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Zur intrinsischen Sauerstoffaffinität: Die Primärstruktur eines weiteren Ruminantia-Hämoglobins: Methionin in β NA2 eines Stirnwaffenträgers, des Nordland-Elches (*Alces alces alces*)

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Zusammenfassung: Die Primärstruktur der α - und β -Ketten des Hämoglobins vom Nordland-Elch (*Alces alces alces*) wurde ermittelt. Die Sequenz

wurde mit den bovinen Ketten verglichen. Die Sauerstoffaffinität wird in bezug auf die Primärstruktur der β -Ketten diskutiert.

*Intrinsic Oxygen Affinity: The Primary Structure of a Ruminantia Hemoglobin: Methionine in β NA2 of a Pecora, the Northern Elk (*Alces alces alces*)*

Summary: The primary structures of the α - and β -chains of hemoglobin from the Northern Elk (*Alces alces alces*) have been determined. The

sequence was compared with the bovine chains. The oxygen affinity regarding the primary structure of the β -chains is discussed.

Key words: *Alces alces alces* haemoglobin, amino-acid sequence, intrinsic oxygen affinity.

Die Hämoglobine der Ruminantia gehören zu den Vertretern mit niedriger intrinsischer Sauerstoffaffinität^[2,3]. Eine Theorie zur Erklärung der Affinität dieser Hämoglobine auf molekularer Ebene wurde von Perutz entwickelt^[4,5]. Ob diese Theorie auch auf einen Vertreter der Unterfamilie der Alcinae anwendbar ist, sollte durch die Primärstrukturaufklärung des Hämoglobins des Nordland-Elches (*Alces alces alces*) abgeklärt werden.

Experimenteller Teil

Gewinnung von α - und β -Ketten

Blut einer adulten Nordland-Elchkuh (*Alces alces alces*) war ein Geschenk von Dr. Wiesner, Tierpark Hellabrunn. Die Erythrozyten wurden wie üblich gewaschen und lysiert. Das Hämoglobin wurde durch Polyacrylamidgel-Elektrophorese auf die Anzahl der Hämoglobinkomponenten untersucht^[6] und mittels dieser Technik in Gegenwart von Triton X-100 und Harnstoff wurde die Anzahl der Globinketten bestimmt^[7] (Abb. 1.).

Abkürzungen:

Quadrol = *N,N,N',N'*-Tetrakis(2-hydroxypropyl)ethylendiamin;
Reagenz I = 1-(Isothiocyanato)benzol-4-sulfonsäure, Natriumsalz;
Reagenz IV = 7-(Isothiocyanato)naphthalin-1,3,5-trisulfonsäure, Trinatriumsalz;
TosPheCH₂Cl = (*N*-Tosyl-L-phenylalanyl)chlormethan.

* 76. Mitteilung über Hämoglobine; 75. Mitteilung s. l.c.^[1].

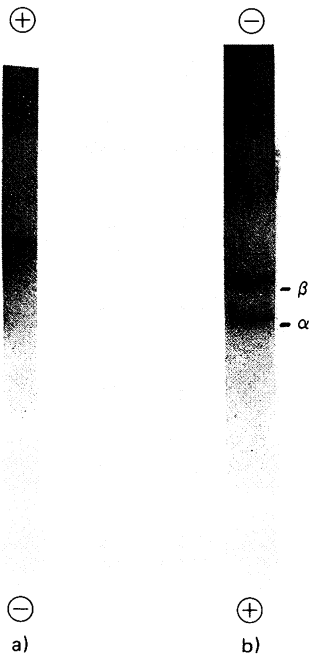


Abb. 1. Acrylamidgel-Elektrophorese des Hämoglobins.
 a) Gel: 10% Polyacrylamid mit 1.6proz. Bis(acrylamido)-methan in 375mM Tris/HCl, pH 8.9; Elektrodenpuffer: 57mM Glycin, 7.4mM Tris, pH 8.3.
 b) Elektrophorese in Gegenwart von 2% Triton X-100 in 8M Harnstoff und 5% Essigsäure.

Die präparative Kettentrennung erfolgte nach Abspaltung des Häms mit 2-Butanon^[8] auf CM-Sepharose CL-6B im Harnstoffpuffer (Abb. 2).

Tryptische Peptide

10 mg lyophilisierte Kette wurden in 500 μ l 50mM Ammoniumacetat/Ammoniak-Puffer, pH 9.0, gelöst und unter Rühren 4 h bei Raumtemperatur mit 2proz. Trypsin (TosPheCH₂Cl-behandelt, Worthington) gespalten. Anschließend wurde lyophilisiert. Die β -Kette wurde in einem Experiment außerdem vor der tryptischen Verdauung mit Perameisensäure oxidiert^[9].

Die tryptischen Hydrolysate wurden anschließend in 500 μ l 50mM Ammoniumacetat/Essigsäure-Puffer, pH 6, aufgenommen, von unlöslichem „core“ durch Zentrifugation befreit und durch Hochdruck-Flüssigkeitschromatographie auf einer 4.6 \times 250-mm-LiChrosorb-RP-2-Säule, 7 μ m Partikelgröße (Merck), in 50mM Ammoniumacetat/Essigsäure-Puffer, pH 6.0, mit einem Acetonitrilgradienten von 0–60% in 60 min bei einem

Durchfluß von 1 ml/min getrennt (HPLC-Gerät der Fa. Beckman Instruments). Das Eluat wurde bei 230 nm vermessen (Abb. 3–5). Einige Fraktionen wurden auf einer 5 μ m 4.6 \times 250-mm-ODS-Hypersil-Säule (Shandon Southern Products Ltd.) unter sonst identischen Bedingungen rechromatographiert.

Der „core Anteil“ wurde auf einer 4.6 \times 250-mm-LiChrosorb-RP-2-Säule, 7 μ m Partikelgröße, mit 0.1proz. Trifluoressigsäure und einem Acetonitrilgradienten von 30–60% in 30 min unter sonst gleichen Bedingungen getrennt.

Saure Hydrolyse der Asp-Pro-Bindungen^[10]

10 mg lyophilisierte Kette wurden in 1 ml 6M Guanidinhydrochlorid in 70proz. Ameisensäure gelöst und 72 h bei 40 °C gespalten. Das Hydrolysat wurde auf einer Sephadex-G-50f-1.6 \times 90-cm-Säule in 6M Guanidiniumhydrochlorid/10proz. Essigsäure/3proz. Mercaptoethanol-Puffer bei einer Durchflußgeschwindigkeit von 6 ml/h fraktioniert. Die Gipfel wurden auf Sephadex G-25 in 5proz. Essigsäure entsalzt und lyophilisiert.

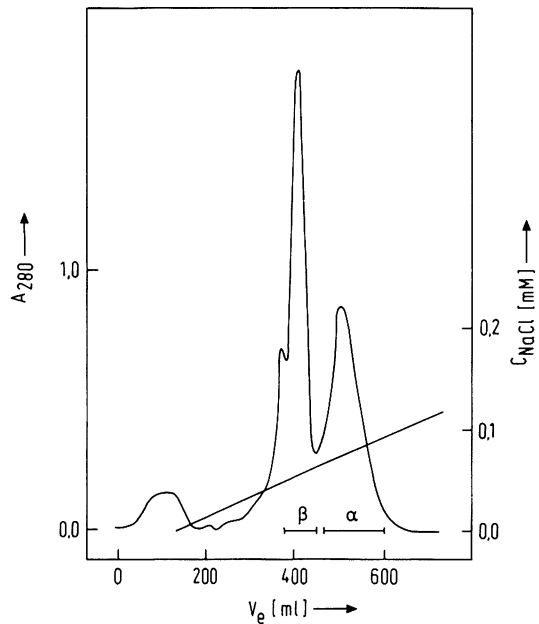


Abb. 2. Kettentrennung.
 200 mg Globin; Säule 2.6 \times 10 cm CM-Sepharose CL-6B; Puffer: 50mM Natriumacetat/HCl in 8M Harnstoff, pH 5.7; linearer Gradient von 0 bis 0.2M NaCl, Gradientenvolumen 1 l; Durchflußgeschwindigkeit 30 ml/h.

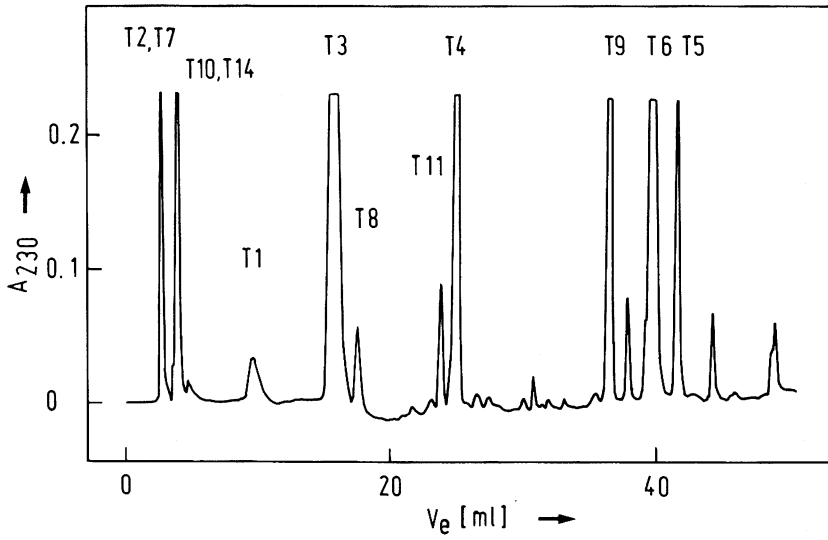


Abb. 3. Trennung der tryptischen Peptide der α -Kette durch Hochdruckflüssigkeitschromatographie. Säule: 4.6×250 mm LiChrosorb RP2; Puffer 50mM Ammoniumacetat/Essigsäure, pH 6.0; linearer Gradient: 0–60proz. Acetonitril in 60 min, Durchflußgeschwindigkeit 1 ml/min.

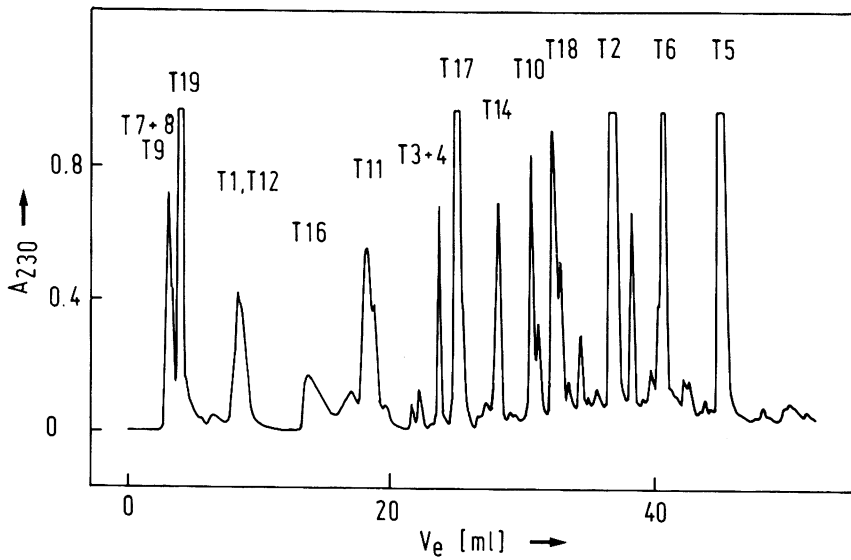


Abb. 4. Trennung der tryptischen Peptide der β -Kette durch Hochdruckflüssigkeitschromatographie. Bedingungen s. Abb. 3.

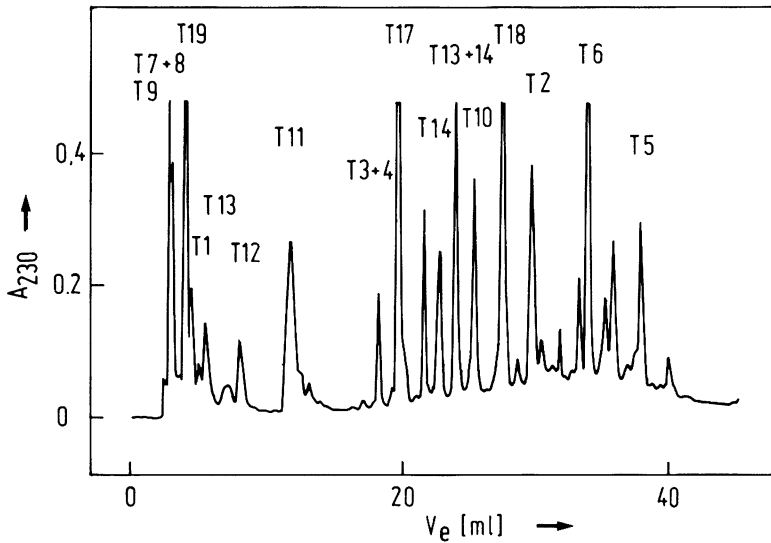


Abb. 5. Trennung der tryptischen Peptide der oxidierten β -Kette durch Hochdruckflüssigkeitschromatographie. Bedingungen s. Abb. 3.

Bromcyanspaltung^[11, 12]

10 mg β -Kette wurden in 70proz. Ameisensäure mit 10 mg Bromcyan 6 h bei Raumtemperatur gespalten und anschließend die Peptide unter den gleichen Bedingungen isoliert wie die Peptide nach saurer Hydrolyse der Asp-Pro-Bindung.

Aminosäureanalyse

200 μ g Protein oder 100 – 50 μ g Peptid wurden 20 h bei 110 °C mit 6M Salzsäure hydrolysiert und anschließend im Aminosäureanalysator Spinco, Modell 121 C (Beckman Instruments) analysiert. Cystein und Methionin wurden nach Oxidation mit Perameisensäure, Tryptophan nach Hydrolyse mit 6proz. Thioglycolsäure (Merck) in 6M Salzsäure bestimmt.

Sequenzanalyse

Die Sequenzanalyse wurde durch automatischen Edman-Abbau^[13] in einem Beckman-Sequenator mit folgenden Methoden durchgeführt:

Methode a: Im 0.25M Quadrolprogramm wurden die Globinketten und Lysinpeptide, die mit Reagenz IV hydrophilisiert worden waren, mit einem Sequencer 890 C abgebaut^[14].

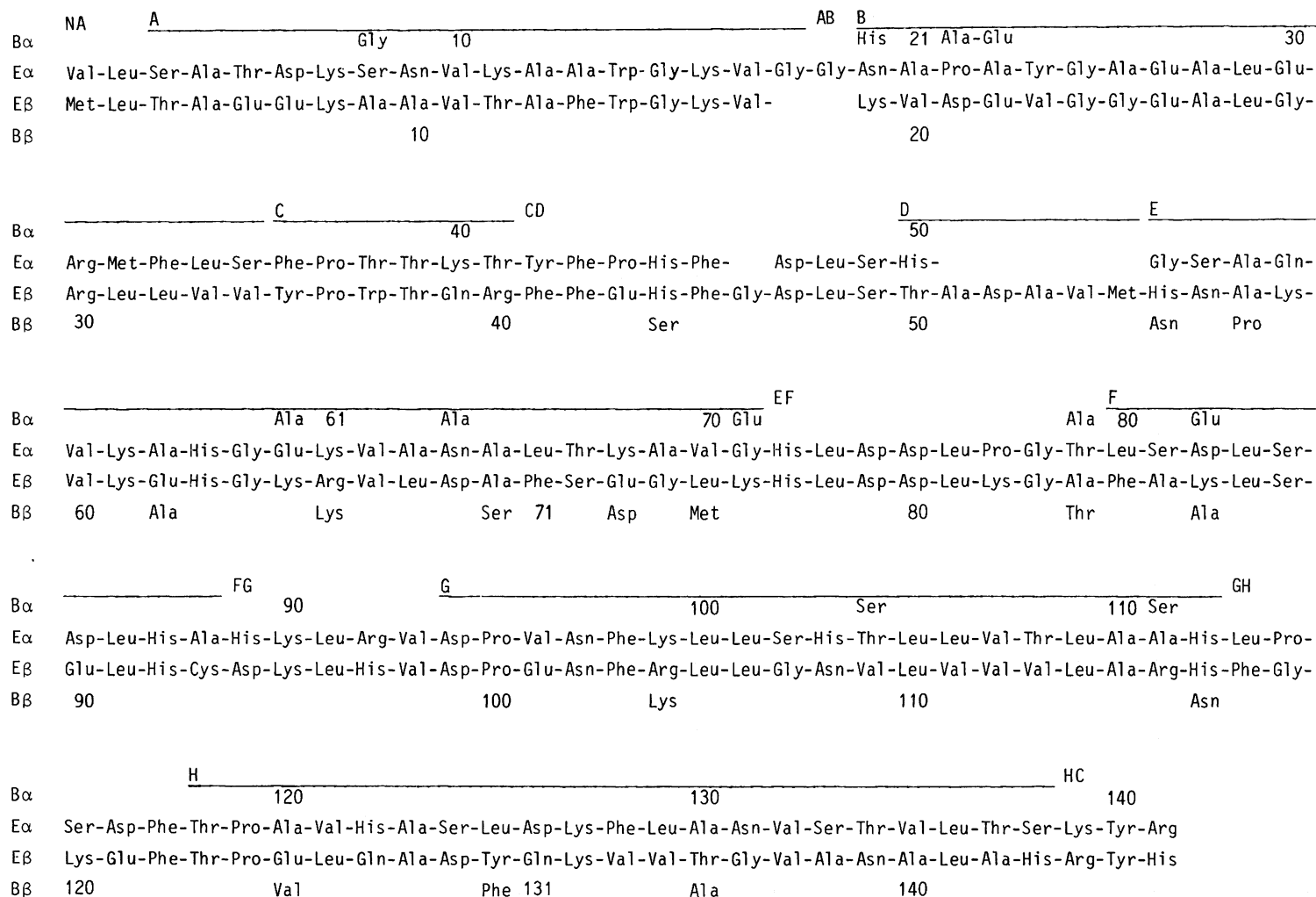
Methode b: Das 1.5M 3-(Diethylamino) propin-Programm^[15] wurde für Arginin-Peptide, Lysin-Peptide, ent-

weder in Gegenwart von Hexadimethrinbromid oder nach Reaktion mit Reagenz I^[16], – und für die Prolin-Peptide nach saurer Hydrolyse der Asp-Pro-Bindungen – in einem Sequencer 890 B angewendet.

Die Identifizierung der Phenylthiohydantoin-Derivate der Aminosäuren erfolgte mittels Dünnschicht-Chromatographie^[17] und Hochdruck-Flüssigkeitschromatographie^[18, 19] auf einem Hochdruck-Flüssigkeitschromatographen der Fa. Hewlett Packard (HP 1084).

Ergebnisse

Die Polyacrylamidgel-Elektrophorese des Hämoglobins bei pH 8.9 zeigte unter nicht dissoziierenden Bedingungen nur eine Bande (Abb. 1a) und unter dissoziierenden Bedingungen zwei Banden (Abb. 1b). Daraus kann man schließen, daß eine Hämoglobinkomponente, bestehend aus zwei Ketten – einer α - und einer β -Kette –, vorhanden ist. Die Ionenaustausch-Chromatographie auf CM-Sepharose CL-6 B lieferte ebenfalls zwei Gipfel, wobei der erste eine leichte Vorschulter besitzt, die sich aber nicht als eine Nebenkomponente identifizieren ließ (Abb. 2).

Abb. 6. Homologer Vergleich der α - und β -Ketten des Elches (E) mit den bovinen Ketten (B), von denen nur die ausgetauschten Aminosäuren angegeben sind.

Der N-terminale Bereich wurde durch Sequenzierung an den beiden Polypeptidketten direkt bestimmt, wobei sich mit Methode a an der α -Kette 42 und an der β -Kette 55 Abbauschritte im Sequenator durchführen ließen. Die übrigen Sequenzen der α -Kette wurden mit tryptischen Peptiden und dem Prolin-Peptid, das nach saurer Hydrolyse der Asp-Pro-Bindung erhalten wurde, bestimmt. Es konnten alle tryptischen Peptide isoliert werden (Abb. 3), die Peptide T2 und T7 erst nach Rechromatographie an ODS-Hypersil. Die „ α -core“-Fraktion enthielt geringe Mengen des tryptischen Doppelpeptides T12+13. Die Hauptkomponente bestand aus dem unvollständig gespaltenen Bruchstück T10+11+12+13. Von den tryptischen Peptiden wurden zur Sequenzermittlung die Peptide T6, T7, T8, T9 und T10+11+12+13 abgebaut. Die Sequenz wurde überlappend und in Homologie zu den bovinen α -Ketten^[20] ermittelt (Abb. 6).

Die restlichen Sequenzen der β -Kette wurden aus den tryptischen Peptiden, den tryptischen Peptiden der oxidierten Kette, den Bromcyanpeptiden (CB 3) und dem Prolin-Peptid, das nach saurer Hydrolyse der Asp-Pro-Bindung erhalten wurde, bestimmt. Das cysteinhaltige Peptid T13 konnte nicht isoliert werden. Aus dem tryptischen Hydrolysat der oxidierten β -Kette konnte das tryptische Doppelpeptid T13+14 erhalten werden (Abb. 5). Die Lysinbindung zwischen den Peptiden T7 und T8 wurde nur unvollständig gespalten. Nach Rechromatographie auf ODS-Hypersil konnten sowohl T7 und T8 als auch T7+8 isoliert werden. Die Peptide T5, T6, T7+8, T13+14, T14 und T18 wurden sequenziert. Aus diesen Daten konnte die Sequenz der β -Kette in überlappender Weise erarbeitet werden. In Abb. 6. ist die Sequenz in Homologie zu den bovinen β -Ketten dargestellt^[21, 22].

Die Analysen der Peptide sind in Tab. 1 und Tab. 2 am Schluß der Arbeit (S. 1330) zusammengestellt.

Diskussion

In der Polyacrylamidgel-Elektrophorese (Abb. 1a) zeigt das Elchhämoglobin eine einzige Bande. Die Ionenaustauschchromatographie auf CM-Sepharose Cl 6B löst das Globin in zwei Ketten auf (Abb. 2). Dieses Ergebnis steht im Einklang mit

der Polyacrylamidgel-Elektrophorese in Gegenwart von Harnstoff und Triton X-100 (Abb. 1b). Die Sequenzen der α - und β -Ketten werden in Abb. 6 wiedergegeben. Der dargestellte homologe Vergleich mit den bovinen Ketten^[20-22] läßt für die α -Kette 11 und für die β -Kette 15 unterschiedliche Aminosäuren erkennen.

Die Säugerhämoglobine können nach Bunn^[2] in zwei Gruppen eingeteilt werden: In solche mit intrinsisch hoher Sauerstoffaffinität, die in den Erythrozyten durch organisches Phosphat (2,3-Bisphosphoglycerat) erniedrigt wird und solche mit intrinsisch niedriger Affinität. Es wurde gezeigt, daß im humanen Desoxyhämoglobin – ein Hämoglobin, das zur ersten Gruppe gehört – vier Aminosäuren (β NA1 Val, β NA2 His, β EF6 Lys und β H21 His) Bindungen mit organischem Phosphat eingehen^[23], und daß auf diese Weise die T-Struktur des Hämoglobins stabilisiert wird. Es sind Beispiele beschrieben worden in denen eine Variation (Erhöhung) der Sauerstoffaffinität durch Aminosäureaustausch in den Phosphatbindungsstellen erreicht wird^[24, 25]. Bei niederaffinen Hämoglobinen der Ruminantia (Rind, Schaf, Hirsch und Yak) besteht die β NA-Region nur aus zwei Aminosäuren^[21, 22, 26-29]. β NA1 ist deletiert und in β NA2 (hier Pos. 2) besitzen diese Ketten mit Methionin eine hydrophobe Aminosäure. Diese Hämoglobine zeigen fast keine Affinität zu organischem Phosphat^[23], vielmehr übernimmt wahrscheinlich die hydrophobe Seitenkette der N-terminalen Aminosäure Methionin diese Funktion, indem sie sich in ähnlicher Weise zwischen die β -Ketten lagert und so die Untereinheiten in der T-Struktur fixiert^[24]. Diese Deletion findet sich ebenfalls in den β -Ketten des Elchhämoglobins. Außerdem unterscheidet es sich nicht in den 2,3-Bisphosphoglycerat-Bindungsstellen von den anderen Ruminantia. Daraus kann geschlossen werden, daß – obwohl keine Messungen vorliegen – sich das Elchhämoglobin den Hämoglobinen mit niedriger Sauerstoffaffinität, die keine Abhängigkeit von organischem Phosphat aufweisen, zuordnen läßt.

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