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Phosphate-Haemoglobin Interaction

The Primary Structure of the Haemoglobin of the African Elephant (*Loxodonta africana*, Proboscidea): Asparagine in Position 2 of the β -Chain*

Gerhard BRAUNITZER^a, Anton STANGL^a, Barbara SCHRANK^a, Claus KROMBACH^a and Henning WIESNER^b

^a Max-Planck-Institut für Biochemie, Abteilung Proteinchemie, Martinsried bei München, and

^b Tierpark Hellabrunn, München

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Summary: The primary structure of the haemoglobin of the African Elephant (*Loxodonta africana*) is reported. The sequence was determined by means of a sequenator. The haemoglobin differs in 26 amino acids in the α -chains and in 27 in the β -chains from that of adult human haemoglobin. The haemoglobin of the African Elephant, like that of the Indian Ele-

phant and llama, has only 5 binding sites for polyphosphate. This finding explains the low $p(O_2)_{50}$ value in whole blood as a result of the lower 2,3-bisphosphoglycerate-haemoglobin interaction. This is discussed in relation to aspects of respiratory physiology; some points are also of interest with regard to the Second Punic War and Hannibal's crossing of the Alps.

Phosphat-Hämoglobin-Wechselwirkung. Die primäre Struktur des Hämoglobins des afrikanischen Elefanten (Loxodonta africana, Proboscidea): Asparagine in Position 2 der β -Kette

Zusammenfassung: Die primäre Struktur des Hämoglobins des afrikanischen Elefanten (*Loxodonta africana*) wird angegeben. Die Sequenz wurde mittels Sequenator erarbeitet. Das Hämoglobin unterscheidet sich in den α -Ketten in 26 und in den β -Ketten in 27 Aminosäuren gegenüber adultem Humanhämoglobin. Das Hämoglobin des afrikanischen Elefanten hat – wie das des indischen Elefanten und des Lamas – nur 5 Bin-

dingsstellen zum Phosphat. Dieser Befund erklärt den niedrigen $p(O_2)_{50}$ -Wert im Vollblut durch die geringere 2,3-Bisphosphoglycerat-Hämoglobin Wechselwirkung. Dieses Ergebnis wird weiterhin in bezug auf Aspekte der Atmungsphysiologie diskutiert. Sie sind auch hinsichtlich einiger Aspekte des Zweiten Punischen Krieges und Hannibals Alpenüberquerung interessant.

Key words: Haemoglobin, African Elephant, primary structure, 2,3-bisphosphoglycerate, oxygen affinity.

Abbreviations:

Hb = Haemoglobin; Quadrol = *N,N,N',N'*-tetrakis-2-(hydroxypropyl)ethylenediamine; Tp = tryptic peptides; Reagent I = sodium 4-(isothiocyanato)benzenesulfonate; Reagent IV = trisodium 7-(isothiocyanato)naphthalene-1,3,5-trisulphenate; TosPheCH₂Cl = *N*-tosyl-L-phenylalanyl-chloromethane; Pth amino acids = phenylhydantoin derivative of amino acids; HbF = human foetal haemoglobin, DPG = 2,3-bisphosphoglycerate; IPP = inositol-1,3,4,5,6-pentakisphosphate.

* 72th Communication on Hemoglobins; 71st communication see ref.[1].

In the course of investigations of oxygen transport in mammals we report the primary structure of the haemoglobin of an African Elephant. These data are compared with the primary structure of the haemoglobin of the Indian Elephant and other mammals; in particular, the binding sites and the interaction of the haemoglobin with 2,3-bisphosphoglycerate are discussed.

Materials and Methods

Isolation of African Elephant haemoglobin

The haemoglobin was collected at the Hellabrunn Zoo in Munich by removing blood from an ear vein. Isolation of the erythrocytes and extraction of the crude haemoglobin were carried out by standard techniques. The preparation was tested for homogeneity by disk electrophoresis: only a single blood band could be detected. Globin was obtained by precipitation with acidic acetone; the preparations were preserved at -30°C . The chains were separated by chromatography on CM cellulose and urea buffer^[2]. For sequence analysis the chains were cleaved with trypsin and cyanogen bromide^[3].

Peptide fractionation

Tryptic peptides were pre-fractionated on Sephadex G-25 (2.5×100 cm) in 0.1M acetic acid, the fractions of the individual peaks were collected, and the material was purified by high-performance liquid chromatography on a RP-2 LiChrosorb (Merck, Darmstadt) column.

Amino-acid analyses

The 121 C apparatus (two-column system, Beckman Instruments, Palo Alto, U.S.A.) was used for amino-acid

analyses. In each case 300 μg protein or 200 μg peptide were hydrolysed and injected.

Sequence determination

The film technique was used and two programmes were applied, the Quadrol programme^[4] and the diethyl- or dimethylaminopropyne programme^[5].

a) Quadrol programme: α - and β -chains were degraded by a procedure similar to that of Edman and Begg in 1M Quadrol. Tryptic lysin-containing peptides were reacted with hydrophilic isothiocyanates, reagent I^[6] or IV^[7], prior to degradation, using 0.2–0.4M Quadrol.

b) Propyne programme: a programme without ethyl acetate^[8] was used for short or hydrophobic peptides with C-terminal arginine. This was carried out at 3500 (high speed) and 2000 (low speed) r.p.m. to obtain the thinnest possible films and to make the washing with ethyl acetate or butyl chloride as efficient as possible. Conversion was carried out with 3M trifluoroacetic acid at 80°C for 14 min^[9] and the Pth amino acids were extracted with ethyl acetate.

The phenylthiohydantoin were identified by thin-layer^[10] or high-performance liquid chromatography^[11]. We used a 890 B sequencer (Beckman Instruments, Palo Alto, U.S.A.) modified by our own workshop.

Discussion and Results

Primary structure

The blood of an African Elephant (*Loxodonta africana*) was removed from an ear vein. Only one haemoglobin band could be detected by electrophoresis under non-dissociating conditions; this findings was confirmed by separating the chains under dissociating conditions, where

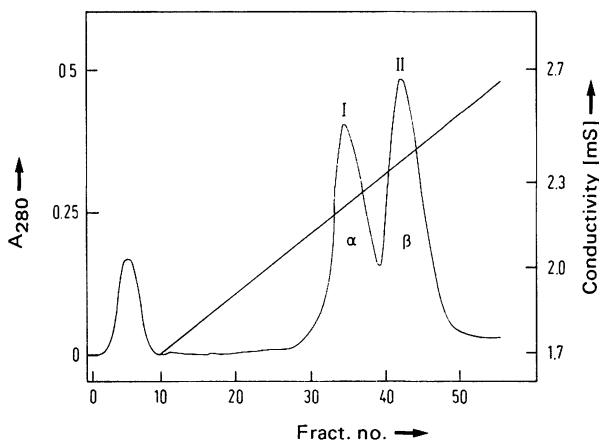


Fig. 1. Chain separation of *Loxodonta* globin.

CM-cellulose-column, 2.6×10 cm, buffer 0.05M sodium acetate/0.01% dithioerythritol/8M urea, pH 5.0; gradient 0.02–0.1M NaCl; 600 ml.

two bands were obtained (Fig. 1). Separations of the tryptic peptides of the α - and β -chains are shown in Figs. 2 and 3 and the amino-acid compositions of the tryptic peptides are given in Tables 3 and 4 in the Supplementary Material.

The sequence of the α - and β -chains is shown in Fig. 4 and the substitutions relative to human haemoglobin A^[12] are given. The number of differences is 26 for the α -chains and 27 for the β -chains (see Fig. 4).

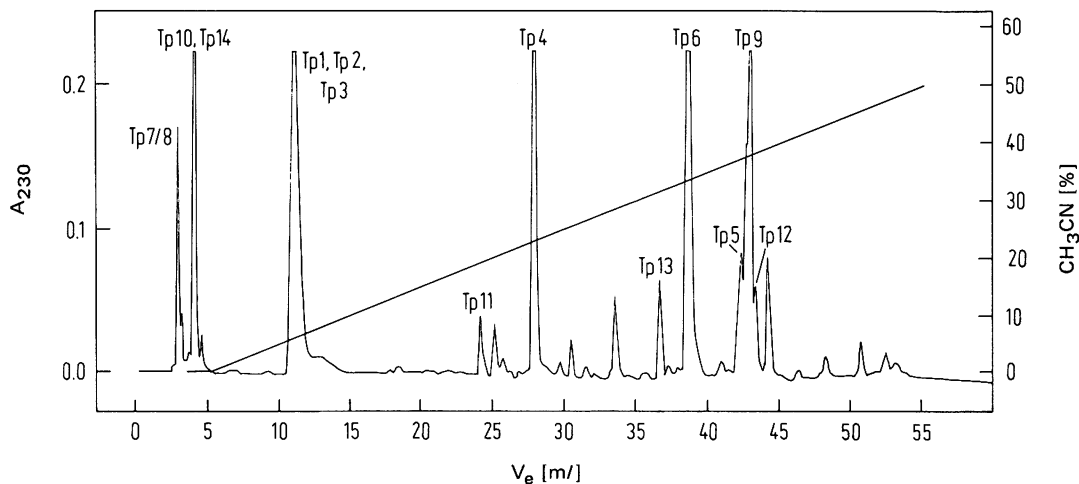


Fig. 2. Separation of tryptic peptides of the α -chains.

Column: RP-2 LiChrosorb (Merck), 4.6×250 mm; Solvent A: 0.05 ammonium acetate, pH 6.0; Solvent B: acetonitrile; 1 ml/min.

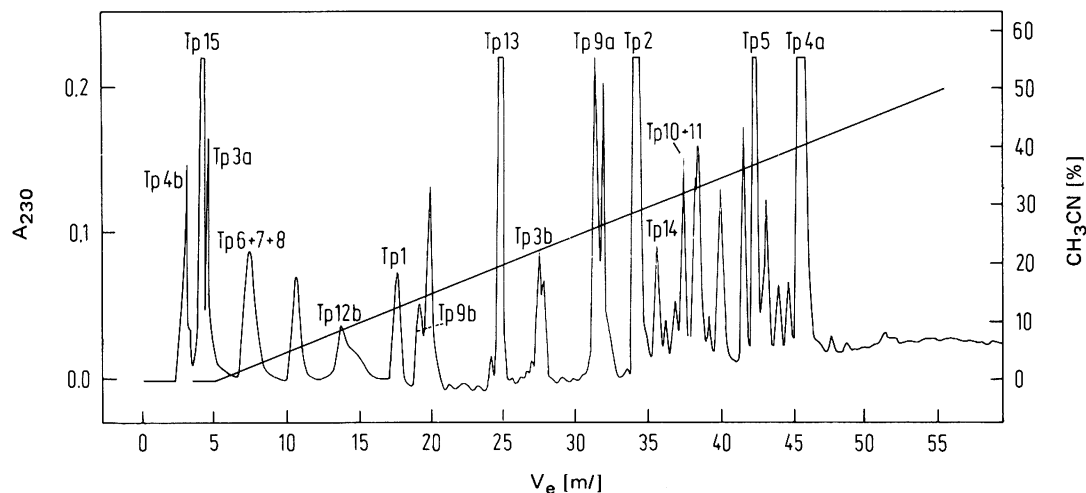


Fig. 3. Separation of tryptic peptides of the β -chains.

Column: RP-2 LiChrosorb (Merck), 4.6×250 mm; Solvent A: 0.05 ammonium acetate, pH 6.0; Solvent B: acetonitrile; 1 ml/min.

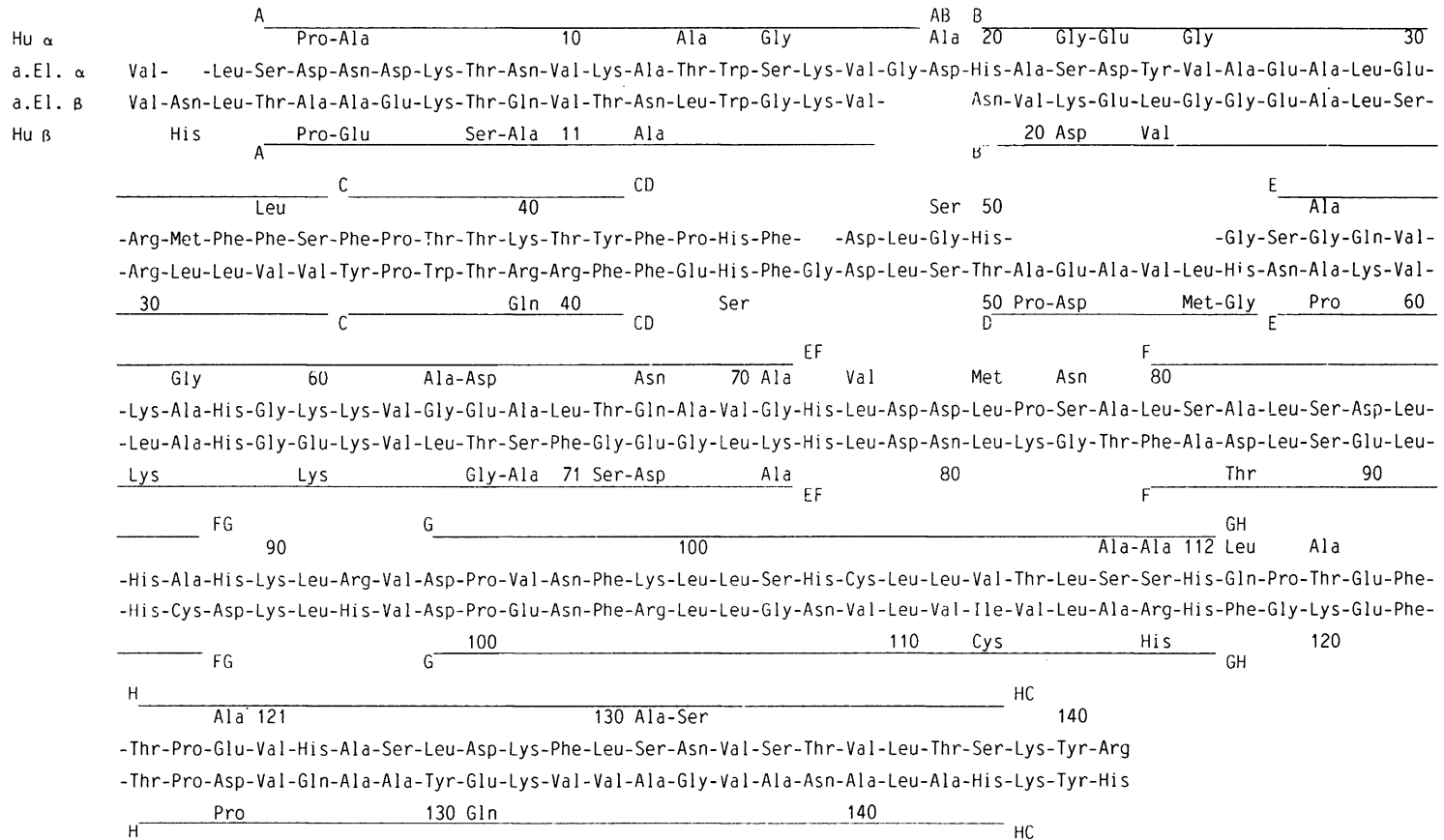


Fig. 4. Amino-acid sequence of the α - and β -chains from HbA of African Elephant (a. El.).
 Hu α and Hu β indicates the differences with respect to the corresponding chains of human haemoglobin. The bars A, B etc. show the helical regions.

Sequence differences between the Indian and the African Elephant

A comparison of the sequences of the Indian^[13] and African Elephant reveals that the differences – as would be expected – are small. A total of 4 substitutions is found.

Indian Elephant $\alpha 5$ Lys $\alpha 49$ Ser $\alpha 57$ Gly $\beta 52$ Asp
African Elephant $\alpha 5$ Asn $\alpha 49$ Gly $\alpha 57$ Ala $\beta 52$ Glu

It is notable that the substitutions are neutral and in particular that the sequence at $\beta 2$ is identical in both elephant species, i.e. asparagine is found, therefore the physiological indications for both species can be considered equivalent.

Oxygen affinity

The $p(O_2)_{50}$ value in absence of 2,3-bisphosphoglycerate and CO_2 , which is a parameter of the intrinsic oxygen affinity of elephant haemoglobin, was 2.06 kPa (= 15.4 torr). The data are similar to those derived in the case of human foetal haemoglobin (HbF)^[14–16].

Earlier investigations revealed that the blood of both Indian and African Elephants has a particularly high oxygen affinity^[17]. The normal blood $p(O_2)_{50}$ value is 3.36 kPa (25.2 torr) at 37 °C and pH 7.4^[18]. The intraerythrocyte 2,3-bisphosphoglycerate concentration (5mM) in the elephant is just as high as in most other mammals^[18]. We were able to show that the intrinsic affinity of elephant haemoglobin is not abnormally high by comparison with other mammal species^[13] and furthermore that it is based on relatively weak binding between haemoglobin and 2,3-bisphosphoglycerate. The effect of 2,3-bisphosphoglycerate on the oxygen affinity was actually even lower with elephant haemoglobin than with human HbF, for which a particularly weak 2,3-bisphosphoglycerate interaction is known.

2,3-Bisphosphoglycerate-haemoglobin interaction

The physiological data of the $p(O_2)_{50}$ value of the Indian Elephant haemoglobin together with the association constant for 2,3-bisphosphoglycerate are plausibly interpreted by the data of this haemoglobin sequence. Asparagine is present at $\beta 2$ in the sequence. The oxygen affinity is known to be controlled by 2,3-bisphosphoglycerate^[19,20]; this bound in the T-form via

the $\beta 1$, $\beta 2$, $\beta 82$, and $\beta 143$ residues, which all contain basic residues (proton acceptors) and hence form salt bridges to the phosphate groups. The oxygen affinity of haemoglobin is reduced to normal blood value and therefore to the physiological value by 2,3-bisphosphoglycerate. The substitutions $\beta 2 \rightarrow$ Asn causes disruption of the binding sites^[13], since the side-chain of asparagine (but not that of glutamine) (Table 1) is too short to enter any interaction. The elephant therefore “breathes” – just like the llama – with only 5 binding sites and not with 7, like the majority of mammals (Table 2). The intrinsic and therefore the phosphate-free oxygen affinity of the haemoglobin is partially reduced in the African Elephant too, and this is responsible for the elevated affinity of its haemoglobin and blood to oxygen.

Hannibal's crossing of the Alps

Investigations of high-altitude respiration have revealed that the particular ability of the llama to breathe at high altitudes must be traced back to the reduced interaction of phosphate and haemoglobin, which was explained on the molecular level by the side chain of $\beta 2$ asparagine (instead of histidine). Exactly the same molecular situation of the phosphate-haemoglobin interaction has been found in the Indian and now in the African Elephant as well. Here Hannibal's crossing of the Alps and the Second Punic War comes to mind^[21–23].

It is said that Hannibal “trained” in the mountains of North Africa before his invasion of the Po plains and before crossing the Alps. He probably noticed on this occasion that elephants work “normally” even at high altitudes and concluded that he could risk crossing the Alps

Table 1. Atomic distances of the amide groups of the $\beta 2$ residues asparagine and glutamine between the $\beta 1$ and $\beta 2$ chains and to the phosphate O-group of 2,3-bisphosphoglycerate, measured from the atomic model (kindly provided by M. F. Perutz).

N δ (Gln2 β ₁) – (N δ (Gln2 β ₂))	15 Å
N γ (Asn2 β ₁) – N γ (Asn2 β ₂)	16.8 Å
N δ (Gln2 β) – O-(PO ₄ of DPG)	3.5–4.0 Å
N γ (Asn2 β) – O-(PO ₄ of DPG)	4.5–5.0 Å

Table 2. Genetic control of the oxygen affinity of some vertebrate haemoglobins by organic polyphosphates and hydrogen carbonate: Reduction in the intrinsic affinity of haemoglobins.

The contact sites are given. Changed phosphate contacts: only the exchanged side chains in haemoglobin are presented. At $\beta 2$ asparagine the side chain is too short and therefore causes disruption of the interaction with polyphosphate. the free carboxyl group of $\beta 2$ glutamic acid allows no interaction as the negative charge causes an – almost quantitative – reduction of interaction with polyphosphate, glutamic acid in $\beta 2$ on the other hand is a binding site for ATP and GTP in fish, etc. This table summarizes the current knowledge regarding the control of haemoglobin oxygen affinity by phosphates and hydrogen carbonate in tetrameric vertebrate haemoglobins.

Helix	NA1	NA2	EF6	H13	H17	H21	H22	Contact number	
Sequence	$\beta 1$	$\beta 2$	$\beta 82$	$\beta 135$	$\beta 139$	$\beta 143$	$\beta 144$		
DPG	Val	His	Lys			His		7	Mammalia
IPP	Val	His	Lys	Arg	His	Arg		10	Aves
ATP, GTP	Val	Glu	Lys			Arg		5	Pisces, Amphibia
HCO_3^-	AcAla		Lys				Glu	6	Crocodylia
<i>Changed phosphate contacts</i>									
DPG		Gln				Ser		5	HbF – Primates
		Asn						7	<i>Equus</i>
		Glu						5	<i>Lama, Elephas, Dasypus</i>
		Gln						0 ?	<i>Rhinozerus</i>
IPP			Asn					10	<i>Struthio camelus</i>
ATP, GTP		His						3 ?	<i>Thunnus</i>
		His						5 ?	<i>Squalus acanthus</i>
		His	Leu					5 ?	<i>Iguana iguana</i>
								?	<i>Chrysemis picta belli</i>

with these animals.* Our biochemical and physiological data imply that Hannibal’s enterprise was facilitated by the distinctive respiratory function of elephant haemoglobin. Our earlier findings in the Indian Elephant and the conclusions drawn from these are therefore correct, since they also apply to the African Elephant ($\beta 2 = \text{Asn}$) which Hannibal had at his disposal. We could even conclude further that Hannibal would have been able to cross the Andes, where it is more likely that he and his soldiers, but not his elephants, would have encountered difficulties.

Miss Barbara Peischl separated the chains and isolated the peptides. We thank Priv.-Doz. Dr. Wolfgang Jelkmann, Regensburg, and Priv.-Doz. Dr. Rosemarie Bau-

* Annotation

Here another point that is not considered on encyclopaedias, but is important, may be discussed. Hannibal thoroughly prepared for the Second Punic War: for example he hired drivers from India for the elephants. In the Rhone crossing, however, all the Indian Elephant keepers drowned when the rafts capsized (loc. cit. chap. 46). This is undoubtedly the first source of the problems that appeared later when crossing the Alps (J. Lindauer, private communication).

mann, Hannover, for valuable discussions as well as OStD Josef Lindauer, Wilhelms-Gymnasium Munich, for valuable advice.

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Prof. Dr. G. Braunitzer, Anton Stangl, Barbara Schrank, Claus Krombach, Max-Planck-Institut für Biochemie, D-8033 Martinsried bei München.

Priv. Doz. Dr. Henning Wiesner, Tierpark Hellabrunn, D-8000 München 90.

Supplementary Material

Table 3. Amino-acid composition of tryptic peptides of the α -chains.

Pept. Pos.	1p1 1-7	1p2 8-11	1p3 12-16	1p4 17-31	1p5 32-40	1p6 41-56	1p7 57-60	1p8 61	1p9 62-90	1p10 91-92	1p11 93-99	1p12 100-127	1p13 128-139	1p14 140-141	α -chain 1-141
Asp	2.99	1.03	-	2.03	-	0.96	-	-	2.86	-	2.09	1.06	1.18	-	(14) 14.16
Thr	-	0.86	0.84	-	1.96	1.02	-	-	1.06	-	-	2.96	2.01	-	(11) 10.78
Ser	0.96	-	1.06	0.94	1.06	1.03	-	-	2.97	-	-	4.19	2.75	-	(15) 14.95
Glu	-	-	-	2.05	-	0.97	-	-	2.21	-	-	2.88	-	-	(9) 8.01
Pro	-	-	-	-	0.95	0.95	-	-	1.07	-	1.02	1.99	-	-	(6) 5.88
Gly	-	-	-	0.96	-	2.78	0.95	-	2.00	-	-	-	-	-	(7) 6.98
Ala	-	-	0.98	2.92	-	-	0.98	-	4.87	-	-	1.16	-	-	(11) 10.85
Cys	-	-	-	-	-	-	-	-	-	-	-	0.96	-	-	(1) 0.96
Val	1.04	0.97	-	1.96	-	0.99	-	-	2.01	-	1.93	1.95	2.02	-	(13) 12.88
Met	-	-	-	-	1.08	-	-	-	-	-	-	-	-	-	(1) 1.06
Ile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leu	0.90	-	-	1.08	-	1.09	-	-	5.91	1.08	-	5.89	2.10	-	(18) 18.07
Tyr	-	-	-	0.96	-	0.87	-	-	-	-	-	-	-	0.98	(3) 2.91
Phe	-	-	-	-	3.08	2.12	-	-	-	-	0.95	1.01	1.06	-	(8) 8.20
His	-	-	-	1.06	-	1.97	1.07	-	3.03	-	-	2.95	-	-	(10) 10.18
Lys	0.96	0.95	1.02	-	0.97	1.03	0.99	1.00	1.47	-	0.97	0.93	0.99	-	(11) 11.08
Arg	-	-	-	1.04	-	-	-	-	-	0.97	-	-	-	0.94	(3) 2.95
Trp	-	-	0.84	-	-	-	-	-	-	-	-	-	-	-	(1) 0.78
total	7	4	5	15	9	16	4	1	29	2	7	28	12	2	

Table 4. Amino-acid composition of tryptic peptides of the β -chains.

Pept. Pos.	1p1 1-8	1p2 9-17	1p3a 18-21	1p3b 22-30	1p4a 31-39	1p4b 40	1p5 41-59	1p6+7+8 60-66	1p9 67-76	1p10 77-82	1p10+11 83-104	1p12b 117-120	1p13 121-132	1p14 133-144	1p15 145-146	β -chain 1-146
Asp	0.99	1.13	1.10	-	-	-	1.86	-	-	2.00	4.12	-	1.05	0.93	-	(14) 13.92
Thr	0.97	1.89	-	-	1.12	-	1.13	-	0.93	-	1.19	-	1.07	-	-	(8) 7.99
Ser	-	-	-	1.05	-	-	1.12	-	0.88	-	1.05	-	-	-	-	(4) 4.28
Glu	1.01	1.65	-	2.10	-	-	2.01	1.06	1.05	-	2.08	-	2.86	-	-	(13) 13.08
Pro	-	-	-	-	1.13	-	-	-	-	-	1.07	-	1.17	-	-	(3) 3.13
Gly	-	1.05	-	1.98	-	-	1.04	0.97	1.98	-	1.07	1.05	0.97	-	-	(11)
Ala	1.94	-	-	0.95	-	-	2.82	1.18	-	-	1.07	-	1.80*	4.10	-	(15) 14.83
Cys	-	-	-	-	-	-	-	-	-	-	0.93	-	-	-	-	(1) 0.96
Val	0.93	1.02	1.85	-	1.95	-	1.11	0.98	0.90	-	1.11	-	0.93	2.90	-	(17) 17.37
Met	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	(1) 0.98
Leu	0.98	1.05	-	1.98	2.16	-	1.86	0.95	1.89	2.05	3.07	-	-	1.06	-	(21) 20.99
Tyr	-	-	-	-	0.92	-	-	-	-	-	-	-	0.97	-	0.86	(3) 2.85
Phe	-	-	-	-	-	-	2.89	-	1.00	-	1.98	1.03	0.98	-	-	(8)
His	-	-	-	-	-	-	1.85	0.86	-	1.01	2.02	0.97	-	1.07	1.05	(9) 8.91
Lys	0.92	1.07	0.98	-	-	-	0.96	1.06	0.96	1.03	1.04	0.97	1.01	1.03	-	(11) 11.03
Arg	-	-	-	0.87	1.02	1.00	-	-	-	-	0.76	-	-	-	-	(5) 4.64
Trp	-	0.87	-	-	0.98	-	-	-	-	-	-	-	-	-	-	(2) 1.86
total	8	9	4	9	9	1	19	7	10	6	22	4	12	12	2	