To align the four cyanogen bromide peptides of *Neurospora* tyrosinase whose amino acid sequences were reported in the preceding paper, suitable methionine-containing overlap peptides were isolated. The required peptides were obtained by tryptic, peptic, and thermolytic digestion of the unmodified protein and of the maleylated derivative. From the partial sequence information of these peptides and a cyanogen bromide overlap peptide, the four cyanogen bromide fragments were aligned in the order CB3-CB1-CB4-CB2. These data establish *Neurospora* tyrosinase as a single-chain protein of 407 amino acids with a molecular weight of 48,000. The single cysteinyl residue 94 was found to be covalently linked via a thioether bridge to histidyl residue 96. The chemical nature of this unusual structure was elucidated by physicochemical analysis of peptides obtained from in *vivo* $^{35}$S, [2,5-3H]histidine, and [5-3H]histidine-labeled *Neurospora* tyrosinase.

In the preceding paper (1), the amino acid sequences of the four CB1 fragments from *Neurospora* tyrosinase were presented. This paper reports the strategy used to delineate the order of the four CB fragments. In addition, a hitherto unknown thioether structure linking cysteinyl residue 94 to histidyl residue 96 is described.

**EXPERIMENTAL PROCEDURES**

**RESULTS AND DISCUSSION**

**Alignment of the Four Cyanogen Bromide Fragments CB1 to CB4**—The strategy of the alignment of the four cyanogen bromide fragments is schematically presented in Fig. 1. Gel filtration of a tryptic digest of apotyrosinase on Sephadex G-50 (Fig. 5) and subsequent ion exchange chromatography of the medium-size molecular weight fraction (pool 2 of Fig. 5) on SE-Sephadex (Fig. 6) allowed the isolation of three fragments (T1 to T3), two of them containing methionine (Table III). Peptide T1 was subjected to automatic Edman degradation (Table V) and its NH$_2$-terminus was found to be identical with that of the COOH-terminal tryptic peptide of the cyanogen bromide fragment CB3. However, since only the first eight residues of T1 were determined, the fragment was further digested with thermolysin and the peptide mixture separated by ion exchange chromatography on Beckman M-72 (Fig. 7). The amino acid sequence of the methionine-containing pentapeptide T1-Th1 (Table III) was elucidated by amionopeptidase M and carboxypeptidase C digestion as Ille-His-Gly-Met-Pro (Table IV). This peptide established the order CB3 $\rightarrow$ CB1, since only fragment CB1 has an NH$_2$-terminal proline residue.

Automated sequence analysis of the tryptic fragment T2 containing two methionine residues allowed the determination of the first 15 residues (Table V). The NH$_2$-terminal sequence (residues 1-7) was found to be identical with the sequence of the COOH-terminal tryptic peptide from CB1, whereas residues 8-15 coincided with the NH$_2$-terminal sequence of CB4. These results unequivocally established the order CB1 $\rightarrow$ CB4. The tryptic peptide T3, although devoid of methionine, was also subjected to automatic Edman degradation (Table VI) and found to be a valuable overlap fragment of three tryptic peptides from CB2 (cf. preceding paper, Ref. 1). The alignment of the four cyanogen bromide fragments was further corroborated by the isolation of methionine-containing peptide CB3 (Fig. 1). Ion exchange chromatography on Beckman M-72 (Fig. 9) and Sephadex G-25 chromatography (Fig. 10) of a tryptic digest of *in vivo* $^{35}$S-labeled *Neurospora* tyrosinase resulted in four radioactively labeled peptides (P1 to P4), three of them containing methionine (Table VIII). Compositional and partial sequence analysis (Table IX) of the peptic peptides P1, P2, and P4 were in complete agreement with the alignment of the CB peptides in the order CB3 $\rightarrow$ CB1 $\rightarrow$ CB4 $\rightarrow$ CB2. This order is further supported by automated sequence analysis of the tryptic fragment Tm1 (Table VII) isolated from maleylated tyrosinase (Fig. 8, Table III) and an overlap cyanogen bromide fragment, CB2-4, (Fig. 1, Table X) whose isolation was described in the preceding paper (1).

**Chemical Structure of the Tripeptide (Residues 94-96)**—As was pointed out in the preceding paper (1) residues 26 and 28 of the cyanogen bromide fragment CB1 (residues 94 and 96 in Fig. 2) could not be unambiguously identified. Although back hydrolysis of PTH derivative 26 had suggested a serine residue, this assignment was not compatible with the amino acid composition of the corresponding peptic peptide (residues 91-96). However, compositional analysis of this peptide revealed, in addition to...
Ac-S TD KF AI TVP VTP TSS NGA VPL RL REL DL
Q N YP E F N L Y L L G R D F Q G L D E A K L D S Y Y
O G A I M F P K W A G V P D T D W S Q G S G F
G Y C T S I L F I T W H R P L A Y E Q A L Y A S V
Q V A K F P V E G L R A K Y V A A K D F R A Y F D
W A S Q P K G T L A F P E S L S R T I Q V D V D G K T
K S I N N P L H R T F H P V N P S P G N F S A A W S R Y P
S T V R Y P N R L P G A S R D E R I A P I L A D E L A S L R
N V S L L L S Y K D F D A F S Y N R W D P N T P G D F
G S L E A V H N E I H D R T G N G H M S S L E V S A F D P
L F W L H H V N V D R L W S I M W D L N P S F M T P R A
P Y S T F V A Q E G S Q S K S T P L E P F W D K S A A N F
W T G V K D S I T F G Y A Y P T Q K W K Y S S V K E Y
Q A A I R K S V T A L Y G S N V F

**Fig. 1. Schematic outline of the peptides used to establish the complete amino acid sequence of *Neurospora* tyrosinase.** The peptides were designated according to the cleavage method used as follows: CB, cyanogen bromide; T, TPCK-trypsin; Tb, TPCK-trypsin of the maleylated derivative; Th, thermolysin. The stippled area of each bar represents the portion of the sequence determined by automatic or manual sequence analysis. Residue numbers above the bar refer to the sequence in Fig. 2.

| Label | Peptide |
|-------|---------|
| P1    | P2      |
| P3    | P4      |

**Table I**  
Specific radioactivities of the sulfur- and histidine-containing peptidase from in vivo $^{35}$S, $[2,5-3^H]$histidine, and $[5-3H]$ histidine-labeled *Neurospora* tyrosinase

| Peptide | $^{35}$S | $[2,5-3^H]$Histidine | $[5-3H]$Histidine |
|---------|---------|---------------------|------------------|
| P1      | 4.4 x 10^5 | 4.6 x 10^5 | 4.5 x 10^5 | 4.7 x 10^5 |
| P2      | 1.9 x 10^5 | 9.3 x 10^4 | 1.8 x 10^5 |
| P3      | 3.5 x 10^5 | 3.6 x 10^5 | 3.4 x 10^5 |

* The radioactivity of peptide P3 if referred to the concentration of Thr.
* Peptide P2 contains no histidine.

for the total of nine histidyl residues in the amino acid sequence of *Neurospora* tyrosinase (Fig. 2), the profile revealed a fifth component eluting in the same position as P3. The specific radioactivity of this fragment was found to be only half of those of the other histidine-containing peptides (Table I) indicating a tritium loss in either the 2 or 5 position of the imidazole nucleus. To determine the position from which tritium was lost, tyrosinase labeled in vivo with $[5-3H]$ histidine was again cleaved with pepsin. The elution profile (Fig. 12) was indistinguishable from the one of Fig. 11 with the exception that the specific radioactivity of P3 was now identical with that of the other histidine-containing peptides (Table I). The results of the radiolabeling experiments are compatible with a covalent linkage between a cysteiny1 residue and C3 of a histidyl residue presumably via a thioether bond. In the presence of 6 N HCl at 110 °C such a structure would be expected to undergo facile cleavage to yield thiolhistidine (SH—His) as one of the products. This conjecture is strongly supported by the observation that synthetic 2-thiolhistidine coelutes with the unknown species of the acid hydrolysate of P3 from cationic exchange resins (Fig. 14). Thus, the linkage of the sulfur in position 2 of the imidazole nucleus is borne out both by the radiolabeling data and by amino acid analysis.

To confirm further the presence of a thioether structure in P3, the 2.5-3H-labeled fragment was cleaved with chymotrypsin yielding two peptides: the tripeptide P3-C2 (Gly 91-Gly 92-Tyr 93) and the radioactively labeled peptide P3-C1 giving rise to Thr and SH—His after acid hydrolysis (Fig. 13, Table XI). Treatment of the acid hydrolysate of P3-C1 with a 10-fold excess of hydrogen peroxide led to the formation of free histidine and threonine, again supporting the presence of His in this fragment. In addition, peptide P3-C1 gave a positive chloroplatinate acid test (7) and yielded cysteic acid after performic acid oxidation (8) of a sample treated with Ag2SO4, a reagent known to cleave thioethers (6). These data are thus compatible with the presence of an intramolecular thioether.

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**Fig. 2. Complete amino acid sequence of *Neurospora* tyrosinase.** Cysteinyl residue 94 is covalently linked to histidyl residue 96 via a thioether bond. For the one-letter notation for amino acid residues, see *J. Biol. Chem.* 243, 3557-3559 (1968).

1.0 Thr, 1.9 Gly, and 1.0 Tyr, an unknown, ninhydrin-positive species eluting just after aspartic acid (Fig. 14). The same peak was also observed upon back hydrolysis of PTH derivative 28 of CB1 (2). The chemical nature of this species remained unclear until in vivo labeling experiments with $[^35]$S sulfate and $[2,5-3^H]$histidine suggested the presence of a sulfur-containing amino acid and histidine in the tripeptide spanning residues 94-96.

The elution profile from the ion exchange resin M-72 of a peptic digest of in vivo labeled $[^35]$S-*Neurospora* tyrosinase is depicted in Fig. 9. In addition to the three methionine-containing peptides P1, P2, and P4 already described, a fourth fragment P3 was isolated with the same amino acid composition (Table VIII, Fig. 14) as the peptic peptide from CB1 mentioned above (residues 91-96). The specific radioactivity of the $[^35]$S-labeled fragment was identical with that of the three methionine-containing peptides (Table I), thus strongly indicating the presence of a modified sulfur-containing amino acid in this peptide. The occurrence of histidine in the same peptide P3 is inferred from the elution profile of a peptic digest of in vivo labeled $[2,5-3^H]$histidine tyrosinase (Fig. 11). In addition to four well resolved radioactive peaks accounting...
bridge between a cysteinyl and a histidyl residue in this fragment. The complete chemical structure of P3-C1 was established by manual Edman degradation (Table XII). The first step yielded Ala after back hydrolysis of the ethyl acetate phase, strongly indicating the presence of a cysteinyl residue in position 1. The second amino acid residue was unambiguously identified as Thr in agreement with the results from automatic Edman degradation of CB1 (1). Direct amino acid analysis of the residual aqueous phase after step 2 gave SH—His in good yield, thus confirming the sequence position of the histidyl residue. The manual Edman degradation of P3-C1 was carried out both with the [2,5-3H]histidine and 35S-labeled peptide. In both instances, the bulk of the radioactivity was confined to SH—His (Table XII).

The presence of a thioether structure between Cys 94 and position 2 of His 96 is also supported by the characteristic absorption features of P3-C1 in the UV region. The absorption spectrum (Fig. 3) was found to be strikingly similar to 2-thiolhistidine. The strong absorption of P3-C1 (ε_{200/260} = 14,400) is also expected to be manifested in the absorption spectrum of Neurospora tyrosinase (Fig. 15). Indeed, the ratio of A_{200/260} was found to be rather low (1.50). The calculated ratio based on the content of aromatic amino acids gave a value of 1.71 for Neurospora tyrosinase. The discrepancy between these two values is accounted for by the presence of the strongly absorbing thioether in Neurospora tyrosinase. The complete chemical structure of the tripeptide P3-C1 is depicted in Fig. 4 with its pertinent characteristics summarized in Table II.

**Amino Acid Sequence of Neurospora Tyrosinase.**—The complete primary structure of Neurospora tyrosinase as deduced from the sequence of the cyanoogen bromide fragments (1) and the methionine-containing overlap peptides (Fig. 1), is shown in Fig. 2. The enzyme consists of 407 amino acids with a molecular weight of 46,000 including two g-atoms of copper. This value is substantially higher than those reported earlier (8, 9); however, the amino acid composition calculated from the amino acid sequence was found to be in good agreement with the published results by Fling et al. (8) if corrected for the larger molecular weight of 46,000.

![Fig. 3](image_url)

**Fig. 3.** UV absorption spectra of 2-thiolhistidine (dashed line) and the chymotryptic tripeptide (residues 94–96, Fig. 2) (solid line). 2-Thiolhistidine (50 μM) and the tripeptide (34.5 μM) were dissolved in 10 mM HCl.

![Chemical structure](image_url)

**Fig. 4.** Chemical structure of the chymotryptic tripeptide (residues 94–96, Fig. 2) of Neurospora tyrosinase. The sulfur of cysteinyl residue 94 is covalently linked to the imidazole nucleus of histidyl residue 96 in position 2.

**Table II**

| Treatment                                    | Result          |
|----------------------------------------------|-----------------|
| Acid hydrolysis (18 h, 6 N HCl)              | 1 mol of Thr; 0.9 mol of SH—His | 1 mol of Thr; 0.8 mol of His |
| Acid hydrolysis, 10-fold molar excess H2O2   |                 |                             |
| Chloroplatinic acid test                     | Positive        |                             |
| Thioether cleavage (AgNO3), performic acid oxidation, and acid hydrolysis | 1 mol of Thr; 0.7 mol of cysteic acid | 1.44 × 10^3 |

**Post-translational Modifications.**—It was recognized very early in the course of the sequence determination of Neurospora tyrosinase that the NH2-terminal residue is blocked. Using mass spectrometry (10), the first amino acid was identified as N-acetylseryl. This is in contrast to the four isozymes of mushroom tyrosinase (11) which were reported to contain a free NH2-terminal isoleucine residue. However, mushroom tyrosinase was recently found to be composed of two subunits (12) and therefore it cannot be ruled out that one of the two subunits is also blocked.

In agreement with earlier findings (8) freshly isolated, denatured Neurospora tyrosinase contains no free sulphydryl group. Hence, the thiol side chain of the sole cysteiny1 residue 94 found in this enzyme is quantitatively linked to histidyl residue 96. Although the possibility of an isolation artifact has to be considered, it seems much more likely that this unusual cross-link is an inherent structural feature of Neurospora tyrosinase, generated in a post-translational event. That some processing does occur is suggested by the findings of Fox and Burnett (13) who showed that in crude extracts of the fungus the enzyme is present in an active and an inactive form (protyrosinase). The results of a kinetic study of the activation process of protyrosinase were interpreted in terms of an enzyme-catalyzed intramolecular rearrangement of the molecule. Thus, it is conceivable that the activation of protyrosinase takes place by the enzymatic formation of the thioether linkage between Cys 94 and His 96. In this context it is of interest, that Neurospora crassa is capable of synthesizing ergothioneine (15), an N-trimethylated derivative of 2-thiolhistidine. Biosynthetic studies have indicated that ergothioneine is derived from histidine and that cysteine is the principal source of the sulfur of ergothioneine (15). Thus, possibly related enzymic processes might be responsible both for parts of the synthesis of ergothioneine and for the generation of the thioether structure in Neurospora tyrosinase.

Finally it was of interest to see if this peculiar thioether structure is a unique feature of Neurospora tyrosinase or if it
occurs also in other copper proteins. By taking advantage of the ease in converting 2-thiolhistidine into histidine with hydrogen peroxide, a diagonal procedure was developed (see "Materials and Methods"). With this method, no histidine was detected in the hydrogen peroxide-treated amino acid eluate of tyrosinase from the procaryote Streptomyces glaucescens (3). The thioether structure was also absent in Neurospora laccase (2) and Cancer pagurus hemocyanin, two copper proteins containing a similar binuclear copper site to Neurospora tyrosinase.

Sequence Homology with Other Copper Proteins—Neurospora tyrosinase is a monooxygenase containing a binuclear copper active site (16–20). This copper complex, referred to as type 3 copper (21), is shared by the oxygen transporting hemocyanins (22) and by the multicopper oxidases laccase, ascorbate oxidase, and ceruloplasmin. Upon comparison of the COOH-terminal part of the 50,000-dalton fragment of ceruloplasmin with the sequence of Neurospora tyrosinase, a common Leu-His-His sequence (255–257 in ceruloplasmin and 304–306 in tyrosinase) was recognized. This admittedly quite limited sequence homology in the active-site residues was observed to the blue copper proteins plastocyanin and azurin as well as to copper-zinc superoxide dismutase. Upon comparison of the COOH-terminal part of the 50,000-dalton fragment of ceruloplasmin with the sequence of Neurospora tyrosinase, a common Leu-His-His sequence (255–257 in ceruloplasmin and 304–306 in tyrosinase) was recognized. This admittedly quite limited sequence homology is of interest since the second of the juxtaposed histidyl residues (residue 306) of Neurospora tyrosinase has recently been demonstrated to be selectively destroyed during active-site directed inactivation by catechol (24). Since, concurrently with the inactivation, one of the two copper atoms was lost, it was suggested that histidyl residue 306 functions as a copper ligand.

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Amino Acid Sequence of Neurospora Tyrosinase

EXPERIMENTAL PROCEDURES

Materials

Neurospora tyrosinase and Neurospora tryptophanase were isolated as described previously (3,13). Both enzymes showed a single band in polyacrylamide gel electrophoresis and had the specific enzymatic activities indicated above. The 2,5-dimethylphenylacetic acid assay was performed as described previously (18). The 2-thiolhistidine assay was performed as described by Olmsted (19) and Neurath et al. (20). The 6 N HCl containing 0.1% mercaptoethanol was purchased from Bio-Rad Laboratories, Richmond, Calif.

Methods

For the isolation and sequencing of the peptides, the procedure described in the Experimental Procedures section of the preceding paper (3,13) was used. The method was essentially the same as that used in the isolation of the tryptic peptides from Neurospora tyrosinase (3,13). The only modification was in the isolation of the tryptic peptide from Neurospora tyrosinase. The tryptic peptides were isolated from the tryptic digest of Neurospora tyrosinase using high-voltage paper electrophoresis at pH 1.9. The peptides were eluted with 5% acetic acid and were further purified as indicated in Table III.

RESULTS

Isolation and Characterization of Neuraminic-Containing Peptides of Neurospora tyrosinase

Fig. 1 - Ion-exchange chromatography of the tryptic peptides from Neurospora tyrosinase on a Superoxide column (2.5 x 140 cm) equilibrated with 0.1 M NaCl. The fraction indicated by the solid bar was pooled. The fractions indicated by the open bars were further purified as indicated in Table III.

Fig. 2 - Ion-exchange chromatography of the tryptic peptides from Neurospora tyrosinase on a Superoxide column (2.5 x 140 cm) equilibrated with 0.1 M NaCl. The fraction indicated by the solid bar was pooled. The fractions indicated by the open bars were further purified as indicated in Table III.

Fig. 3 - Ion-exchange chromatography of the tryptic peptides from Neurospora tyrosinase on a Superoxide column (2.5 x 140 cm) equilibrated with 0.1 M NaCl. The fraction indicated by the solid bar was pooled. The fractions indicated by the open bars were further purified as indicated in Table III.

Fig. 4 - Ion-exchange chromatography of the tryptic peptides from Neurospora tyrosinase on a Superoxide column (2.5 x 140 cm) equilibrated with 0.1 M NaCl. The fraction indicated by the solid bar was pooled. The fractions indicated by the open bars were further purified as indicated in Table III.

Fig. 5 - High-voltage paper electrophoresis of the tryptic peptides from Neurospora tyrosinase on a Whatman 1 paper. The peptides were eluted with 5% acetic acid and were further purified as indicated in Table III.
Amino Acid Sequence of Neurospora Tyrosinase

Table III - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table IV - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table V - Amino acid compositions of the peptide derived from the thrombin fragment of Neurospora tyrosinase.

Table VI - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table VII - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table VIII - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table IX - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table X - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table XI - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table XII - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table XIII - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table XIV - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table XV - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table XVI - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table XVII - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table XVIII - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table XIX - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.

Table XX - Amino acid compositions of the large tryptic peptide and a thrombin fragment from intact and deficient Neurospora tyrosinase.
Primary structure of tyrosinase from Neurospora crassa. II. Complete amino acid sequence and chemical structure of a tripeptide containing an unusual thioether.

K Lerch

J. Biol. Chem. 1982, 257:6414-6419.

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