org Chem **60**: 2786
302. Risse D, Beiderbeck H, Taraz K, Budzikiewicz H, Gustin D (1998) Corrugatin, a Lipopeptide Siderophore from *Pseudomonas corrugata*. Z Naturforsch **53c**: 295
303. Robinson JP, Wawrousek EF, McArdle JV, Coyle G, Adler I (1984) X-ray Photoelectron and Electron Spin Resonance Spectra of Iron(III) Parabactin. Inorg Chim Acta **92**: L19
304. Ruangviryachai C, Barelmann I, Fuchs R, Budzikiewicz H (2000) An Exceptionally Large Pyoverdin from a *Pseudomonas* Strain Collected in Thailand. Z Naturforsch **55c**: 323
305. Ruangviriyachai C, Uría Fernández D, Fuchs R, Meyer JM, Budzikiewicz H (2001) A New Pyoverdin from *Pseudomonas aeruginosa* R'. Z Naturforsch **56c**: 933
306. Ruangviriyachai C, Uría Fernández D, Schäfer M, Budzikiewicz H (2004) Structure Proposal for a New Pyoverdin from a Thai *Pseudomonas putida* Strain. Spectroscopy **18**: 453
307. Rue E, Bruland K (2001) Domoic Acid Binds Iron and Copper: a Possible Role for the Toxin Produced by the Marine Diatom *Pseudo-nitzschia*. Mar Chem **76**: 127
308. Sakakura A, Umemura S, Ishihara K (2008) Convergent Total Syntheses of Fluvibactin and Vibriobactin Using Molybdenum(VI) Oxide-catalyzed Dehydrative Cyclization as a Key Step. Chem Commun 3561
309. Salah-el-Din ALM, Kyslík P, Stephan D, Abdallah MA (1997) Bacterial Iron Transport: Structure Elucidation by FAB-MS and by 2D NMR (^{1}H, ^{13}C, ^{15}N) of Pyoverdin G4R, a Peptidic Siderophore Produced by a Nitrogen-Fixing Strain of *Pseudomonas putida*. Tetrahedron **53**: 12539
310. Sansinenea E, Ortiz A (2009) Bacterial Siderophores Containing a Thiazoline Ring. Mini-Rev Org Chem **6**: 120
311. Sattely ES, Walsh CT (2008) A Latent Oxazoline Electrophile for N-O-C Bond Formation in Pseudomonine Biosynthesis. J Am Chem Soc **130**: 12282
312. Saxena B, Modi M, Modi VV (1986) Isolation and Characterization of Siderophores from *Azospirillum lipoferum* D-2. J Gen Microbiol **132**: 2219
313. Sayer JM, Emery TF (1968) Structures of the Naturally Occurring Hydroxamic Acids, Fusarinines A and B. Biochemistry **7**: 184
314. Schaffner EM, Hartmann R, Taraz K, Budzikiewicz H (1996) Structure Elucidation of Azotobactin 87, Isolated from *Azotobacter vinelandii* ATCC 12837. Z Naturforsch **51c**: 139
314a. Schalk IJ, Hennard C, Dugave C, Poole K, Abdallah MA, Pattus F (2001) Iron-free Pyoverdin Binds to its Outer Membrane Receptor FpvA in *Pseudomonas aeruginosa*: a New Mechanism for Membrane Iron Transport. Mol Microbiol **39**: 351
314b. Schalk IJ, Kyslik P, Prome D, van Dorsselaer A, Poole K, Abdallah MA, Pattus F (1999) Copurification of the FpvA Ferric Pyoverdin Receptor of *Pseudomonas aeruginosa* with its Iron-Free Ligand: Implications for Siderophore-Mediated Iron Transport. Biochemistry **38**: 9357
315. Schlegel K, Fuchs R, Schäfer M, Taraz K, Budzikiewicz H, Geoffroy V, Meyer JM (2001) The Pyoverdins of *Pseudomonas* sp. 96-312 and 96-318. Z Naturforsch **56c**: 680
316. Schlegel K, Lex J, Taraz K, Budzikiewicz H (2006) The X-ray Structure of the Pyochelin Fe^{3+} Complex. Z Naturforsch **61c**: 263

317. Schlegel K, Taraz K, Budzikiewicz H (2004) The Stereoisomers of Pyochelin, a Siderophore of *Pseudomonas aeruginosa*. BioMetals **17**: 409
318. Schröder H, Adam J, Taraz K, Budzikiewicz H (1995) Dihydropyoverdinsulfonsäuren – Zwischenstufen bei der Biogenese? Z Naturforsch **50c**: 616
319. Seinsche D, Taraz K, Budzikiewicz H, Gondol D (1993) Neue Pyoverdin-Siderophore aus *Pseudomonas putida* C. J Prakt Chem **335**: 157
320. Shah S, Rao KK, Desai A (1993) Production of Catecholate Type of Siderophores by *Azospirillum lipoferum* M. Indian J Exp Biol **31**: 41
321. Shanzer A, Libman J (1983) Total Synthesis of Enterobactin *via* an Organotin Template. J Chem Soc Chem Commun 846
322. Sharman GJ, Williams DH, Ewing DF, Ratledge C (1995) Isolation, Purification and Structures of Exochelin MS, the Extracellular Siderophore from *Mycobacterium smegmatis*. Biochem J **305**: 187
323. Sharman GJ, Williams DH, Ewing DF, Ratledge C (1995) Determination of the Structure of Exochelin MN, the Extracellular Siderophore from *Mycobacterium neoaurum*. Chem Biol **2**: 553
324. Shiman R, Neilands JB (1965) Isolation, Characterization and Synthesis of Pyrimine, an Iron(II) Binding Agent from *Pseudomonas* GH. Biochemistry **4**: 2233
325. Shirahata K, Deguchi T, Hayashi T, Matsubara I, Suzuki T (1970). The Structures of Fluopsins C and F. J Antibiotics **23**: 546
326. Simpson FB, Neilands JB (1976) Siderochromes in Cyanophyceae: Isolation and Characterization of Schizokinen from *Anabena* sp. J Phycol **12**: 44
327. Skorupska A, Choma A, Derylo M, Lorkiewicz Z (1988) Siderophore Containing 2,3-Dihydroxybenzoic Acid and Threonine Formed by *Rhizobium trifolli* (*sic*!). *Acta Biochim Polon* **35**: 119
328. Smith MJ, Shoolery JN, Schwyn B, Holden I, Neilands JB (1985) Rhizobactin, a Structurally Novel Siderophore from *Rhizobium meliloti*. J Am Chem Soc **107**: 1739
329. Snow GA (1965) The Structure of Mycobactin P, a Growth Factor for *Mycobacterium johnei*, and the Significance of its Iron Complex. Biochem J **94**: 160
330. Snow GA (1965) Isolation and Structure of Mycobactin T, a Growth Factor from *Mycobacterium tuberculosis*. Biochem J **97**: 166
331. Snow GA (1970) Mycobactins: Iron-chelating Growth Factors from Mycobacteria. Bacteriol Rev **34**: 99
332. Snow GA, White AJ (1969) Chemical and Biological Properties of Mycobactins Isolated from Various Mycobacteria. Biochem J **115**: 1031
333. Sokol PA, Lewis CJ, Dennis JJ (1992) Isolation of a Novel Siderophore from *Pseudomonas cepacia*. J Med Microbiol **36**: 184
333a. Spiro TG, Bates G, Saltman P (1989) The Hydrolytic Polymerization of Ferric Citrate. II. The Influence of Excess Citrate. J Am Chem Soc **89**: 5559
333b. Spiro TG, Pape L, Saltman P (1989) The Hydrolytic Polymerization of Ferric Citrate. I. The Chemistry of the Polymer. J Am Chem Soc **89**: 5555
334. Steglich W, Steffan B, Stroech K, Wolf M (1984) Pistillarin, ein charakteristischer Inhaltsstoff der Herkuleskeule (*Clavariadelphus pistillaris*) und einiger *Ramaria*-Arten (Basidiomycetes). Z Naturforsch. **39c**: 10
335. Stephan H, Freund S, Beck W, Jung G, Meyer JM, Winkelmann G (1993) Ornibactins – a New Family of Siderophores from *Pseudomonas*. BioMetals **6**: 93
336. Stephan H, Freund S, Meyer JM, Winkelmann G, Jung G (1993) Structure Elucidation of the Gallium-Ornibactin Complex by 2D-NMR Spectroscopy. Liebigs Ann Chem 43
337. Stintzi A, Barnes C, Xu J, Raymond KN (2000) Microbial Iron Transport via a Siderophore Shuttle: a Membrane Ion Transport Paradigm. Proc Natl Acad Sci USA **97**: 10691
338. Stoll A, Renz J, Brack A (1951) Beiträge zur Konstitutionsaufklärung des Nocardamins. 10. Mitteilung über antibakterielle Stoffe. Helv Chim Acta **34**: 862
339. Storey EP, Boghozian R, Little JL, Lowman DW, Charkraborty R (2006) Characterization of 'Schizokinen'; a Dihydroxamate-type Siderophore Produced by *Rhizobium leguminosarum* IARI 917. BioMetals **19**: 637

340. Stuart SJ, Prpic JK, Robins-Browne RM (1986) Production of Aerobactin by some Species of the Genus *Yersinia*. J Bacteriol **166**: 1131
341. Suenaga K, Kokubo S, Shinohara C, Tsuji T, Uemura D (1999) Structures of Amamistatins A and B, Novel Growth Inhibitors of Human Tumor Cell Lines from an Actinomycete. Tetrahedron Lett **40**: 1945
342. Sultana R, Fuchs R, Schmickler H, Schlegel K, Budzikiewicz H, Siddiqui BS, Geoffroy V, Meyer JM (2000) A Pyoverdin from *Pseudomonas* sp. CFML 95-275. Z Naturforsch **55c**: 857
343. Sultana R, Siddiqui BS, Taraz K, Budzikiewicz H, Meyer JM (2000) A Pyoverdine from *Pseudomonas putida* CFML 90-51 with a Lys ε-Amino Link in the Peptide Chain. BioMetals **13**: 147
344. Sultana R, Siddiqui BS, Taraz K, Budzikiewicz H, Meyer JM (2001) An Isopyoverdin from *Pseudomonas putida* CFML 90-44. Z Naturforsch **56c**: 303
345. Sultana R, Siddiqui BS, Taraz K, Budzikiewicz H, Meyer JM (2001) An Isopyoverdin from *Pseudomonas putida* CFML 90-33. Tetrahedron **57**: 1019
346. Tabata N, Tomoda H, Ōmura S (1999) Ferroverdins, Inhibitors of Cholesteryl Ester Transfer Protein Produced by *Streptomyces* sp. WK-5344. II. Structure Elucidation. J Antibiotics **52**: 1108
347. Tait GH (1975) The Identification and Biosynthesis of Siderochromes Formed by *Micrococcus denitrificans*. Biochem J **146**: 191
348. Takahashi A, Nakamura H, Kameyama T, Kurasawa S, Naganawa H, Okami Y, Takeuchi T, Umezawa H, Iitaka Y (1987) Bisucaberin, a New Siderophore, Sensitizing Tumor Cells to Macrophage-mediated Cytolysis. II. Physico-chemical Properties and Structure Determination. J Antibiotics **40**: 1671
349. Tappe R (1991) Ferribactin 3b, ein Siderophor von *Pseudomonas aptata* 3b. Diplomarbeit, Universität zu Köln
350. Tappe R, Taraz K, Budzikiewicz H, Meyer JM, Lefèvre JF (1993) Structure Elucidation of a Pyoverdin Produced by *Pseudomonas aeruginosa* ATCC 27853. J Prakt Chem **335**: 83
351. Taraz K, Ehlert G, Geisen K, Budzikiewicz H, Korth H, Pulverer G (1990) Protochelin, ein Catecholat-Siderophor aus einem Bakterium (DMS Nr. 5746). Z Naturforsch **45b**: 1327
352. Taraz K, Seinsche D, Budzikiewicz H (1991) Pseudobactin- und Pseudobactin A-Varianten: Neue Peptidsiderophore vom Pyoverdin-Typ aus *Pseudomonas fluorescens* "E2". Z Naturforsch **46c**: 522
353. Teintze M, Hossain MB, Barnes CL, Leong J, van der Helm D (1981) Structure of Ferric Pseudobactin, a Siderophore from a Plant Growth Promoting *Pseudomonas*. Biochemistry **20**: 6446
354. Teintze M, Leong J (1981) Structure of Pseudobactin A, a Second Siderophore from Plant Growth Promoting *Pseudomonas* B10. Biochemistry **20**: 6457
355. Telford JR, Leary JA, Tunstad LMG, Byers BR, Raymond KN (1994) Amonabactin: Characterization of a Series of Siderophores from *Aeromonas hydrophila*. J Am Chem Soc **116**: 4499
356. Telford JR, Raymond KN (1997) Amonabactin: a Family of Novel Siderophores from a Pathogenic Bacterium. J Biol Inorg Chem **2**: 750
357. Telford JR, Raymond KN (1998) Coordination Chemistry of the Amonabactins, Bis(catecholate) Siderophores from *Aeromonas hydrophila*. Inorg Chem **37**: 4578
357a. Temirov YuV, Esikova TZ, Kashporov IA, Balashova TA, Vinokurov LM, Alakhov YuB (2003) A Catecholic Siderophore Produced by the Thermoresistant *Bacillus licheniformis* VK21 Strain. Russian J Bioorg Chem **29**: 542 (translated from Bioorg Khim **29**: 597)
358. Thieken A, Winkelmann G (1992) Rhizoferrin: a Complexon Type Siderophore of the Mucorales and Entomophthorales (Zygomycetes). FEMS Microbiol Lett **94**: 37
359. Thomas MS (2007) Iron Acquisition Mechanisms of the *Burkholderia cepacia* Complex. Biometals **20**: 431

360. Tindale AE, Mehrotra M, Ottem D, Page WJ (2000) Dual Regulation of Catecholate Siderophore Biosynthesis in *Azotobacter vinelandii* by Iron and Oxidative Stress. Microbiology **146**: 1617

361. Tomada H, Tabata N, Shinose M, Takahashi Y, Woodruff HB, Ōmura S (1999) Ferroverdins, Inhibitors of Cholesteryl Ester Transfer Protein Produced by *Streptomyces* sp. WK-5344. I. Production, Isolation and Biological Properties. J Antibiotics **52**: 1101

362. Torres L, Pérez-Ortín JE, Tordera V, Beltrán JP (1986) Isolation and Characterization of an Fe(III)-Chelating Compound Produced by *Pseudomonas syringae*. Appl Environ Microbiol **2**: 157

363. Uría Fernández D**,** Fuchs R**,** Schäfer M, Budzikiewicz H**,** Meyer JM (2003) The Pyoverdin of *Pseudomonas fluorescens* G173, a Novel Structural Type Accompanied by Unexpected Natural Derivatives of the Corresponding Ferribactin. Z Naturforsch **58c**: 1

364. Uría Fernández D, Fuchs R, Taraz K, Budzikiewicz H, Munsch P, Meyer JM (2001) The Structure of a Pyoverdine Produced by a *Pseudomonas tolaasii*-like Isolate. BioMetals **14**: 81

365. Uría Fernández D, Geoffroy V; Schäfer M, Meyer JM, Budzikiewicz H (2003) Structure Revision of Several Pyoverdines Produced by Plant-Growth Promoting and Plant-Deleterious *Pseudomonas* Species. Monatsh Chem **134**: 1421

366. van der Helm D, Jalal MAF, Hossain MB (1987) The Crystal Structures, Conformations, and Configurations of Siderophores. In: Winkelmann G, van der Helm D, Neilands JB (eds) Iron Transport in Microbes, Plants and Animals. VCH, Weinheim, p 135

366a. van der Helm D, Poling M (1976) The Crystal Structure of Ferrioxamine E. J Am Chem Soc **98**: 82

367. van de Woestyne M, Bruyneel B, Mergeay M, Verstraete W (1991) The Fe^{2+} Chelator Proferrorosamine A is Essential for the Siderophore-mediated Uptake of Iron by *Pseudomonas roseus fluorescens*. Appl Environ Microbiol **57**: 949

368. Van Tiel-Menkveld GJ, Mentjox-Vervuurt JM, Oudega B, de Graaf FK (1982) Siderophore Production by *Enterobacter cloacae* and a Common Receptor Protein for the Uptake of Aerobactin and Cloacin DF13. J Bacteriol **150**: 490

369. Vergne AF, Walz AJ, Miller MJ (2000) Iron Chelators from Mycobacteria (1954-1999) and Potential Therapeutic Applications. Nat Prod Rep **17**: 99

370. Visca P, Colotti G, Serino L, Verzili D, Orsi N, Chiancone E (1992) Metal Regulation of Siderophore Synthesis in *Pseudomonas aeruginosa* and Functional Effects of Siderophore-Metal Complexes. Appl Environ Microbiol **58**: 2886

371. Voss J, Taraz K, Budzikiewicz H (1999) A Pyoverdin from the Antarctica Strain 51W of *Pseudomonas fluorescens*. Z Naturforsch **54c**: 156

372. Voßen W, Fuchs R, Taraz K, Budzikiewicz H (2000) Can the Peptide Chain of a Pyoverdin be Bound by an Ester Bond to the Chromophore? – The Old Problem of Pseudobactin 7SR1. Z Naturforsch **55c**: 153

373. Voßen W, Taraz K (1999) Structure of the Pyoverdin PVD 2908 – a New Pyoverdin from *Pseudomonas* sp. 2908. BioMetals **12**: 323

374. Wallner A, Blatzer M, Schrettl M, Sarg B, Lindner H, Haas H (2009) Ferricrocin – a Siderophore Involved in Intra- and Transcellular Iron Distribution in *Aspergillus fumigatus*. Appl Envir Microbiol **75**: 4194

374a. Wang W, Chi Z, Liu G., Buzdar MA, Chi Z, Gu Q (2009) Chemical and Biological Characterization of Siderophores Produced by the Marine-derived *Aureobasidium pullulans* HN6.2 and its Antibacterial Activity. Biometals **22**: 965

375. Wang QX, Phanstiel O IV (1998) Total Synthesis of Acinetoferrin. J Org Chem **63**: 1491

376. Warner PJ, Williams PH, Bindereif A, Neilands JB (1981) CoIV Plasmid-Specific Aerobactin Synthesis by Invasive Strains of *Escherichia coli*. Infect Immunol **33**: 540

377. Wasielewski E, Adkinson RA, Abdallah MA, Kieffer B (2002). The Three-Dimensional Structure of the Gallium Complex of Azoverdin, a Siderophore of *Azomonas macrozytogenes* ATCC 12334, Determined by NMR Using Residual Dipolar Coupling Constants. Biochemistry **41**: 12488

378. Wawszkiewicz EJ, Schneider HA (1975) Control of Salmonellosis Pacifarin Biosynthesis by Iron. Infect Immunol **11**: 69
379. Weber M, Taraz K, Budzikiewicz H, Geoffroy V, Meyer JM (2000) The Structure of a Pyoverdine from *Pseudomonas* sp. CFML 96.188 and its Relation to other Pyoverdines with a Cyclic C-terminus. *BioMetals* **13**: 301
380. Westervelt P, Bloom ML, Mabbott GA, Fekete FA (1985) The Isolation and Identification of 3,4-Dihydroxybenzoic Acid Formed by Nitrogen-fixing *Azomonas macrocytogenes*. FEMS Microbiol Lett **30**: 331
381. White AJ, Snow GA (1969) Isolation of Mycobactins from Various Mycobacteria. The Properties of Mycobactins S and H. Biochem J **111**: 785
382. Wilson MK, Abergel RJ, Raymon J, Arceneaux JE, Byers BR (2006) Siderophores from *Bacillus anthracis*, *Bacillus cereus*, and *Bacillus thuringiensis*. Biochem Biophys Res Commun **348**: 320
383. Winkelmann G (1990) Structural and Stereochemical Aspects of Iron Transport in Fungi. Biotech Adv **8**: 207
384. Winkelmann G (1991) Specificity of Iron Transport in Bacteria and Fungi. In: Winkelmann G (ed) CRC Handbook of Microbial Iron Chelates. CRC, Boca Raton, FL, p 65
385. Winkelmann G, Huschka HG (1989) Molecular Recognition and Transport of Siderophores in Fungi. In: Winkelmann G, van der Helm D, Neilands JB (eds) Iron Transport in Microbes, Plants and Animals. VCH, Weinheim, p 317
386. Winkler S, Ockels W, Budzikiewicz H, Korth H, Pulverer G (1986) 2-Hydroxy-4-methoxy-5-methylpyridin-N-oxid, ein Al^{3+}-bindender Metabolit von *Pseudomonas cepacia*. Z Naturforsch **41c**: 807
387. Wong-Lun-Sang S, Bernardini JJ, Hennard C, Kyslík P, Dell A, Abdallah MA (1996) Bacterial Siderophores: Structure Elucidation, 2D ^{1}H and ^{13}C NMR Assignments of Pyoverdins Produced by *Pseudomonas fluorescens* CHA0. Tetrahedron Lett **37**: 3329
388. Wuest WM, Sattely ES, Walsh CT (2009) Three Siderophores from one Bacterial Enzymatic Assembly Line. J Am Chem Soc **131**: 5056
389. Xu G, Martinez JS, Groves JT, Butler A (2002) Membrane Affinity of the Amphiphilic Marinobactin Siderophores. J Am Chem Soc **124**:13408
390. Yamada Y, Seki N, Kitahara T, Takahashi M, Matsui M (1970) Structure and Synthesis of Aeruginoic Acid (2-*o*-hydroxyphenylthiazole-4-carboxylic acid). Agric Biol Chem **34**: 780
391. Yamamoto S, Okujo N, Fujita Y, Saito M, Yoshida T, Shinoda S (1993) Structures of Two Polyamine-containing Catecholate Siderophores from *Vibrio fluvialis*. J Biochem **113**: 538
392. Yamamoto S, Okujo N, Sakakibara Y (1994) Isolation and Structure Elucidation of Acinetobactin, a Novel Siderophore from *Acinetobacter baumannii*. Arch Mikrobiol **162**: 249
393. Yamamoto S, Okujo N, Yoshida T, Matsuura S, Shinoda S (1994) Structure and Iron Transport Activity of Vibrioferrin, a New Siderophore of *Vibrio parahaemolyticus*. J Biochem **115**: 868
394. Youard ZA, Mislin GLA, Majcherczyk PA, Schalk IJ, Reimmann C (2007) *Pseudomonas fluorescens* CHA0 Produces enantio-Pyochelin, the Optical Antipode of the *Pseudomonas aeruginosa* Siderophore Pyochelin. J Biol Chem **282**: 35546
395. Zähner H, Keller-Schierlein W, Hütter R, Hess-Leisinger K, Deér A (1963) Stoffwechselprodukte von Mikroorganismen. 40. Mitteilung. Sideramine aus Aspergillaceen. Arch Mikrobiol **45**: 119
396. Zalkin A, Forrester JD, Templeton DH (1966) Ferrichrome A Tetrahydrate. Determination of Crystal and Molecular Structure. J Am Chem Soc **88**: 1810
397. Zamri A, Abdallah MA (2000) An Improved Stereocontrolled Synthesis of Pyochelin, Siderophore of *Pseudomonas aeruginosa* and *Burkholderia cepacia*. Tetrahedron **56**: 249
398. Zawadzka AM, Vandecasteele FPJ, Crawford RL, Paszczynski AJ (2006) Identification of Siderophores from *Pseudomonas stutzeri*. Can J Microbiol **52**: 1164

399. Abergel RJ, Zawadzka AM, Hoette TM, Raymond KM (2009) Enzymatic Hydrolysis of Trilactone Siderophores: Where Chiral Recognition Occurs in Enterobactin and Bacillibactin Iron Transport. J Am Chem Soc **131**: 12682
400. Amin SA, Green DH, Küpper FC, Carrano CJ (2009) Vibrioferrin, an Unusual Marine Siderophore: Iron Binding, Photochemistry and Biological Implications. Inorg Chem **48**: 11451
401. Barbeau K (2006) Photochemistry of Organic Iron (III) Complexing Ligands in Oceanic Systems. Photochem Photobiol **82**: 1505
402. Bergeron RJ, McManis JS, Perumal PT, Algee SE (1991) The Total Synthesis of Alcaligin. J Org Chem **56**: 5560
403. Crosa JH, Walsh CT (2002) Genetics and Assembly Line Enzymology of Siderophore Biosynthesis in Bacteria. Microbiol Mol Biol Rev **66**: 223
404. Fadeev E, Luo M, Groves JT (2005) Synthesis and Structural Modeling of the Amphiphilic Siderophore Rhizobactin-1021 and its Analogs. Bioorg Med Chem Lett **15**: 3771
405. Ghosh A, Miller MJ (1993) Synthesis of Novel Citrate-Based Siderophores and Siderophore-β-lactam Conjugates. Iron Transport-mediated Drug Delivery Systems. J Org Chem **58**: 7652
406. Lemenceau P, Expert D, Gaymard F, Bakker PAHM, Briat JF (2009) Role of Iron in Plant-Microbe Interaction. Adv Bot Res **51**: 491
407. Mukai A, Komaki H, Takagi M, Shin-ya K (2009) Novel Siderophore, JBIR-16, Isolated from *Nocardia tenerifensis* 101015. J Antibiot **62**: 601
408. Peuckert F, Miethke M, Albrecht AG, Essen LO, Marahiel MA (2009) Structural Basis and Stereochemistry of Tricatecholate Siderophore Binding by FeuA. Angew Chemie Int Ed **48**: 7924
409. Ravel J, Cornelis P (2003) Genomics of Pyoverdin-mediated Iron Uptake in Pseudomonads. Trends Microbiol **11**: 195
410. Sandy M, Butler A (2009) Microbial Iron Acquisition: Marine and Terrestrial Siderophores. Chem Rev **109**: 4580
411. Takeuchi Y, Nagao Y, Toma K, Yoshikawa Y, Akiyama T, Nishioka H, Abe H, Harayama T, Yamamoto S (1999) Synthesis and Siderophore Activity of Vibrioferrin and One of its Diastereomeric Isomers. Chem Pharm Bull **47**: 1284
412. Lautru S, Deeth RJ, Bailey LM, Challis GL (2005) Discovery of a New Peptide Natural Product by *Streptomyces coelicolor* Genome Mining. Nature Chem Biol **1**: 65
413. Robbel L, Knappe TA, Linne U, Xie X, Marahiel MA (2009) Erythrochelin - a Hydroxamate-type Siderophore Predicted from the Genome of *Saccharopolyspora erythraea*. FEBS J published online DOI 10.1111/j.1742-4658.2009.07512.x