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The Amino Acid Sequence of Canada Goose (*Branta canadensis*) and Mute Swan (*Cygnus olor*) Hemoglobins

Two Different Species with Identical β -Chains*

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Summary: The amino acid sequences of the α - and β -chains from the major hemoglobin component (HbA) of Canada goose (*Branta canadensis*) and mute swan (*Cygnus olor*) are given. The α -chains are of the α^A -type, since α^D -type was expressed but only found in low concentrations. By homologous comparison, greylag goose hemoglobin (*Anser anser*) and Canada goose hemoglobin α -chains differ by two exchanges, and β -chains by three exchanges. A valine substitution for threonine was found at position $\alpha 34$ (B15). This exchange is a result of a two point mutation. Thus, there are three nucleotide mutations in α -chains, as in β -chains. Substitutions in positions

$\alpha 34$ (B15) and $\beta 125$ (H3) have modified inter-subunit contacts ($\alpha_1\beta_1$ -contacts). A comparison of mute swan hemoglobin with greylag goose hemoglobin shows four exchanges in α -chains and three in β -chains. Canada goose and mute swan have identical β -chains, while α -chains differ in two amino acids. One of these exchanges is implicated in one of the $\alpha_1\beta_1$ -contact points ($\alpha 34$) where isoleucine substitution for valine was found. Comparison of hemoglobins from different species in the same tribe (Anserini) shows a high homology between Canada goose and mute swan hemoglobins.

Die Aminosäuresequenz der Hämoglobine von Kanadagans (Branta canadensis) und Höckerschwan (Cygnus olor): Zwei verschiedene Arten mit identischen β -Ketten

Zusammenfassung: Die Primärstrukturen der α - und β -Ketten der Hauptkomponenten (HbA) von Kanadagans (*Branta canadensis*) und Höckerschwan (*Cygnus olor*) werden angegeben. Die α -Ketten sind vom α^A -Typ, der α^D -Typ wird ebenfalls exprimiert, aber nur in geringen Konzen-

trationen nachgewiesen. Beim homologen Vergleich mit dem Hämoglobin der Graugans (*Anser anser*) findet man bei der Kanadagans in den α -Ketten zwei, in den β -Ketten drei Unterschiede. Der Austausch $\alpha 34$ (B15) Thr \rightarrow Val muß auf eine Zweipunktmutation zurückgeführt werden. Da-

Abbreviations:

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-trisulphonate; TosPheCH₂Cl = chloro-(*N*-tosyl-L-phenylalanyl)methane; BG = barheaded goose; CG = Canada goose; CH = chicken; GG = greylag goose; PH = pheasant; SW = mute swan; inositol-P₅ = inositol-1,3,4,5,6-pentaphosphate;

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her haben sowohl in den α -Ketten als auch in den β -Ketten drei Mutationen stattgefunden. In α 34 (B15) Val und β 125 (H3) Asp sind $\alpha_1\beta_1$ -Bindungsstellen verändert. Das Hämoglobin des Höckerschwans unterscheidet sich von dem der Graugans in den α -Ketten in vier, in den β -Ketten in drei Aminosäuren. Die β -Ketten von Kanadagans und Höckerschwan sind identisch. Die

α -Ketten unterscheiden sich in zwei Aminosäuren. Eine Mutation findet man mit α 34 (B15) Val \rightarrow Ile an einer $\alpha_1\beta_1$ -Bindungsstelle. Der Vergleich der Hämoglobine verschiedener Arten aus verschiedenen Gattungen der Gattungsgruppe Gänse (Anserini) ergibt die größte Homologie zwischen Kanadagans und Höckerschwan.

Key words: Hemoglobin, sequence, canada goose, mute swan.

Birds occupy an important position in biological evolution. A comparative study of the primary structure of bird hemoglobin and hemoglobin from other species is very interesting from the aspect of biochemical evolution and respiratory function. Studies of greylag goose (*Anser anser*)^[2], barheaded goose (*Anser indicus*)^[3,4] ostrich (*Struthio camelus*)^[3], chicken (*Gallus gallus*)^[5] and pheasant (*Phasianus colchicus colchicus*)^[6] hemoglobins have already been published. In this paper we report the primary structures of Canada goose and mute swan hemoglobins A.

Materials and Methods

Isolation of hemoglobin

Blood was obtained from the major leg vein of mute swan and Canada goose. Erythrocytes were separated from the plasma by centrifugation and washed 3 times with physiological saline. Hemolysate was prepared by lysing the cells with distilled water. It was analysed by electrophoresis on polyacrylamide disc gels^[7]; the results are shown in Fig. 1. Without prior separation of the hemoglobin components, globin was prepared from the whole hemolysate according to the method of Rossi-Fanelli and Antonini^[8].

Separation of the chains

The native globin was separated into α - and β -subunit chains by chromatography on CM-Cellulose in 8M urea buffers in the pH range 5.0 to 5.8^[9]. According to this method two α -chains (α^A and α^D) and one β -chain were isolated (Fig. 2). Between the two α -chains of the Canada goose an additional chain was found and degraded in the sequenator for 45 steps. The sequence was identical with the α^A -chain.

Furthermore, the polypeptide chains were resolved by polyacrylamide disc gel electrophoresis in presence of

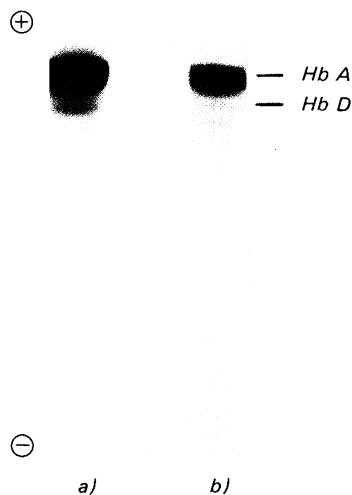


Fig. 1. Disc electrophoresis of a) Canada goose and b) mute swan hemoglobins.

urea and Triton X-100 according to Alter et al.^[10] (Fig. 3).

Modification of the protein

Oxydation was carried out with performic acid^[11], reduction with 2-mercaptoethanol and carboxymethylation with iodoacetamide^[12].

Enzymatic digestion

Tryptic peptides of native globin were obtained by digestion with TosPheCH₂Cl-treated trypsin. Digestion was carried out at pH 9 to 10 for 4 h at room temperature. The peptides were first fractionated by gel filtration on Sephadex G-25 in 0.1M acetic acid. The single peaks were subsequently chromatographed on Dowex 50X4 42 °C with pyridine buffers and linear gradients (Fig. 4).

Fig. 2. Separation of the chains from Canada goose hemoglobin on a carboxymethyl-cellulose CM-52 column (2.5 × 12 cm) at a flow rate of 40 ml/h with a linear salt gradient.

Starting buffer: 8M urea + 0.02M sodium acetate + 0.02% 2-mercaptoethanol, pH 5.6. Final buffer: starting buffer + 0.4M NaCl pH 5.6. Fraction vol. 10 ml.

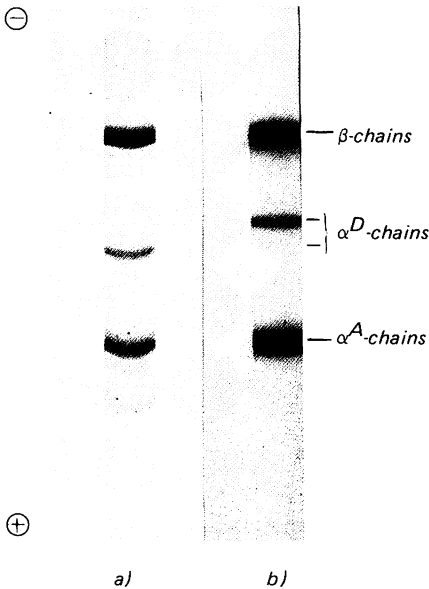
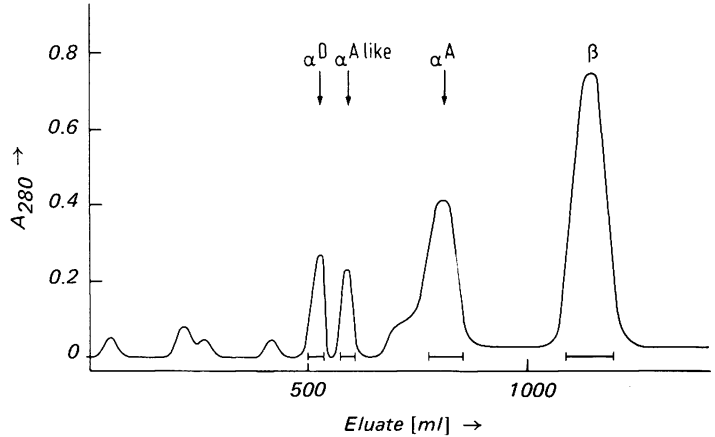


Fig. 3. Triton X-100 electrophoresis of a) Canada goose b) mute swan globins.

Asp-Pro cleavage

The cleavage of Asp-Pro bonds was carried out with 80% formic acid/6M guanidinium chloride solution at 42 °C for 60 h^[13]. The peptides were then chromatographed on a Sephadex G-50 column in 8M urea/10% formic acid.

Amino acid analysis

Samples were hydrolysed in constant boiling hydrochloric acid at 110 °C for 20 h. The analyses were performed

with a Beckman Model 121 C amino analyzer (Tables 1-5).

Sequence determination

Sequence determination was done by automatic Edman degradation^[14] in a Beckman sequencer using Quadrol^[14] and *N,N*-diethylaminopropyl^[15] programs. The Quadrol programme was applied for sequencing the intact polypeptide chains, large peptides and lysine peptides which had been reacted with reagent I or IV^[16,17]. The *N,N*-diethylaminopropyl programme was applied for sequencing arginine peptides.

Identification of phenylthiohydantoin derivatives of amino acids

The derivatives were identified by thin-layer chromatography on silica gel (E. Merck, Darmstadt) using the solvent systems of Braunitzer et al.^[18]. Some results were confirmed by high performance liquid chromatography^[19]. The results of sequence determination corroborate the data of amino acid composition of the peptides and intact chains.

Results and Discussion

Polymorphism of Canada goose and mute swan hemoglobins

The red blood cells of the birds contain multiple types of hemoglobins which vary at different stages of development and during the life cycle. The hemoglobins found in early embryonic stages are called hemoglobins E, P, P' and M, in the late embryo HbH, and in the adult bird are called HbA and HbD^[20].

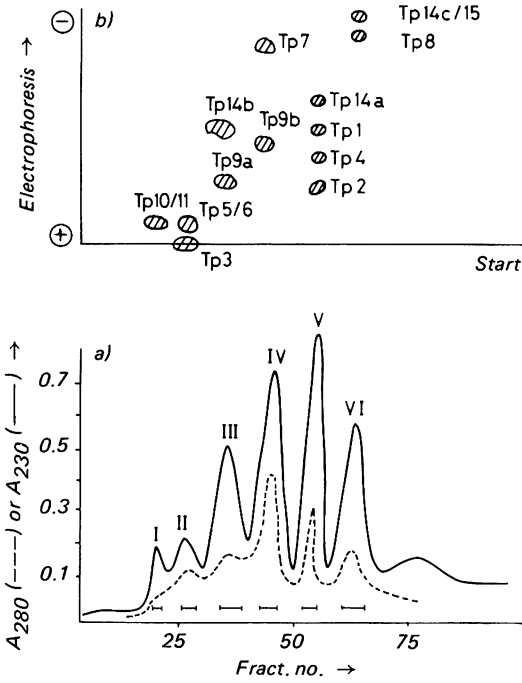


Fig. 4. a) Fractionation of β -chain soluble tryptic peptides from mute swan hemoglobin on a Sephadex G-25 (2.5 x 130 cm) at a flow rate 20 ml/h.

Buffer: 0.1M acetic acid. Fraction vol. 5 ml. b) The peptide map was obtained by high voltage electrophoresis.

Early embryonic fetal globin chains and adult globin chains are encoded by two developmentally regulated multigene families^[21,22]. The two adult hemoglobins have different α -chains (α^A and α^D) and identical β -chains^[20].

These two α -chains appear to be present in all birds, but the expression in different species differs. The α^D -gene is expressed in high levels in chicken and pheasant (about 20%) but in lower levels in geese and swan (about 5–10%). A larger difference in amino acid sequence was found between α^D - and α^A -chains of one species than between α^D -chains of different species^[6]. This indicates that these globins are products of very old gene duplication. By homologous comparison of the same type of chains from different species, α^D -chains show a high, α^A -chains a normal and β -chains a reduced evolution rate.

We have analysed the partial sequence of hemoglobin D from Canada goose, and found that this amino acid sequence is very similar to the α^D -chains of chicken and pheasant hemoglobins (Fig. 5). The β -chains in the major and minor components are identical.

Physiology of Canada goose hemoglobin

In all birds inositol- P_5 is the major allosteric effector in hemoglobin^[23,24]. The concentration

PH	Asn	Glu	Leu	Gln	Ala
CH		Glu	Leu	Gln	Ala
CG	Met-Leu-Thr-Ala-Asp-Asp-Lys-Lys-Ile-Ile-Ala-Gln-Leu-Trp-Glu-				
		5		10	15
PH	Ala	Ser	Gln	Ala	Thr
CH	Ala	Ser	Gln	Ala	Val
CG	-Lys-Val-Ala-Gly-His-Gln-Asp-Glu-Phe-Gly-Asn-Glu-Ala-Leu-Glu-				
		20		25	30
PH	Thr-Ala				
CH	Thr	Glu			
CG	-Arg-Met-Phe-Val-Thr-Tyr-Pro-Gln-Thr-Lys-Thr-Tyr				
		35		40	

Fig. 5. Sequence of α^D -chains from hemoglobin D of Canada goose. The sequence is homologously aligned with α^D -chains from pheasant^[6] and chicken HbD^[29].

Table 1. Canada goose hemoglobin, α^A -chains.
Amino acid composition of the soluble tryptic peptides.

	Tp5	Tp6	Tp7	Tp8	Tp9a	Tp9b	Tp10	Tp11	Tp14
Asx	—	1.02	—	—	2.98	1.00	—	2.01	—
Thr	1.11	0.78	—	—	—	—	—	—	—
Ser	—	1.03	—	—	0.87	0.96	—	—	—
Glx	1.00	1.99	—	—	0.95	1.02	—	—	—
Pro	0.85	0.90	—	—	—	—	—	0.72	—
Gly	—	0.99	1.00	—	0.94	—	—	—	—
Ala	1.02	1.01	1.03	—	5.29 (6)	0.98	—	—	—
Val	1.12	—	—	—	3.23	—	—	1.77	—
Ile	—	0.82	—	—	2.03	—	—	—	—
Leu	—	1.52 (1)	—	—	2.28	1.91	1.07	—	—
Tyr	0.88	0.89	—	—	—	—	—	—	0.98
Phe	0.92	1.94	—	—	—	—	—	0.87	—
Lys	1.02	1.05	1.00	1	1.37	1.07	—	0.93	—
His	—	2.03	0.97	—	1.03	1.04	—	—	—
Arg	—	—	—	—	—	—	0.93	—	1.02
Met	1.04	—	—	—	—	—	—	—	—
Cys	—	—	—	—	—	—	—	—	—
Sum.	9	16	4	1	21	8	2	7	2

Table 2. Canada goose hemoglobin, β -chains.
Amino acid composition of the soluble tryptic peptides.

	Tp5/6	Tp7	Tp8	Tp9a	Tp9b	Tp10/11	Tp14b	Tp14c/15
Asx	2.33	—	—	1.08	3.07	3.95	—	—
Thr	1.00	—	—	1.02	—	0.84	—	—
Ser	3.87	—	—	0.88	—	1.14	—	—
Glx	—	—	—	—	—	3.01	—	—
Pro	1.63	—	—	—	—	0.86	—	—
Gly	1.81	0.99	—	0.96	—	—	—	—
Ala	1.28	1.00	—	0.97	—	1.07	2.95	—
Val	1.27	—	—	1.78	—	0.87	1.16 (2)	—
Ile	1.03	—	—	—	0.92	—	—	—
Leu	2.52 (2)	—	—	1.21	1.04	3.05	1.42 (1)	—
Tyr	—	—	—	—	—	—	—	1.01
Phe	2.81	—	—	1.04	—	1.94	—	—
Lys	—	1.04	1	1.03	0.99	1.19	—	1.02
His	—	0.97	—	—	—	2.03	1.39 (1)	0.97
Arg	1.30 (1)	—	—	—	—	1.00	1.05	—
Met	0.90	—	—	—	—	—	—	—
Cys	—	—	—	—	—	1.01	—	—
Sum.	21	4	1	10	6	22	8	3

Table 3. Mute swan hemoglobin, α^A -chains.
Amino acid composition of the soluble tryptic peptides.

	Tp1	Tp2	Tp3	Tp4	Tp5	Tp6	Tp7	Tp8	Tp9a	Tp9b	Tp10	Tp11	Tp14
Asx	1.07	1.03		1.97		0.96			2.96	1.16		2.41	
Thr		0.98		1.06	1.21	0.88			1.14				
Ser	1.00		1.00			0.90			1.23	1.09			
Glx				2.02	1.15	1.93				1.17			
Pro					1.05	0.90						0.79	
Gly			0.98	2.84		1.20	1.10		1.22				
Ala	1.92			1.89	0.90	1.15	1.13		5.84	1.15			
Val	1.03	1.02	0.92						2.89			1.81	
Met					0.89								
Ile				0.94	0.93	0.86			1.81				
Leu	0.99			1.03		0.98			2.00	2.21	0.87		
Tyr				0.91	0.96	0.88							0.98
Phe			0.95		0.92	1.88						0.84	
Lys	0.97	0.98	1.14		0.98	1.22	0.90	1	1.23	1.00		0.89	
His				1.31		2.22	0.86		1.15	1.00			
Arg				1.00							1.12		1.01
Sum.	7	4	5	15	9	16	4	1	21	8	2	7	2

Table 4. Mute swan hemoglobin, β -chains.
Amino acid composition of the soluble tryptic peptides.

	Tp1	Tp2	Tp3	Tp4	Tp5/6	Tp7	Tp8	Tp9a	Tp9b	Tp10/11	Tp14a	Tp14b	Tp14c/15
Asx			2.16		2.13			1.02	2.76	3.85			
Thr	1.12	1.17		1.00	1.01			0.95		0.83			
Ser					3.78			0.89		0.97			
Glx	1.99	1.13	1.01	1.15						2.60			
Pro				1.07	2.12					0.87			
Gly		2.03	1.30		2.09	0.98		1.05					
Ala	0.99		3.89		1.26	1.07		1.05		1.25		3.26	
Val	0.95		1.74	0.78	1.06			1.81		1.28	0.96	1.48 (2)	
Met					1.06								
Ile		0.96		0.76	0.95				1.02				
Leu		2.00	1.19	2.18	2.14			1.03	1.19	2.86	1.05	1.12	
Tyr				1.02									0.83
Phe					2.99			0.93		1.73			
Lys	1.03	0.89						0.98	1.09	1.12			1.00
His	0.86						1	0.98		2.08		1.06	1.19
Arg			0.97	1.08	1.00					0.93	0.99	1.27	
Cys			0.87							1.01			
Trp	1.00	1.00		1.00									
Sum.	8	9	13	10	21	4	1	10	6	22	3	8	3

Table 5. Canada goose hemoglobin. Amino acid composition of the complete α^A - and α^D -chains and of the C-terminal peptides HP-2 after hydrolytic cleavage (Asp-Pro bond).

TH = Determination after total hydrolysis; SA = sequence determination; values in brackets indicate the differences in comparison to the graylag goose.

	α^A -Chains				β -Chains				α^D -Chains
	Complete chains		HP-2 peptide		Complete chains		HP-2 peptide		Compl. chains
	TH	SA	TH	SA	TH	SA	TH	SA	TH
Asx	11.30	11 (+ 1)	2.30	2	14.73	15 (+ 2)	4.30	4 (+ 2)	12.52
Thr	7.57	8 (-1)	2.77	3	6.47	7 (+ 1)	0.94	1	5.33
Ser	6.97	7	1.91	2	6.02	6 (-1)	-	-	6.77
Glx	9.30	9 (-1)	1.19	1	10.29	10 (-2)	3.14	3 (-2)	13.94
Pro	4.24	5	2.53	3	5.34	5	1.98	2	5.05
Gly	8.78	9	2.12	2	7.90	8	1.10	1	7.03
Ala	19.02	19	5.32	5	17.07	17	7.51	8	15.55
Val	14.65	15 (+ 1)	6.55	7	11.85	12	3.95	4	10.49
Ile	4.50	5	1.02	1	6.61	7	2.86	3	3.33
Leu	14.50	14	6.09	6	17.68	18	5.97	6	15.32
Tyr	3.75	4	1.00	1	2.20	2	1.01	1	4.31
Phe	8.07	8	3.48	4	8.14	8	3.00	3	7.18
Lys	12.00	12	3.20	3	10.13	10	3.16	3	10.29
His	9.61	10	3.52	4	7.17	7	2.69	3	6.11
Arg	2.91	3	1.00	1	5.86	6	3.05	3	3.94
Met	1.38	1	-	-	1.05	1	-	-	2.55
Cys	1.95	2	2.11	2	4.10	4	0.94	1	
Trp	-	-	-	-	2.73	3	0.85	1	
Sum.		141		47		146		47	141

of inositol- P_5 in Canada goose erythrocytes is $5.2\mu\text{M}$ ^[25], which is 20% higher than in graylag goose ($4.3\mu\text{M}$) and barheaded goose ($4.5\mu\text{M}$). In addition low levels of ATP ($0.6\mu\text{M}$) and 2,3-diphosphoglycerate ($0.3\mu\text{M}$) are present^[25]. The concentration of ATP in Canada goose erythrocytes is about 30% higher than in erythrocytes of barheaded goose and 10% higher than in graylag goose red blood cells. The $p(\text{O}_2)_{50}$ for the whole blood of Canada goose is 5.6 kPa indicating a lower oxygen affinity compared to that of the graylag goose. The $p(\text{O}_2)_{50}$ estimate for geese hemoglobin without phosphate is 0.1–0.3 kPa, but is increased in the presence of phosphate. It was found that the highest influence of phosphate is in Canada goose red blood cells. This result correlates with the high concentration of inositol- P_5 and other phosphates and also with mutations in the primary structure of

the chains. We suggest that substitution in $\alpha_1\beta_1$ -contact sites may account for higher influence of inositol- P_5 on Canada goose hemoglobin.

Table 6. Comparison of amino acid and nucleotide substitutions in the hemoglobins of graylag goose (GG), barheaded goose (BG), Canada goose (CG) and mute swan (SW).

	Amino Acid α/β	Nucleotide α/β
CG/SW	2/0	2/0
GG/BG	3/1	3/1
CG/GG	2/3	3/3
SW/GG	4/3	4/3
CG/BG	5/2	6/2
SW/BG	7/2	7/2

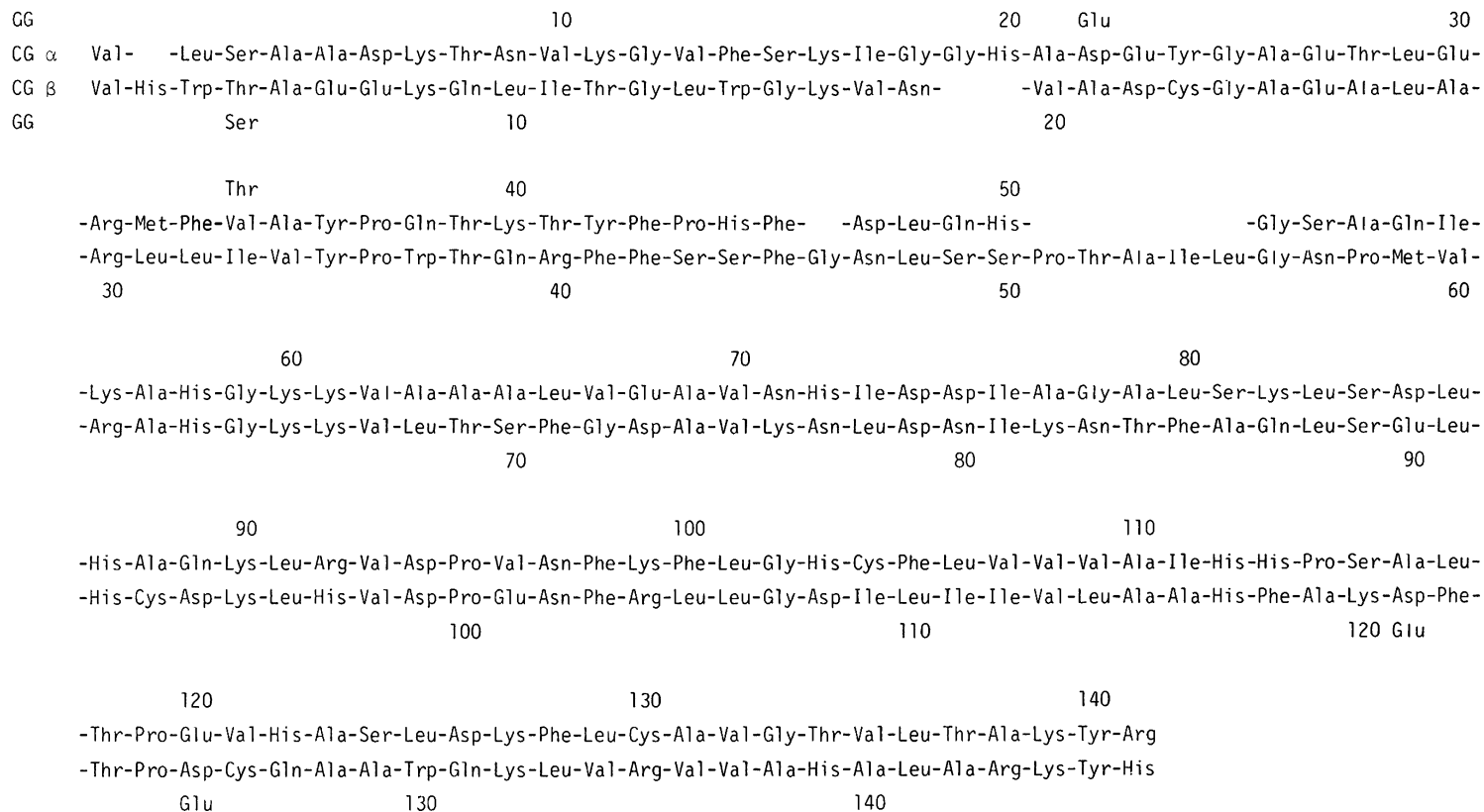


Fig. 6. Sequence of α^A - and β -chains from hemoglobin A of Canada goose. The sequence is homologously aligned with greylag goose hemoglobin^[2].

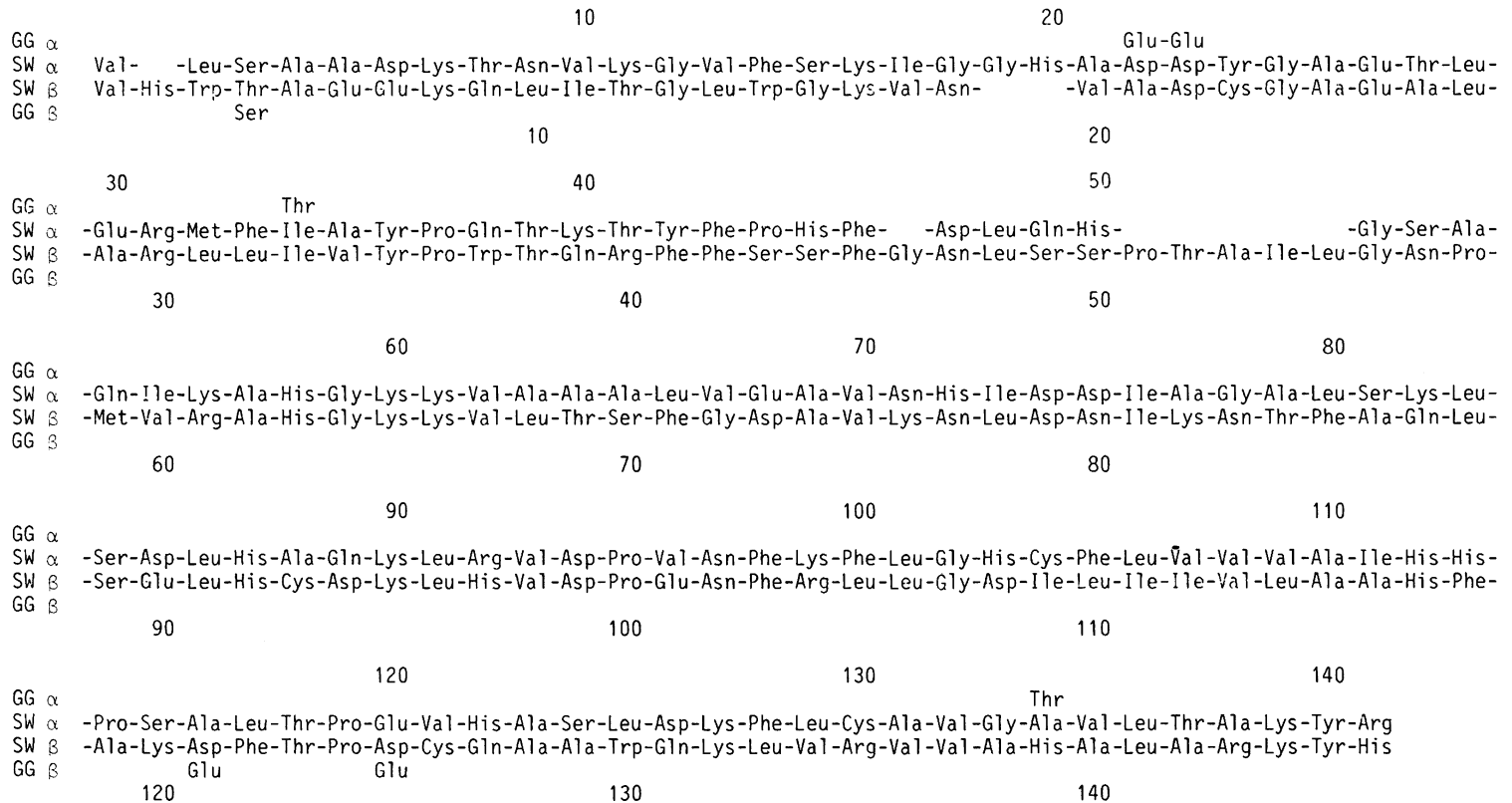


Fig. 7. Sequence of α^A - and β -chains from hemoglobin A of mute swan. The sequence is homologously aligned with greylag goose hemoglobin^[2].

Comparison of Canada goose hemoglobin with greylag goose hemoglobin shows five exchanges (Fig. 6). Two of these substitutions are in $\alpha_1\beta_1$ -contacts but only one [$\alpha 34$ (B15), Thr→Val] could make a significant contribution to the elevated influence of inositol- P_5 on Canada goose hemoglobin. Substitution at position $\beta 125$ (H3, Glu→Asp) was also found in barheaded goose hemoglobin.

Physiology of mute swan hemoglobin

Investigations on the affinity of oxygen for hemoglobin of mute swan are not reported here. Bech and Johnsen^[26] measured ventilation and gas exchange in this hemoglobin, and from their data we have estimated the $p(O_2)_{50}$ for mute swan whole blood to be 5.1 kPa. This value is lower than that reported for Canada goose and therefore indicates a higher oxygen affinity. A high concentration of inositol- P_5 or Ile-substitution for Val at position $\alpha 34$ may be responsible for elevated oxygen affinity of mute swan hemoglobin.

Classification and biology of Canada goose and mute swan

The Canada goose belongs to the genus *Branta*, the mute swan to the genus *Cygnus*. Both genera belong to the family Anatidae. The Canada goose is the most common goose in North America and gives rise to the most subspecies. They inhabit low lying areas. Mute swans inhabit Europe and middle Asia. Mute swans differ from geese in their larger size and longer necks. Of the tribe Anserini (geese) which consists of four genera, the primary structures of hemoglobins from genus *Cygnus*, *Anser* and *Branta* have already been published. Table 6 shows the lowest number of mutations between Canada goose and mute swan α - and β -chains of both species are identical. According to homologous comparison of hemoglobins, Canada goose and mute swan must be closely related, although they belong to two different tribes. This could be mean that classification from biological data should be revised or that the real genetic distance between these two species is not apparent because of their parallel evolution. A close relationship between *Cygnus* and *Branta* is also indicated by the comparative analysis of lysozymes. Most avian species possess either the

goose type or chick type of lysozyme in their egg white. In contrast, the Australian black swan (*Cygnus astratus*) and Canada goose have mixture of both types of lysozymes^[27,28].

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Stichwortregister

- Acetonitrile**, purification for high performance liquid chromatography, G. Braunitzer, P. Rücknagel and W. Oberthür, 485
- 9(8)-O-Acetylated sialic acids**, fluorimetric determination, A.K. Shukla and R. Schauer, 255
- Acetyl-CoA**, enzymatic preparation of (3*S*)-citryl-CoA, G. Löhlein and H. Eggerer, 1103
- N*-Acetylgalactosaminol**, paper chromatography, M.-L. Rasilo and O. Renkonen, 89
- N*-Acetylglucosamine-1-phosphotransferase**, mucopolidosis III. A. Waheed, A. Hasilik, M. Cantz and K.v. Figura, 169
- β -*N*-Acetyl-D-glucosaminidase (EC 3.2.1.30)**, inactivation by nonenzymatic glucosylation, R. Dolhofer, E. A. Siess and O.H. Wieland, 1427
- N*-Acetylglucosaminol**, paper chromatography, M.-L. Rasilo and O. Renkonen, 89
- Acetylruthenocene**, steroid hormones, M. Wenzel, G. Schachschneider, M. Schneider and R. Herken, 693
- Acinar cells (human)**, localization of kallikrein, M. Amouric, P. Lechene de la Porte and C. Figarella, 515
- 4-(9-Acridinylamino)aniline**, interaction with DNA, J.-P. Hélichart, J.-L. Bernier and J.-P. Catteau, 835
- Acrosin (EC 3.4.21.10) (boar)**, two active forms, B. Železná and D. Čechová, 757
- Active site**, hemocyanins, H.-J. Schneider, U. Illig, E. Müller, B. Linzen, F. Lottspeich and A. Henschen, 487
- Acylation**, s. deacylation, transacylation
- Acylchymotrypsin**, nucleophilic deacylation, V. Kasche and R. Zöllner, 531
- Adenosinetriphosphate**, arginyl-tRNA synthetase, E. Gerlo, W. Freist and J. Charlier, 365
- Adenosinetriphosphate analogues**, arginyl-tRNA synthetase, E. Gerlo, W. Freist and J. Charlier, 365
- , reaction with phenylalanyl-tRNA synthetase, H. J. Gabius, W. Freist and F. Cramer, 1241
- Adenosinetriphosphatases**, comparative aspects, 38th Conference of the Gesellschaft für Biologische Chemie 459
- Adenylate**, s. polyadenylate, polyadenylation
- Adenylate cyclase (EC 4.6.1.1)**, prostaglandin E₁ action, J. Mruk, A. Bakardjiev and W. Burgermeister, 745
- Adipocytes (rat, isolated)**, glucose uptake effected by guanidino derivatives, G. Weitzel and A. Hadjianghelu, 45
- (epididymal of rats), insulin analogues, C. Diaconescu, D. Saunders, H.-G. Gattner and D. Brandenburg, 187
- ADP/ATP carrier (beef heart mitochondria)** amino acid sequence, H. Aquila, D. Misra, M. Eulitz and M. Klingenberg, 345
- Adrenal gland**, cortisol, J. Voigt and C. E. Sekeris, 159
- Adsorbents**, improved adsorbents for affinity chromatography of aminopeptidases, K.-H. Röhm, 641
- Affinity chromatography**, s.a. immunoaffinity chromatography
- , aminopeptidases, K.-H. Röhm, 641
- , sialidase from human liver, J.-C. Michalski, A.P. Corfield and R. Schauer, 1097
- Affinity labelling**, vasopressin analogs, F. Fahrenholz, H.S. Hussein, J.L. Morgat and K.-H. Thierauch, 1415
- Age**, regulation in lipogenesis, M. Boll, E. Brückner and J. Berndt, 103
- Aggregation (of cells)**, s. cell adhesion
- Agmatine**, glucose uptake, G. Weitzel and A. Hadjianghelu, 45
- Alanine aminopeptidase (human leukocytes)**, separation from other leukocyte enzymes, S. Engelbrecht, E. Pieper, H.W. Macartney, W. Rautenberg, H.R. Wenzel and H. Tschesche, 305
- Alkaline phosphatase (EC 3.1.3.1)**, retinoic acid binding, B. Gmeiner and G. Zerlauth, 337
- 1-Alkenyl-*sn*-glycero-3-phosphoethanolamine**, glial cells, H.K. Illig, B. Witter, J. Gunawan, P. Ahrens and H. Debuch, 709
- Alloantigens**, induced lymphocyte proliferation, D. Fuchs, A. Hausen, C. Huber, R. Margreiter, G. Reibnegger, M. Spielberger and H. Wachter, 661
- , partial amino acid sequence, C. Yang, H. Kratzin, H. Götz, F.P. Thinnes, T. Kruse, G. Egert, E. Pauly, S. Kölbl, P. Wernet and N. Hilschmann, 671
- Allergy**, serine protease inhibitors, M. Muramatu, T. Satoh, Y. Yanagimoto, Y. Kanamoto, I. Katsuyama, M. Kanamoto and K. Taguchi, 203
- Amadori compounds**, *N*^α-glycosylgastrin, A. Previero, G. Mourier, J.-P. Bali, M.F. Lignon and L. Moroder, 813

- Amatoxin**, amatoxin-binding protein, O.G. Brodner, M. Salbagh and T. Wieland, 273
- Ambiquitous enzymes**, membrane-bound hexokinase, P.A. Lazo and L. Bosca, 635
- Amino acids**, s.a. aromatic-amino-acid aminotransferase, Boc-amino acid derivatives
- , fermentation by *Clostridium sporogenes*, C. Pitsch and H. Simon, 1253
- Amino acid sequence**, hemoglobins of *Equus hemionus kulan* (asiatic wild ass) and *Equus zebra* (mountain zebra), G. Mazur and G. Braunitzer, 59
- (partial), human urokinase, W.A. Günzler, G.J. Steffens, F. Ötting, G. Buse and L. Flohé, 133
 - , pheasant hemoglobin, G. Braunitzer and J. Godovac, 229
 - , armadillo hemoglobin α -chain, T. Kleinschmidt, W.W. de Jong and G. Braunitzer, 239
 - , ADP/ATP carrier from beef heart mitochondria, H. Aquila, D. Misra, M. Eulitz and M. Klingenberg, 345
 - , similarities among biologically active peptides, H. Jörnvall, V. Mutt and M. Persson, 475
 - , hemoglobin of *Anser indicus* (bar-headed goose), W. Oberthür, G. Braunitzer and I. Würdinger, 581
 - , histocompatibility antigen, C. Yang, H. Kratzin, H. Götz, F.P. Thinnies, T. Kruse, G. Egert, E. Pauly, S. Kölbl, P. Wernet and N. Hilschmann, 671
 - , hemoglobin of the indian elephant, G. Braunitzer, W. Jelkmann, A. Stangl, B. Schrank and C. Krombach, 683
 - , contact site A glycoprotein of *Dictyostelium discoideum* (N-terminus), J. Stadler, C. Bordier, F. Lottspeich, A. Hensch and G. Gerisch, 771
 - , hemoglobins of Canada goose and mute swan, W. Oberthür, J. Godovac-Zimmermann, G. Braunitzer and H. Wiesner, 777
 - , hemoglobins of sheep and goat, T. Kleinschmidt and G. Braunitzer, 789
 - , C-terminal region of a brain proteolipid apoprotein, W. Stoffel, H. Hillen, W. Schroeder and R. Deutzmann, 855
 - , low-molecular mass urokinase from human urine, G.J. Steffens, W.A. Günzler, F. Ötting, E. Frankus and L. Flohé, 1043
 - , anti-streptococcal group A polysaccharide antibody light chain, H. Herbst, J.Y. Chang, R. Aebersold and D.G. Braun, 1069
 - , hemoglobin from a rhinoceros, G. Mazur, G. Braunitzer and P.G. Wright, 1077
 - , protein CM-2 from *Bitis arietans* venom, F. J. Joubert, T. Haylett, D.J. Strydom and N. Taljaard, 1087
 - , proteolytic fragments of a proteolipid apoprotein, W. Stoffel, W. Schröder, H. Hillen and R. Deutzmann, 1117
 - , polypeptide VI a of cytochrome *c* oxidase, R. Biewald and G. Buse, 1141
 - , A chain of high-molecular mass urokinase from human urine, W.A. Günzler, G.J. Steffens, F. Ötting, S.-M.A. Kim, E. Frankus and L. Flohé, 1155
 - , hemoglobin of the egyptian fruit bat (*Rousettus aegyptiacus*), T. Kleinschmidt and G. Braunitzer, 1209
 - , L-1 light chain of chicken fast skeletal muscle myosin, T. Umegane, T. Maita and G. Matsuda, 1321
 - , variable part of Bence-Jones protein Mev., M. Eulitz and R. P. Linke, 1347
 - , proteolytic fragments of a brain proteolipid apoprotein, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- Aminoacyl-tRNA synthetases**, s. arginyl-tRNA synthetase, phenylalanyl-tRNA synthetase
- ϵ -Aminocaproic acid**, inhibits carboxypeptidase N, L. Juillerat-Jeanneret, M. Roth and J.-P. Bargetzi, 51
- 5-Aminolaevulinate**, biosynthesis, O. Klein and R. J. Porra, 551
- Aminopeptidases**, s.a. alanine aminopeptidase
- , ϵ -peptide bond, A. Plessing, G. Siebert, J.H. Wissler, A. J. Puigserver and P. Pfaender, 279
 - , improved affinity chromatography, K.-H. Röhm, 641
- Amino-protecting groups**, peptide synthesis, E. Wünsch, L. Moroder, R. Nyfeler and E. Jaeger, 197
- [1,6- α -Aminosuberic acid, 8-arginine]vasopressin**, synthesis of the tritium-labelled, reactive compound, F. Fahrenholz, H.S. Husseini, J. L. Morgat and K.-H. Thierrauch, 1415
- Aromatic-amino-acid aminotransferase (EC 2.6.1.57)**, chloramphenicol-resistant flavobacteria, H.G. Beschle, R. Süßmuth and F. Lingens, 1365
- Aniline**, s. 4-(9-acridinylamino)aniline
- Anionic protease**, *Thermoactinomyces vulgaris*, R. Kleine and U. Kettmann, 843
- Anser indicus*** (bar-headed goose), amino acid sequence of hemoglobin, W. Oberthür, G. Braunitzer and I. Würdinger, 581
- Anthranilic acid**, s. 5-hydroxyanthranilic acid
- Antiallergic effects**, serine-protease inhibitors, M. Muramatu, T. Satoh, Y. Yanagimoto, Y. Kanamoto, I. Katsuyama, M. Kanamoto and K. Taguchi, 203
- Antibody** (monoclonal), contact site A glycoprotein, J. Stadler, C. Bordier, F. Lottspeich, A. Hensch and G. Gerisch, 771

- (anti-streptococcal group A polysaccharide antibody light chain), amino acid sequence, H. Herbst, J. Y. Chang, R. Aebersold and D.G. Braun, 1069
- Antibody production**, "facteur thymique serique", G. Auger, D. Blanot, E. Bricas, J.-M. Pléau, M. Dardenne and J.-F. Bach, 331
- Antigenicity**, in normal and malignant cells, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 894
- Antigens**, s.a. alloantigens, histocompatibility antigens, HLA-D antigen, SV40 T-antigen
 - , zona pellucida, J. Dietl, A. Czuppon and L. Mettler, 381
 - , synthetic spermatozoal antigen, A. B. Czuppon and L. Mettler, 1465
- Antiserum**, detection of toxin T-2, H. Peters, M.P. Dierich and K. Dose, 1437
- Anti-streptococcal group A polysaccharide antibody light chain**, amino acid sequence, H. Herbst, J. Y. Chang, R. Aebersold and D.G. Braun, 1069
- Apoprotein** (of a proteolipid from bovine brain), amino acid sequence of a C-terminal fragment, W. Stoffel, H. Hillen, W. Schroeder and R. Deutzmann, 855
 - , amino acid sequence of proteolytic fragments, W. Stoffel, W. Schröder, H. Hillen and R. Deutzmann, 1117
 - , partial amino acid sequence, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- Aprotinin**, soluble carrier, M. Havranová, D. Čechová, V. Saudek, M. Metalová and J. Drobník, 295
- Arginine carboxypeptidase (EC 3.4.17.3)**, properties, L. Juillerat-Jeanneret, M. Roth and J.-P. Bargetzi, 51
- Arginine acid**, inhibits carboxypeptidase N, L. Juillerat-Jeanneret, M. Roth and J.-P. Bargetzi, 51
- Arginyl bonds**, cleavage, R. Biewald and G. Buse, 1141
- Arginyl-tRNA synthetase (EC 6.1.1.19)** (from *E. coli*), specificity with regard to ATP analogues, E. Gerlo, W. Freist and J. Charlier, 365
- Armadillo**, s. *Dasybus novemcinctus*
- Arthropods**, hemocyanins, H.-J. Schneider, U. Illig, E. Müller, B. Linzen, F. Lottspeich and A. Henschen, 487
- Aryl trans-4-(aminomethyl)cyclohexanecarboxylate and aryl trans-4-(guanidinomethyl)cyclohexanecarboxylate**, serine-protease inhibitors, M. Muramatu, T. Satoh, Y. Yanagimoto, Y. Kanamoto, I. Katsuyama, M. Kanamoto and K. Taguchi, 203
- Arylsulfatase A (EC 3.1.6.1)**, synthesis and processing, A. Waheed, A. Hasilik and K.v. Figura, 425
- Ascites tumor cells**, membrane-bound hexokinase, P.A. Lazo and L. Bosca, 635
- Asparagine derivatives**, soluble carrier polymers, M. Havranová, D. Čechová, V. Saudek, M. Metalová and J. Drobník, 295
- Aspartic proteinases**, autolysis studies, T. Lah and V. Turk, 247
- Ass** (asiatic wild ass), s. *Equus hemionus kulan*
- Assembly**, 50S ribosomal subunits, R. Röhl, H.E. Roth and K.H. Nierhaus, 143
- Association**, s. cell association
- ATP** s. adenosinetriphosphate
- ATP analogues**, s. adenosinetriphosphate analogues
- Autolysis**, cathepsin D, T. Lah and V. Turk, 247
- Azido-labelling**, lipids, W. Stoffel, K.-P. Salm and M. Müller, 1
 - , lipids in HDL, W. Stoffel and P. Metz, 19
- Azodicarboxylic acid derivatives**, disulfide synthesis, E. Wünsch and S. Romani, 449
- Bacteriochlorophyll**, biosynthesis, O. Klein and R. J. Porra, 551
- Bat** (egyptian fruit bat) s. *Rousettus aegyptiacus*
- Bence-Jones protein Mev** (amyloidogenic), amino acid sequence, M. Eulitz and R.P. Linke, 1347
- Bestatin**, affinity chromatography of aminopeptidases, K.-H. Röhm, 641
- Binding parameters**, 4-(9-acridinylamino)aniline and DNA, J.-P. Hélichart, J.-L. Bernier and J.-P. Catteau, 835
- Binding region**, between polysaccharide and core protein, T. Stein, R. Keller, H.W. Stuhlsatz, H. Greiling, E. Ohlst, E. Müller and H.-D. Scharf, 825
- Binding sites**, plasma lipoproteins, E. Koller, F. Koller and W. Doleschel, 395
- Biocompatible derivatives**, trypsin-kallikrein inhibitor, M. Havranová, D. Čechová, V. Saudek, M. Metalová and J. Drobník, 295
- Bioenergetics** (molecular), aspects, 43rd Conference of the Gesellschaft für Biologische Chemie, 535
- Biological clock**, and cycles, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 952
- Biopterin**, s. dihydrobiopterin, tetrahydrobiopterin
- Bis(monoacylglycero)phosphate**, chloroquine effect, G. Pakalapati and H. Debuch, 573
- 2,3-Bisphosphoglycerat**, hemoglobin, G. Braunitzer, W. Jelkmann, A. Stangl, B. Schrank and C. Krombach, 683
- Bitis arietans** (puff adder), amino acid sequence of protein CM-2, F. J. Joubert, T. Haylett, D.J. Strydom and N. Taljaard, 1087
- Blood** (dog), excretion of tissue kallikrein from blood into urine, E. Fink and M. Schleuning, 1331
- Blood coagulation**, separation of fibrinogen chains, M. Kehl, F. Lottspeich and A. Henschen, 1501

- Blood platelets**, s. thrombocytes
- Blood pressure** (rat), tissue kallikrein, L. Schack and T. Dietl, 107
- Blot hybridization**, demonstration of SV40 gene fragment, J. Horst, E. Jacob, C. Weckler and W. Deppert, 445
- B-Lymphocytes**, mitogenicity, W.G. Bessler, R.B. Johnson, K. Wiesmüller and G. Jung, 767
- Boc-Amino acid derivatives**, liquid-phase peptide synthesis, B. Hemmasi, W. Stüber and E. Bayer, 701
- Bone marrow cells** (human, murine), colony-stimulating factors, R. Neumeier, H.R. Maurer, M. Arnold, U. Gerlach, K. Glendinning, H. Renner and J.H. Wissler, 193
- Bradykinin**, high performance liquid chromatography, R. Geiger, R. Hell and H. Fritz, 527
- , rat uterus homogenates, M. Marin-Grez, G. Schaechtelin and K. Hermann, 1359
- Brain** (bovine), proteolipid apoprotein from myelin, W. Stoffel, H. Hillen, W. Schroeder and R. Deutzmann, 855
- , –, W. Stoffel, W. Schröder, H. Hillen and R. Deutzmann, 1117
- , –, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- , structural similarities among biologically active peptides, H. Jörnvall, V. Muttand M. Persson, 475
- Branta canadensis** (canada goose), amino acid sequence of hemoglobin, W. Oberthür, J. Godovac-Zimmermann, G. Braunitzer and H. Wiesner, 777
- (tert-Butyldithio)carbonyl**, amino-protecting group, E. Wünsch, L. Moroder, R. Nyfeler and E. Jaeger, 197
- S-tert-Butylthio group**, introduction into cysteine and cysteine derivatives, E. Wünsch, L. Moroder and S. Romani, 1461
- Calcium ions**, coagulation factors IX and X, J. Kárpáti, K. Váradi and S. Elödi, 521
- Cancer**, s. teratocarcinoma cells (human)
- Capra aegagrus** (goat), amino acid sequence of hemoglobin, T. Kleinschmidt and G. Braunitzer, 789
- Captopril**, kininase II inhibition, L. Schack and T. Dietl, 107
- Carboxylic acids**, s. azidocarboxylic acid derivatives
- 6-(Carboxymethoxymino)-2-methoxy-1,3,5(10)-estratriene-3,17 β -diol**, synthesis, D. Berg, H.-H. Warnecke and E. Kuss, 737
- 6-(Carboxymethoxymino)-3-hydroxy-2-methoxy-1,3,5(10)-estratrien-17-one**, synthesis, D. Berg, H.-H. Warnecke and E. Kuss, 737
- Carboxypeptidase N**, s. arginine carboxypeptidase
- Carcinoma**, s. teratocarcinoma cells (human)
- Carcinus maenas** (crab), ecdysteroids, F. Lachaise and J.A. Hoffmann, 1059
- Carrier** (soluble), trypsin-kallikrein inhibitor, M. Havranová, D. Čechová, V. Saudek, M. Metalová and J. Drobník, 295
- (ADP/ATP carrier from mitochondria), amino acid sequence, H. Aquila, D. Misra, M. Eulitz and M. Klingenberg, 345
- Catecholestrogens**, immunogenicity, D. Berg, H.-H. Warnecke and E. Kuss, 737
- Cathepsin D (EC 3.4.23.5)**, autolysis studies, T. Lah and V. Turk, 247
- , fibronectin fragments, H. Richter and H. Hörmann, 351
- Cathepsin G (EC 3.4.21.20)**, separation from other leukocyte enzymes, S. Engelbrecht, E. Pieper, H.W. Macartney, W. Rautenberg, H.R. Wenzel and H. Tschesche, 305
- Cationic protease**, *Thermoactinomyces vulgaris*, R. Kleine and U. Kettmann, 843
- Cations** (divalent), effect on 3-hydroxy-3-methylglutaryl-CoA reductase, G. Gil, V.E. Calvet, A. Ferrer and F.G. Hegardt, 1217
- Cell adhesion**, contact site A glycoprotein of *Dictyostelium discoideum*, J. Stadler, C. Bordier, F. Lottspeich, A. Henschen and G. Gerisch, 771
- Cell association**, gangliosides, K. Radsak, G. Schwarzmann and H. Wiegandt, 263
- Cell culture**, s. primary culture
- Cell heterogeneity**, rat liver, W. Fischer, M. Ick and N.R. Katz, 375
- Cell to cell contact**, s. cell adhesion, cell association
- Cell surface**, seminal and colostrum protease inhibitors, L. Veselsky, D. Čechová, V. Hruban and J. Klaudy, 113
- Cellular compartments**, RNA labelling, C. Scholtissek, D. Evans and H. Bürger, 1389
- Cell wall** (bacterial), mitogenic activity, W.G. Bessler, R.B. Johnson, K. Wiesmüller and G. Jung, 767
- Ceratotherium simum**, (white rhinoceros), amino acid sequence of hemoglobin, G. Mazur, G. Braunitzer and P.G. Wright, 1077
- Chelators**, iron (II) ions, H. Nohl, W. Jordan and D. Hegner, 599
- Chicken**, amino acid sequence of L-1 light chain of fast skeletal muscle myosin, T. Umegane, T. Maita and G. Matsuda, 1321
- Chloramine-T iodination**, glucagon, O. Sonne, U.D. Larsen and J. Markussen, 95
- Chloramphenicol**, degradation, H.G. Beschle, R. Süßmuth and F. Lingens, 439
- , resistant flavobacteria, H.G. Beschle, R. Süßmuth and F. Lingens, 1365
- Chlorohydroxyphenylacetic acids**, syntheses, A. Markus, U. Klages and F. Lingens, 431

- Chlorophyll**, s.a. bacteriochlorophyll
 –, biosynthesis, O. Klein and R. J. Porra, 551
- Chloroquine**, fatty acid liberation, G. Pakalapati and H. Debuch, 573
 –, phospholipids of lysosomes, A. Harder and H. Debuch, 717
- Cholamic acid**, s. oxocholanic acid
- Cholesterol**, azido fatty acid-substituted, W. Stoffel, K.-P. Salm and M. Müller, 1
 –, 3-hydroxy-3-methylglutaryl-CoA reductase, H.-S. Jenke, M. Löwel and J. Berndt, 725
- Chondroitin sulfate oligosaccharides**, β -D-glucuronidase, R. Niemann and E. Buddecke, 591
- Chromatography**, s. affinity chromatography, high-performance liquid chromatography, immuno-affinity chromatography, reversed-phase high-pressure liquid chromatography
 –, controlled pore glass, R. Kleine and U. Kettmann, 843
- Chromosomes**, structure and function, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 922
- Chymotrypsin (EC 3.4.21.1)**, s.a. acyl-chymotrypsin
 –, synthetic inhibitors, M. Muramatu, T. Satoh, Y. Yanagimoto, Y. Kanamoto, I. Katsuyama, M. Kanemoto and K. Taguchi, 203
 –, inhibitor in skeletal muscle, M. Dudai, M. Mayer and M. Kidron, 651
- Chymotrypsinogen A**, interaction with human α_1 -protease inhibitor, H. Löbermann, F. Lottspeich, W. Bode and R. Huber, 1377
- Cigarette smoke**, α_1 -proteinase inhibitor, R. A. Stockley, S. C. Afford and D. Burnett, 387
- Circular dichroism**, autolysis studies of proteinases, T. Lah and V. Turk, 247
- Citraconylation**, insulin, V. K. Naithani and H. G. Gattner, 1443
- (3S)-Citryl-CoA**, enzymatic preparation, G. Löhlein and H. Eggerer, 1103
- Clearance**, s. renal clearance
- Cloning**, SV40 gene fragment, J. Horst, E. Jacob, C. Weckler and W. Deppert, 445
- Clostridium barkeri***, 2,3-dimethylmalate lyase, G. Löhlein and H. Eggerer, 1103
- Clostridium sporogenes***, amino acid fermentation, C. Pitsch and H. Simon, 1253
- Coagulation factors IX and X (EC 3.4.21.22 and EC 3.4.21.6)**, granulocyte proteases, J. Kárpáti, K. Váradi and S. Elödi, 521
- Coenzyme A**, s. acetyl-CoA, (3S)-citryl-CoA, propionyl-CoA
- Collagenase (EC 3.4.24.7)**, separation from other leukocyte enzymes, S. Engelbrecht, E. Pieper, H. W. Macartney, W. Rautenberg, H. R. Wenzel and H. Tschesche, 305
- Colony-stimulating factors** (porcine), identification, R. Neumeier, H. R. Maurer, M. Arnold, U. Gerlach, K. Glendinning, H. Renner and J. H. Wissler, 193
 – (bovine), isolation from bovine lung conditioned medium, R. Neumeier and H. R. Maurer, 1493
- Colostrum protease inhibitors**, on leukocytes, L. Veselský, D. Čechová, V. Hruban and J. Klauudy, 113
- Compartmentation**, RNA labelling, C. Scholtissek, D. Evans and H. Bürger, 1389
- Computer averaging**, electron microscopy, H. J. Schramm and W. Schramm, 803
- Conformational adjustment**, insulin, D. Saunders and K. Freude, 655
- Conformational changes**, membrane-bound hexokinase, P. A. Lazo and L. Bosca, 635
- Contact (cell to cell)**, s. cell adhesion, cell association
- Contact site A glycoprotein (*Dictyostelium discoideum*)**, amino acid sequence of N-terminus, J. Stadler, C. Bordier, F. Lottspeich, A. Henschen and G. Gerisch, 771
- Controlled pore glass**, s. pore glass (controlled)
- Copper protein complex**, hemocyanins, H.-J. Schneider, U. Illig, E. Müller, B. Linzen, F. Lottspeich and A. Henschen, 487
- Core protein**, linkage region between polysaccharide and protein, T. Stein, R. Keller, H. W. Stuhlsatz, H. Greiling, E. Ohlst, E. Müller and H.-D. Scharf, 825
- Cornea** (bovine), proteokeratan sulfate, T. Stein, R. Keller, H. W. Stuhlsatz, H. Greiling, E. Ohlst, E. Müller and H.-D. Scharf, 825
- Cortisol**, adrenal gland, J. Voigt and C. E. Sekeris, 159
- C₅ Pathway**, biosynthesis of chlorophyll, O. Klein and R. J. Porra, 551
- Crab**, s. *Carcinus maenas*
- Crayfish**, s. *Orconectes limosus*
- Crosslinking** (photochemical), in liposomes, W. Stoffel, K.-P. Salm and M. Müller, 1
 –, azido-labelled lipids in HDL, W. Stoffel and P. Metz, 19
 –, insulin, A. Schüttler and D. Brandenburg, 317
 –, fibronectin, H. Richter and H. Hörmann, 351
 –, insulin analogues, D. Saunders and K. Freude, 655
- Cyanogen bromide fragments**, distribution of crosslinks, W. Stoffel and P. Metz, 19
 –, proteolipid apoprotein, W. Stoffel, H. Hillen, W. Schroeder and R. Deutzmann, 855
- (Cyclohexyldithio)carbonyl**, amino-protecting group, E. Wünsch, L. Moroder, R. Nyfeler and E. Jaeger, 197
- Cyclovoltograms**, electron transport, P. Egerer, M. Bühler and H. Simon, 627

- Cygnus olor* (mute swan), amino acid sequence of hemoglobin, W. Oberthür, J. Godovac-Zimmermann, G. Braunitzer and H. Wiesner, 777
- Cysteine and cysteine derivatives**, introduction of the *S*-tert-butylthio protecting group, E. Wünsch, L. Moroder and S. Romani, 1461
- α -Cysteine proteinase inhibitor, assay, K. Minakata, M. Asano, T. Sato and N. Harada, 493
- Cystine peptides**, new method for synthesis, E. Wünsch and S. Romani, 449
- Cytochemical localization**, s. immunocytochemical localization
- Cytochrome *c* oxidase (EC 1.9.3.1)**, tissue specificity vs. species specificity, J. Jarausch and B. Kadenbach, 1133
- , amino acid sequence of polypeptide VIa, R. Biewald and G. Buse, 1141
- Cytochrome P-450**, hydroxylations, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 971
- Cytoplasm** (rat liver), cortisol-binding proteins, J. Voigt and C.E. Sekeris, 159
- (hen liver), phenylalanyl-tRNA synthetase, H.-J. Gabius, W. Freist and F. Cramer, 1241
- (chick embryo), compartmentation of influence on RNA labelling, C. Scholtissek, D. Evans and H. Bürger, 1389
- (yeast and hen liver), phenylalanyl-tRNA synthetase compared to that from mitochondria, H.J. Gabius and F. Cramer, 1473
- Cytoskeleton**, polyribosomes, P. Traub and W.J. Nelson, 1177
- Dansyl-Edman degradation**, uremic toxins, G. Bovermann, H. Rautenstrauch, G. Seybold and G. Jung, 1187
- Dasyus novemcinctus* (armadillo), amino-acid sequence of hemoglobin α -chains, G. Braunitzer and J. Godovac, 239
- Deacylation** (nucleophilic), acyl-chymotrypsin, V. Kasche and R. Zöllner, 531
- Decapeptide**, spermatozoal antigen, A.B. Czuppon and L. Mettler, 1465
- Density gradient media**, iodination, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 999
- Deoxyribonucleic acid**, intercalating reagent, J.-P. Hélichart, J.-L. Bernier and J.-P. Catteau, 835
- Dephosphorylation**, retinoic acid binding in tumor cytosol, B. Gmeiner and G. Zerlauth, 337
- Diabetes**, mutant insulins, C. Diaconescu, D. Saunders, H.-G. Gattner and D. Brandenburg, 187
- Dictyostelium discoideum*, contact site A glycoprotein J. Stadler, C. Bordier, F. Lottspeich, A. Henschen and G. Gerisch, 771
- Diet**, effect of lipids on 3-hydroxy-3-methylglutaryl-CoA reductase, H.-S. Jenke, M. Löwel and J. Berndt, 725
- Dietary regulation**, lipogenic enzymes, M. Boll E. Brückner and J. Berndt, 103
- Differentiation**, s.a. embryonic development
- , morphogenesis, 33. Mosbacher Kolloquium der Gesellschaft für Biologische Chemie, 119
- , promyelocytes, M. Kidron, D.B. Friedman, M. Mayer, Y. Klemes and E. Fibach, 865
- Dihydrobiopterin**, determination, M. Bräutigam, R. Dreesen and H. Herken, 341
- 3,5-Diiodosalicylate**, solubilization of antigens, J. Dietl, A. Czuppon and L. Mettler, 381
- 3,4-Dimethoxyphenylacetic acid**, degradation, B. Hauer, K. Haase-Aschoff and F. Lingens, 499
- (2R, 3S)-2,3-Dimethylmalate-lyase reaction**, stereochemical course, G. Löhlein and H. Eggerer, 1103
- Dimethylsulfoxid**, proteolytic activity in promyelocytes, M. Kidron, D.B. Friedman, M. Mayer, Y. Klemes and E. Fibach, 865
- Disulfide bonds**, fibronectin, H. Richter and H. Hörmann, 351
- Disulfide bridges**, cleavage by sulfite, M. Schleyer, H. Etzrodt, T. J. Trah and K.-H. Voigt, 1111
- Disulfides** (unsymmetrical), selective synthesis, E. Wünsch and S. Romani, 449
- Dithiothreitol**, somatotropin activity, M. Schleyer, H. Etzrodt, T. J. Trah, and K.-H. Voigt, 1111
- DNA restriction**, SV40 gene, J. Horst, E. Jacob, C. Weckler and W. Deppert, 445
- Drug disposition**, steroid hormones, M. Wenzel, G. Schachschneider, M. Schneider and R. Herken, 693
- Ecdysteroid receptors**, crayfish, M. Londershausen, P. Kuppert and K.-D. Spindler, 797
- Ecdysteroids**, shore crab (*Carcinus maenas*), F. Lachaise and J.A. Hoffmann, 1059
- Eglin**, elastase, W. Hornebeck and H.P. Schnebli, 455
- Ehrlich ascites tumor cells**, cytoskeleton, P. Traub and W.J. Nelson, 1177
- Elastase (EC 3.4.21.37)** (human leukocytes), separation from other leukocyte enzymes, S. Engelbrecht, E. Pieper, H.W. Macartney, W. Rautenberg, H.R. Wenzel and H. Tschesche, 305
- (human leukocytes), elastin, W. Hornebeck and H.P. Schnebli, 455
- Elastin**, elastase, W. Hornebeck and H.P. Schnebli, 455

- Electrochemical detection**, reduced bipterins, M. Bräutigam, R. Dreesen and H. Herken, 341
 –, tetrahydrobiopterin, M. Bräutigam and R. Dreesen, 1203
- Electron microscopy**, computer averaging, H. J. Schramm and W. Schramm, 803
- Electron spin resonance**, interaction of 4-(9-acridinyl-amino)aniline with DNA, J.-P. Hélichart, J.-L. Bernier and J.-P. Cateau, 835
- Electron transport particles**, rhein, P. Egerer, M. Bühler and H. Simon, 627
- Electrophoresis**, α_1 -proteinase inhibitor, R.A. Stockley, S.C. Afford and D. Burnett, 387
- Elephant** (indian elephant) s. *Elephas maximus*
- Elephas maximus*** (indian elephant), amino acid sequence of hemoglobin, G. Braunitzer, W. Jelkmann, A. Stangl, B. Schrank and C. Krombach, 683
- ELISA**, s. enzyme-linked immunosorbent assay
- Embryogenesis**, and retroviruses, R. Jaenisch, 1267
- Embryonic development**, vegetalizing inducer protein, K. Asahi, M. Asashima, H.-P. Geithe, J. Born, H. Tiedemann and H. Tiedemann, 563
 –, ecdysteroids in a crab, F. Lachaise and J.A. Hoffmann, 1059
- Energy transduction**, organelles, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 909
- Enoate reductase**, on the kinetics and mechanism, M. Bühler and H. Simon, 609
- Enzyme conversion**, microbial proteases, R. Kleine and U. Kettmann, 843
- Enzyme inhibitors**, biochemical tools, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 944
- Enzyme-linked immunosorbent assay (ELISA)**, detection of T-2 Toxin, H. Peters, M.P. Dierich and K. Dose, 1437
- Enzymes**, (lipogenic), age differences, M. Boll, E. Brückner and J. Berndt, 103
 – (lysosomal), phosphorylation, A. Waheed, A. Hasilik, M. Cantz and K.v. Figura, 169
 –, with unknown biological roles, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 958
- 12,13-Epoxytrichothecens**, detection of T-2 toxins, H. Peters, M.P. Dierich and K. Dose, 1437
- Equus hemionus kulan*** (asiatic wild ass), amino acid sequence of hemoglobin, G. Mazur and G. Braunitzer, 59
- Equus zebra*** (zebra), amino acid sequence of hemoglobin, G. Mazur and G. Braunitzer, 59
- Erythrocytes** (rat, mouse, guinea pig), sialic acid determination, A.K. Shukla and R. Schauer, 255
 – (anomalous from rabbit), liver steatosis, C.L. Balduini, F. Sinigaglia, E. Ascari, U. Magrini, C. Seppi and C. Balduini, 1341
- Escherichia coli***, phenylalanyl-tRNA synthetase, H.-J. Gabius, W. Freist and F. Cramer, 1241
- Estradiol-17 β** , s. 6-(carboxymethoxyimino)-2-methoxy-1,3,5(10)-estratriene-3,17 β -diol, 2-methoxyestradiol-17 β
- Estrogen-C-6-conjugates**, immunogenicity, D. Berg, H.-H. Warnecke and E. Kuss, 737
- Estrogens**, s. catecholestrogens
- Estrone**, s. 6-(carboxymethoxyimino)-3-hydroxy-2-methoxy-1,3,5(10)-estratrien-17-one, 2-methoxy-esterone
- Ether lipids**, metabolism in glial cells, H.K. Illig, B. Witter, J. Gunawan, P. Ahrens and H. Debuch, 709
- Eurypelma californicum***, (= tarantula), subunit assembly of hemocyanin, J. Markl, H. Decker, B. Linzen, W.G. Schutter and E.F.J. van Bruggen, 73
 –, active-site sequence of hemocyanin, H.-J. Schneider, U. Illig, E. Müller, B. Linzen, F. Lottspeich and A. Henschen, 487
- Evolution**, biologically active peptides, H. Jörnvall, V. Mutt and M. Persson, 475
 –, geese hemoglobins, W. Oberthür, G. Braunitzer and I. Würdinger, 581
 –, cytoplasmic and mitochondrial phenylalanyl-tRNA synthetases, H.J. Gabius and F. Cramer, 1473
- Excimer formation**, pyrenedecanoic acid, J. Mruk, A. Bakardjiev and W. Burgermeister, 745
- “Facteur thymique serique”**, synthesis of a conjugate and two derivatives, G. Auger, D. Blanot, E. Bricas, J.-M. Pléau, M. Dardenne and J.-F. Bach, 331
- Fat** (dietary), 3-hydroxy-3-methylglutaryl-CoA reductase, H.-S. Jenke, M. Löwel and J. Berndt, 725
- Fat cells**, s. adipocytes
- Fatty acid dimers**, NH-crosslinked, W. Stoffel, K.-P. Salm and M. Müller, 1
- Fatty acid liberation**, chloroquine effect, G. Pakalapati and H. Debuch, 573
- Fatty acids**, chloroquine, A. Harder and H. Debuch, 717
- Fibrinogen chains**, high-performance liquid chromatography, M. Kehl, F. Lottspeich and A. Henschen, 1501
- Fibroblasts**, mucopolydosis III, A. Waheed, A. Hasilik, M. Cantz and K.v. Figura, 169
 – (mouse cell line), association of gangliosides, K. Radsak, G. Schwarzmann and H. Wiegandt, 263
 – (human skin), arylsulfatase A, A. Waheed, A. Hasilik and K.v. Figura, 425

- (bovine lung), isolation of granulocyte colony-stimulating factor, R. Neumeier and H.R. Maurer, 1493
- Ficin**, assay for inhibitor, K. Minakata, M. Asano, T. Sato and N. Harada, 493
- Filaments**, on the association to polyribosomes, P. Traub and W. J. Nelson, 1177
- Flavobacteria**, tyrosine aminotransferase, H.G. Beschle, R. Süßmuth and F. Lingens, 439
- , aromatic-amino-acid aminotransferase, H.G. Beschle, R. Süßmuth and F. Lingens, 1365
- Flavoproteins**, electron acceptor, P. Egerer, M. Bühler and H. Simon, 627
- Fluorescent probe**, pyrenedecanoic acid, J. Mruk, A. Bakardjiev and W. Burgermeister, 745
- Fluorimetry**, determination of sialic acids, A.K. Shukla and R. Schauer, 255
- Formaldehyde formation**, periodate oxidation of sialic acids, A.K. Shukla and R. Schauer, 255
- Fragment condensations**, s. peptide synthesis
- Ganglioside analogues**, cell association, K. Radsak, G. Schwarzmann and H. Wiegandt, 263
- Gangliosides**, cell association, K. Radsak, G. Schwarzmann and H. Wiegandt, 263
- , specific sialidase, J.-C. Michalski, A.P. Corfield and R. Schauer, 1097
- Gastric acid**, secretion, E. Wünsch, L. Moroder, D. Gillissen, U.B. Soerensen and J.-P. Bali, 665
- Gastrin**, s. N^{α} -glycosylgastrin
- Gastrin I analogs**, immunoreactivity, E. Wünsch, L. Moroder, D. Gillissen, U.B. Soerensen and J.-P. Bali, 665
- Gastrointestinal hormones**, structural similarities, H. Jörnvall, V. Mutt and M. Persson, 475
- Geese**, s. *Anser indicus* (bar-headed goose), *Branta canadensis* (canada goose)
- Gene cloning**, s. cloning
- Gene duplication**, cytoplasmic and mitochondrial phenylalanyl-tRNA synthetases, H.J. Gabius and F. Cramer, 1473
- Gene transfer**, SV40 gene fragment, J. Horst, E. Jacob, C. Weckler and W. Depert, 445
- Glass**, s. pore glass (controlled)
- Glial cells**, phospholipid metabolism, H.K. Illig, B. Witter, J. Gunawan, P. Ahrens and H. Debuch, 709
- Glucagon**, s. monoiodoglucagon
- Glucokinase (EC 2.7.1.2)**, distribution reciprocal to hexokinase, W. Fischer, M. Ick and N.R. Katz, 375
- Glucose**, uptake effected by guanidino derivatives, G. Weitzel and A. Hadjianghelu, 45
- Glucosylation**, nonenzymatic of β -*N*-acetyl-D-glucosaminidase, R. Dolhofer, E. A. Siess and O.H. Wieland, 1427
- β -D-Glucuronidase (EC 3.2.1.31)** (rat liver), substrate specificity and regulation, R. Niemann and E. Buddecke, 591
- Glutamyl-peptide- γ -glutamyltransferase (EC 2.3.2.13)**, effect on trypsin- α -macroglobulin complex uptake, K. Ohlsson, A. Polling and P. Stenberg, 213
- Glutathione**, biosynthesis and function, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 963
- , conjugation of sulfobromophthalein, L.R. Schwarz, 1225
- Glycerate**, s. 2,3-bisphosphoglycerate
- Glycine**, exchange with L- and D-tryptophan in insulin pos. A1, R. Geiger, K. Geisen and H.-D. Summ, 1231
- Glycoconjugates**, structure metabolism and function, 41 st Conference of the Gesellschaft für Biologische Chemie, 1015
- Glycopeptides**, in human teratocarcinoma cells, M.-L. Rasilo and O. Renkonen, 89
- , N^{α} -glycosylgastrin, A. Previero, G. Mourier, J.-P. Bali, M.F. Lignon and L. Moroder, 813
- Glycoprotein**, contact site A glycoprotein of *Dictyostelium discoideum*, J. Stadler, C. Bordier, F. Lottspeich, A. Henschen and G. Gerisch, 771
- , low-molecular mass urokinase from human urine, G. J. Steffens, W.A. Günzler, F. Ötting, E. Frankus and L. Flohé, 1043
- N^{α} -Glycosylgastrin**, synthesis of related peptides, A. Previero, G. Mourier, J.-P. Bali, M.F. Lignon and L. Moroder, 813
- Glycyllysine peptides** (α - and ϵ -substituted), enzymatic cleavage, A. Plessing, G. Siebert, J.H. Wissler, A. J. Puigserver and P. Pfaender, 279
- Goat** s. *Capra aegagrus*
- Gold**, s. protein A-gold technique
- Granulocytes**, seminal and colostrum protease inhibitors, L. Veselský, D. Čechová, V. Hruban and J. Klauudy, 113
- Granulocyte colony-stimulating factors**, identification from porcine leukocyte cultures, R. Neumeier, H.R. Maurer, M. Arnold, U. Gerlach, K. Glendinning, H. Renner and J.H. Wissler, 193
- , isolation from bovine lung conditioned medium, R. Neumeier and H.R. Maurer, 1493
- Granulocyte elastase**, s. leukocyte elastase
- Granulocyte protease (human)**, coagulation factors IX and X, J. Kárpáti, K. Váradí and S. Elödi, 521
- Guanidino derivatives**, glucose uptake, G. Weitzel and A. Hadjianghelu, 45

- Haber-Weiss cycle**, iron-catalysed, H. Nohl, W. Jordan and D. Hegner, 599
- Hapten-carrier conjugate**, detection of toxin T-2, H. Peters, M.P. Dierich and K. Dose, 1437
- Hemocyanins** (spiders), subunit assembly, J. Markl, H. Decker, B. Linzen, W.G. Schutter and E.F.J. van Bruggen, 73
- (arthropods), presumptive active-site sequence, H.-J. Schneider, U. Illig, E. Müller, B. Linzen, F. Lottspeich and A. Henschen, 487
- Hemodialysate** (uremic patients), toxic hexapeptide, G. Bovermann, H. Rautenstrauch and G. Jung, 1187
- Hemoglobins** (asiatic wild ass and mountain Zebra), amino acid sequence, G. Mazur and G. Braunitzer, 59
- (pheasant), amino acid sequence, G. Braunitzer and J. Godovac, 229
 - (armadillo), amino acid sequence of α -chain, T. Kleinschmidt, W.W. de Jong and G. Braunitzer, 239
 - (bar-headed goose), amino acid sequence, W. Oberthür, G. Braunitzer and I. Würdinger, 581
 - (indian elephant), amino acid sequence, G. Braunitzer, W. Jelkmann, A. Stangl, B. Schrank and C. Krombach, 683
 - (canada goose and mute swan), amino acid sequences, W. Oberthür, J. Godovac-Zimmermann, G. Braunitzer and H. Wiesner, 777
 - (fetal of sheep and goat), amino acid sequence of γ -chains, T. Kleinschmidt and G. Braunitzer, 789
 - (white rhinoceros), amino acid sequence, G. Mazur, G. Braunitzer and P.G. Wright, 1077
 - (egyptian fruit bat), amino acid sequence, T. Kleinschmidt and G. Braunitzer, 1209
- Heparin**, heparin-binding domains in fibronectin, H. Richter and H. Hörmann, 351
- Hepatocytes** (rat, isolated), uptake of sulfobromophthalein, L.R. Schwarz, 1225
- Hexokinase** (EC 2.7.1.1) (rat liver acinus), distribution reciprocal to glucokinase, W. Fischer, M. Ick and N.R. Katz, 375
- (ascites tumor cells), lysine residues, P.A. Lazo and L. Bosca, 635
- High-altitude respiration**, hemoglobin of geese, W. Oberthür, G. Braunitzer and I. Würdinger, 581
- High-density lipoprotein**, photochemical crosslinking, W. Stoffel and P. Metz, 19
- High-performance liquid chromatography**, bradykinin and kallidin, R. Geiger, R. Hell and H. Fritz, 527
- , proteolipid apoprotein, W. Stoffel, H. Hillen, W. Schroeder and R. Deutzmann, 855
 - , fibrinogen chains, M. Kehl, F. Lottspeich and A. Henschen, 1501
- High-pressure liquid chromatography**, s. reversed-phase high-pressure liquid chromatography
- Hippuryl-arginine**, carboxypeptidase N, L. Juillerat-Jeanneret, M. Roth and J.-P. Bargetzi, 51
- Hippuryl-lysine**, carboxypeptidase N, L. Juillerat-Jeanneret, M. Roth and J.-P. Bargetzi, 51
- Histamine release**, serine-protease inhibitors, M. Muramatu, T. Satoh, Y. Yanagimoto, Y. Kanamoto, I. Katsuyama, M. Kanamoto and K. Taguchi, 203
- Histocompatibility**, s. major histocompatibility complex
- Histocompatibility antigens** (human, class II), partial amino acid sequence, C. Yang, H. Kratzin, H. Götz, F.P. Thinnis, T. Kruse, G. Egert, E. Pauly, S. Kölbl, P. Wernet and N. Hilschmann, 671
- HLA-D antigen**, partial amino acid sequence, C. Yang, H. Kratzin, H. Götz, F.P. Thinnis, T. Kruse, G. Egert, E. Pauly, S. Kölbl, P. Wernet and H. Hilschmann, 671
- HL-60 cells**, s. promyelocytes
- Hyaluronate oligosaccharides**, β -D-glucuronidase, R. Niemann and E. Buddecke, 591
- Hybridization**, s. blot hybridization
- , lactate dehydrogenase subunits, R. Hermann, R. Rudolph and R. Jaenicke, 1259
- Hydrophobicity**, proteolipid apoprotein from brain, W. Stoffel, W. Schröder, H. Hillen and R. Deutzmann, 1117
- , separation of hydrophobic peptides, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- 5-Hydroxyanthranilic acid**, tryptophan metabolism, B. Hauer and F. Lingens, 507
- Hydroxylation**, cytochrome P-450-dependent, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 971
- 3-Hydroxy-3-methylglutaryl-CoA reductase** (NADPH) (EC 1.1.1.34), dietary lipids, H.-S. Jenke, M. Löwel and J. Berndt, 725
- , inactivation-reativation cycles, G. Gil, V.E. Calvet, A. Ferrer and F.G. Hegardt, 1217
- Hypodermis** (crayfish), ecdysteroid receptors, M. Londershausen, P. Kuppert and K.-D. Spindler, 797
- Imidoesters**, modification of lysine residues, P.A. Lazo and L. Bosca, 635
- Immune response** (cell-mediated), allograft rejection, D. Fuchs, A. Hausen, C. Huber, R. Margreiter, G. Reibnegger, M. Spielberger and H. Wachter, 661
- Immuno-affinity chromatography**, antigens, J. Dietl, A. Czuppon and L. Mettler, 381
- , spermatozoal polypeptide antigens, A. B. Czuppon and L. Mettler, 1465

- Immunoassay**, s. enzyme-linked immunosorbent assay (ELISA)
- Immunocytochemical localization**, kallikrein, M. Amouric, P. Lechene de la Porte and C. Figarella, 515
- Immunodetection blot**, cytochrome *c* oxidase, J. Jarausch and B. Kadenbach, 1133
- Immunogenic conjugate**, "facteur thymique serique", G. Auger, D. Blanot, E. Bricas, J.-M. Pléau, M. Dardenne and J.-F. Bach, 331
- Immunogen steroid derivatives**, characterization of antisera, D. Berg, H.-H. Warnecke and E. Kuss, 737
- Immunoglobulins**, lipoprotein-activated B-lymphocyte development, W.G. Bessler, R.B. Johnson, K. Wiesmüller and G. Jung, 767
- , unusual insertion in a human κ -immunoglobulin light chain, M. Eulitz and R.P. Linke, 1347
- Immunological methods**, detection of protease inhibitors, L. Veselsky, D. Čechová, V. Hruban and J. Klauudy, 113
- Immunological properties**, urinary and pancreatic kallikrein, E. Fink, M.A. Amouric, R. Geiger and C. Figarella, 819
- Immunological rejection**, neopterin secretion, D. Fuchs, A. Hausen, C. Huber, R. Margreiter, G. Reibneger, M. Spielberger and H. Wachter, 661
- Immunoreactivity**, gastrin I analogs, E. Wünsch, L. Moroder, D. Gillissen, U.B. Soerensen and J.-P. Bali, 665
- Immunosorbent test**, s. enzyme-linked immunosorbent test (ELISA)
- Inactivation-reactivation cycles**, 3-hydroxy-3-methylglutaryl-CoA reductase, G. Gil, V.E. Calvet, A. Ferrer and F.G. Hegardt, 1217
- Inducer protein (vegetalizing)**, radioactive labelling, K. Asahi, M. Asashima, H.-P. Geithe, J. Born, H. Tiedemann and H. Tiedemann, 563
- Influenza virus**, determinants of pathogenicity, R. Rott, 1273
- Inhibition**, s.a. inactivation-reactivation cycles
- (noncompetitiv), lipoproteins, E. Koller, F. Koller and W. Doleschel, 395
- Inhibitor assay**, α -cysteine proteinase inhibitor, K. Minakata, M. Asano, T. Sato and N. Harada, 493
- Inhibitors**, s.a. enzyme inhibitors, protease inhibitors, proteinase inhibitors, α_1 -proteinase inhibitor, trypsin kallikrein inhibitor, trypsin inhibitor
- , of enoate reductase, M. Bühler and H. Simon, 609
- Insulin** (bovine), preparation of dimers, A. Schüttler and D. Brandenburg, 317
- (bovine), conformational adjustment to the receptor, D. Saunders and K. Freude, 655
- , citraconylation, V.K. Naithani and H.G. Gattner, 1443
- Insulin analogues**, lipogenesis, C. Diaconescu, D. Saunders, H.-G. Gattner and D. Brandenburg, 187
- (bovine), [Trp^{A1}]insulin, R. Geiger, K. Geisen and H.D. Summ, 1231
- (porcine), [D-Arg^{B22}]insulin, R. Knorr, W. Danho, E.E. Büllesbach, H.-G. Gattner, H. Zahn, G.L. King and C.R. Kahn, 1449
- Intercalation**, 4-(9-acridinylamino)aniline, J.-P. Hénichart, J.-L. Bernier and J.-P. Catteau, 835
- Interferon**, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 985
- Intestinal mucosa**, cleavage of ϵ -substituted peptides, A. Plessing, G. Siebert, J.H. Wissler, A.J. Puigserver and P. Pfaender, 279
- Intestinal peptides**, s. gastrointestinal hormones
- Iodination**, s.a. radioiodination
- , density gradient media, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 999
- Iodoglucagon**, s. monoiodoglucagon
- ¹²⁵**Iodo labeling**, antigens, J. Dietl, A. Czuppon and L. Mettler, 381
- Iodosalicylate**, s. 3,5-diiodosalicylate
- Iron ions**, Haber-Weiss cycle, H. Nohl, W. Jordan and D. Hegner, 599
- Isoenzymes**, cytochrome *c* oxidase, J. Jarausch and B. Kadenbach, 1133
- , porcine lactate dehydrogenase, R. Hermann, R. Rudolph and R. Jaenicke, 1259
- Isolated perfused liver**, s. liver (isolated perfused)
- Isomeric forms**, s. multiple forms
- Isotope effect**, enoate reductase reaction, M. Bühler and H. Simon, 609
- Isozymes**, s. isoenzymes
- Kallidin**, high performance liquid chromatography, R. Geiger, R. Hell and H. Fritz, 527
- , rat uterus homogenate, M. Marin-Grez, G. Schaechtelin and K. Hermann, 1359
- Kallikrein**, s. plasma kallikrein, tissue kallikrein
- Keratan sulfate**, s. proteokeratan sulfate
- Kidney** (bovine), β -*N*-acetyl-D-glucosaminidase, R. Dolhofer, E.A. Siess and O.H. Wieland, 1427
- Kinin**, liberation by kallikrein, L. Schack and T. Dietl, 107
- , rat uterus homogenate, M. Marin-Grez, G. Schaechtelin and K. Hermann, 1359
- Kininase I**, carboxypeptidase N, L. Juillerat-Jeanneret, M. Roth and J.-P. Bargetzi, 51
- Kinigenase**, rat uterus homogenate, M. Marin-Grez, G. Schaechtelin and K. Hermann, 1359

- Lactate dehydrogenase (EC 1.1.1.27)** (porcine), subunit hybridisation, R. Hermann, R. Rudolph and R. Jaenicke, 1259
- Lactoperoxidase iodination**, glucagon, O. Sonne, U.D. Larsen and J. Markussen, 95
- Lactose permease**, and the molecular biology of transport, 39th Conference of the Gesellschaft für Biologische Chemie, 1409
- Leukemia**, maturation of promyelocytes, M. Kidron, D.B. Friedman, M. Mayer, Y. Klemes and E. Fibach, 865
- Leukocyte elastase (EC 3.4.21.37)** (human granulocytes), urinary trypsin inhibitor, B.-M. Jönsson, C. Löffler and K. Ohlsson, 1167
- Leukocytes**, seminal and colostrum protease inhibitors, L. Veselský, D. Čechová, V. Hruban and J. Klauudy, 113
- (porcine), colony-stimulating factors, R. Neumeier, H.R. Maurer, M. Arnold, U. Gerlach, K. Glendinning, H. Renner and H. J. Wissler, 193
 - (human), separation of enzymes, S. Engelbrecht, E. Pieper, H.W. Macartney, W. Rautenberg, H.R. Wenzel and H. Tschesche, 305
 - (human), elastase, W. Hornebeck and H.P. Schnebli, 455
- Leukodystrophy**, s. metachromatic leukodystrophy
- Lewis lung tumor**, retinoic acid binding, B. Gmeiner and G. Zerlauth, 337
- Light**, s. crosslinking (photochemical), photo-label
- Limulus polyphemus**, active-site sequence of hemocyanins, H.-J. Schneider, U. Illig, E. Müller, B. Linzen, F. Lottspeich and A. Henschen, 487
- Linkage monosaccharides**, glycopeptides in teratocarcinoma cells, M.-L. Rasilo and O. Renkonen, 89
- Lipidosis**, s. mucopolipidosis III
- Lipid phase transition** (temperature-induced), prostaglandin E₁, J. Mruk, A. Bakardjiev and W. Burgermeister, 745
- Lipids**, s.a. ether lipids, phospholipids, proteolipid, steatosis
- , azido- and ³H-labelled, W. Stoffel, K.-P. Salm and M. Müller, 1
 - , azido-labelled in HDL, W. Stoffel and P. Metz, 19
 - (dietary), 3-hydroxy-3-methylglutaryl-CoA reductase, H.-S. Jenke, M. Löwel and J. Berndt, 725
 - , membrane lipid phase transition, J. Mruk, A. Bakardjiev and W. Burgermeister, 745
- Lipogenesis**, age-related differences, M. Boll, E. Brückner and J. Berndt, 103
- , insulin analogues, C. Diaconescu, D. Saunders, H.-G. Gattner and D. Brandenburg, 187
 - , insulin action, A. Schüttler and D. Brandenburg, 317
- Lipopptide** (synthetic), mitogenicity, W.G. Bessler, R.B. Johnson, K. Wiesmüller and G. Jung, 767
- Lipophilin**, partial primary structure, W. Stoffel, H. Hillen, W. Schroeder and R. Deutzmann, 855
- , amino acid sequence of proteolytic fragments, W. Stoffel, W. Schröder, H. Hillen and R. Deutzmann, 1117
 - , amino acid sequence of some fragments, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- Lipopolypeptides**, crosslinked, W. Stoffel and P. Metz, 19
- Lipopolysaccharides**, mitogenicity, W.G. Bessler, R.B. Johnson, K. Wiesmüller and G. Jung, 767
- Lipoproteins** (human plasma), blood platelets, E. Koller, F. Koller and W. Doleschel, 395
- (bacterial), mitogenic activity, W.G. Bessler, R.B. Johnson, K. Wiesmüller and G. Jung, 767
 - , structure and metabolism, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 948
- Liposomes**, photochemical crosslinking, W. Stoffel, K.-P. Salm and M. Müller, 1
- Liquid-phase peptide synthesis**, derivatives of Boc-amino acids, B. Hemmasi, W. Stüber and E. Bayer, 701
- Lithium 3,5-diiodosalicylate**, solubilization of antigens, J. Dietl, A. Czuppon and L. Mettler, 381
- Liver**, s.a. hepatocytes
- (rat), regulation of lipogenic enzymes, M. Boll, E. Brückner and J. Berndt, 103
 - (rat), cytoplasmic proteins, J. Voigt and C.E. Sekeris, 159
 - , cell heterogeneity, W. Fischer, M. Ick and N.R. Katz, 375
 - (rat), fatty acid liberation, G. Pakalapati and H. Debuch, 573
 - (rat, isolated perfused), oxocholanic acid metabolism, M.S. Anwer and D. Hegner, 731
 - (human), sialidase, J.-C. Michalski, A.P. Corfield and R. Schauer, 1097
- Liver acinus** (rat), glucokinase and hexokinase distribution, W. Fischer, M. Ick and N.R. Katz, 375
- Liver damage** (rabbits), anomalous erythrocytes, C.L. Balduini, F. Sinigaglia, E. Ascari, U. Magrini, C. Seppi and C. Balduini, 1341
- Localization**, pancreatic kallikrein, M. Amouric, P. Lechene de la Porte and C. Figarella, 515
- Lung**, s. a. Lewis lung tumor
- (bovine), granulocyte colony-stimulating factor, R. Neumeier and H.R. Maurer, 1493
- Lung secretion**, α_1 -proteinase inhibitor, R.A. Stockley, S.C. Afford and D. Burnett, 387
- Lymphocytes**, s.a. B-lymphocytes, T-lymphocytes
- , seminal and colostrum protease inhibitors, L. Veselský, D. Čechová, V. Hruban and J. Klauudy, 113
- Lymphoma cells** (mouse), polyadenylate-protein complex, A. Bernd, R.K. Zahn, A. Maidhof and W.E.G. Müller, 221

- Lysine peptides** (α - and ϵ -substituted), enzymatic cleavage, A. Plessing, G. Siebert, J.H. Wissler, A. J. Puigserver and P. Pfaender, 279
- Lysine residues**, function in hexokinase, P.A. Lazo and L. Bosca, 635
- 2-Lysophosphatidylcholin**, fatty acid liberation, G. Pakalapati and H. Debuch, 573
- Lysophospholipase** (EC 3.1.1.5), chloroquine effect, G. Pakalapati and H. Debuch, 573
- Lysosomal enzymes**, arylsulfatase A, A. Waheed, A. Hasilik and K.v. Figura, 425
- Lysosomes** (human fibroblasts), enzyme phosphorylation, A. Waheed, A. Hasilik, M. Cantz and K.v. Figura, 169
- (rat liver), chloroquine, G. Pakalapati and H. Debuch, 573
 - (rat liver), chloroquine treatment, A. Harder and H. Debuch, 717
- Lysylglycin**, influence on binding of 4-(9-acridinylamino)aniline to DNA, J.-P. Hénichart, J.-L. Bernier and J.P. Cateau, 835
- α_2 -Macroglobulin**, uptake of the trypsin complex, K. Ohlsson, A. Polling and P. Stenberg, 213
- , assay of α -cysteine proteinase inhibitors, K. Minakata, M. Asano, T. Sato and N. Harada, 493
 - (rat), subunit structure of α -macroglobulin proteinase inhibitors, L.P. Nelles and H.P. Schnebli, 677
 - (rat and human), subunit structure of α -macroglobulin proteinase inhibitors, L.P. Nelles and H.P. Schnebli, 677
 - , electron microscopy, H. J. Schramm and W. Schramm, 803
- Macrophages**, colony-stimulating factors, R. Neumeier, H.R. Maurer, M. Arnold, U. Gerlach, K. Glendingning, H. Renner and J.H. Wissler, 193
- , trypsin- α -macroglobulin complex, K. Ohlsson, A. Polling and P. Stenberg, 213
- Magnesium**, ATP complexes, E. Gerlo, W. Freist and J. Charlier, 365
- Major histocompatibility complex**, *N*-terminus of an alloantigen, C. Yang, H. Kratzin, H. Götz, F.P. Thinnes, T. Kruse, G. Egert, E. Pauly, S. Kölbl, P. Wernet and N. Hilschmann, 671
- Malignant cells**, membranes, transport, antigenicity, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 894
- Mass spectrometry**, uremic toxins, G. Bovermann, H. Rautenstrauch and G. Jung, 1187
- Mass spectroscopy**, azido fatty acid-substituted lipids, W. Stoffel, K.-P. Salm and M. Müller, 1
- Mast cells**, histamine release, M. Muramatu, T. Satoh, Y. Yanagimoto, Y. Kanamoto, I. Katsuyama, M. Kanemoto and K. Taguchi, 203
- Membrane protein**, *Dictyostelium discoideum*, J. Stadler, C. Bordier, F. Lottspeich, A. Henschen and G. Gerisch, 771
- Membranes** (mitochondrial), hexokinase, P.A. Lazo and L. Bosca, 635
- , lipid phase transitions, J. Mruk, A. Bakardjiev and W. Burgermeister, 745
 - , membrane-bound proteins, B. Železná and D. Čechová, 757
 - , in normal and malignant cells, including transport and antigenicity, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 894
 - , of reticulocytes during liver steatosis, C.L. Balduini, F. Sinigaglia, E. Ascari, U. Magrini, C. Seppi and C. Balduini, 1341
 - (bovine brain white matter), lipophilin, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- Messenger**, second messengers, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 938
- Messenger RNA**, polyadenylate-protein complex, A. Berndt, R.K. Zahn, A. Maidhof and W.E.G. Müller, 221
- Metabolic zonatron**, hexokinase and glucokinase distribution, W. Fischer, M. Ick and N.R. Katz, 375
- Metachromatic leukodystrophy**, processing of arylsulfatase A, A. Waheed, A. Hasilik and K.v. Figura, 425
- Metalloenes**, steroid hormones, M. Wenzel, G. Schachschneider, M. Schneider and R. Herken, 693
- Methionine residue**, receptor-binding affinity, O. Sonne, U.D. Larsen and J. Markussen, 95
- Methoxinine**, gastrin I analogs, E. Wünsch, L. Moroder, D. Gillissen, U.B. Soerensen and J.-P. Bali, 665
- 2-Methoxyestradiol-17 β** , synthesis, D. Berg, H.-H. Warnecke and E. Kuss, 737
- 2-Methoxyestrone**, synthesis, D. Berg, H.-H. Warnecke and E. Kuss, 737
- Methylation**, of RNA in vitro, K.P. Schäfer, 33
- (reductive), tritium labelling, K. Asahi, M. Asashima, H.-P. Geithe, J. Born, H. Tiedemann and H. Tiedemann, 563
- Met-Lys-Bradykinin**, high-performance liquid chromatography, R. Geiger, R. Hell and H. Fritz, 527
- Microbial degradation**, 4-chlorophenylacetic acid, A. Markus, U. Klages and F. Lingens, 431
- Microbial protease**, chromatography on controlled pore glass, R. Kleine and U. Kettmann, 843
- Mitochondria** (beef heart), ADP/ATP carrier, H. Aquila, D. Misra, M. Eulitz and M. Klingenberg, 345

- (rat heart), formation of OH[•] radicals, H. Nohl, W. Jordan and D. Hegner, 599
- , membrane-bound hexokinase, P. A. Lazo and L. Bosca, 635
- , cytochrome P-450-dependent hydroxylation, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 971
- (hen liver), phenylalanyl-tRNA synthetase, H.-J. Gabius, W. Freist and F. Cramer, 1241
- (yeast and hen liver), phenylalanyl-tRNA synthetase compared to that from cytoplasm, H. J. Gabius and F. Cramer, 1473
- Mitogenicity**, synthetic lipopeptide, W. G. Bessler, R. B. Johnson, K. Wiesmüller and G. Jung, 767
- Molecular arrangement**, lipophilin in bovine brain white matter, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- Molecular bioenergetics**, aspects, 43rd Conference of the Gesellschaft für Biologische Chemie, 535
- Monoiodoglucagon**, receptor-binding affinity, O. Sonne, U. D. Larsen and J. Markussen, 95
- Monosaccharides**, s. linkage monosaccharides
- Morphogenesis**, differentiation, 33. Mosbacher Kolloquium der Gesellschaft für Biologische Chemie, 119
- Mouse L cells**, subcellular system for RNA synthesis and processing, K. P. Schäfer, 33
- Mucin** (equine submandibular gland), specific sialidase, J.-C. Michalski, A. P. Corfield and R. Schauer, 1097
- Mucopolidosis III**, deficiency of *N*-acetylglucosamine-1-phosphotransferase, A. Waheed, A. Hasilik, M. Cantz and K. v. Figura, 169
- Mucosa (intestinal)**, cleavage of ϵ -substituted peptides, A. Plessing, G. Siebert, J. H. Wissler, A. J. Puigserver and P. Pfaender, 279
- Multiple forms**, porcine somatotropin, M. Schleyer, T. Trah and I. Schleyer, 179
- Muscle**, s.a. skeletal muscle
 - (fast skeletal from chicken), amino acid sequence of myosin L-1 light chain, T. Umegane, T. Maita and G. Matsuda, 1321
- Mutants**, papaverine degradation, B. Hauer, K. Haase-Aschoff and F. Lingens, 499
- Myelin** (from bovine brain), proteolipid apoprotein, W. Stoffel, W. Schröder, H. Hillen and R. Deutzmann, 1117
 - (bovine brain white matter), lipophilin, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- Myeloperoxidase**, s. Peroxidase
- Myofibrils** (rat), protease, M. Dudai, M. Mayer and M. Kidron, 651
- Myosin** (chicken fast skeletal muscle), amino acid sequence of myosin L-1 light chain, T. Umegane, T. Maita and G. Matsuda, 1321
- NADH dehydrogenase (EC 1.6.99.3)**, rhein, P. Egerer, M. Bühler and H. Simon, 627
- Neopterin**, allograft rejection, D. Fuchs, A. Hausen, C. Huber, R. Margreiter, G. Reibnegger, M. Spielberger and H. Wachter, 661
- Nervous system**, biochemistry, 44th Conference of the Gesellschaft für Biologische Chemie, 1283
- Neuraminidase**, s. sialidase
- Neurochemistry**, biochemistry of the nervous system, 44th Conference of the Gesellschaft für Biologische Chemie, 1283
- Neuropeptides**, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 941
- Nicotinic acid**, (2*R*, 3*S*)-2,3-dimethylmalate-lyase reaction, G. Löhlein and H. Eggerer, 1103
- Nocardia spec.*** papaverine degradation, B. Hauer, K. Haase-Aschoff and F. Lingens, 499
 - , tryptophan metabolism, B. Hauer and F. Lingens, 507
- Norleucine**, in pos. 8 of an analogue of somatostatin-28, L. Moroder, E. Wunsch, N. Vaysse and A. Ribet, 1247
- Nuclear magnetic resonance**, uremic toxins, G. Bovermann, H. Rautenstrauch and G. Jung, 1187
- Nuclei**, compartmentation of influence on RNA labelling, C. Scholtissek, D. Evans and H. Bürger, 1389
- Nucleophilic deacylation**, acyl-chymotrypsin, V. Kasche and R. Zöllner, 531
- Nucleosides**, influence on RNA labelling with ³²P_i, C. Scholtissek, D. Evans and H. Bürger, 1389
- Oligosaccharides**, β -D-glucuronidase, R. Niemann and E. Buddecke, 591
 - , structure in proteokeratan sulfate, T. Stein, R. Keller, H. W. Stuhlsalz, H. Greiling, E. Ohst, E. Müller and H.-D. Scharf, 825
- Orconectes limosus*** (crayfish), ecdysteroid receptors, M. Londershausen, P. Kuppert and K.-D. Spindler, 797
- Organelles**, energy transduction, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 909
- Ornithine peptides**, synthesis of [perornithine]thynnine fragments, F. Marchiori, G. Borin, D. Stivanello, V. Moretto and G. Chessa, 1483
- Ovis ammon*** (sheep), amino acid sequence of fetal hemoglobin, T. Kieinschmidt and G. Braunitzer, 789
- Oxidation**, s. periodate oxidation
- Oxocholanic acids**, metabolism in liver, M. S. Anwer and D. Hegner, 731

- Oxygen affinity**, hemoglobin of armadillo, T. Kleinschmidt, W.W. de Jong and G. Braunitzer, 239
- , hemoglobin of the indian elephant, G. Braunitzer, W. Jelkmann, A. Stangl, B. Schrank and C. Krombach, 683
- , fetal hemoglobins, T. Kleinschmidt and G. Braunitzer, 789
- , hemoglobin of egyptian fruit bat *Rousettus aegyptiacus*, T. Kleinschmidt and G. Braunitzer, 1209
- Oxygen binding**, hemocyanin, H.-J. Schneider, U. Illig, E. Müller, B. Linzen, F. Lottspeich and A. Henschen, 487
- Pancreas** (human), localization of kallikrein, M. Amouric, P. Lechene de la Porte and C. Figarella, 515
- (human), comparison of urinary and pancreatic kallikrein, E. Fink, M. Amouric, R. Geiger and C. Figarella, 819
- Papaverine**, degradation, B. Hauer, K. Haase-Aschoff and F. Lingens, 499
- , –, B. Hauer and F. Lingens, 507
- Parathyrin** (human), partial synthesis, M. Casaretto, W. Danho, R.-D. Hesch and H. Zahn, 407
- Pathogenicity** (influenza virus), determinants, R. Rott, 313
- Peptidases**, and Proteinases, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 976
- ε-Peptide bond**, enzymatic cleavage, A. Plessing, G. Siebert, J.H. Wissler, A. J. Puigserver and P. Pfaender, 279
- Peptides**, s.a. brain intestinal peptides, cystine peptides, decapeptide, glycopeptides, lipopeptide, lipopoly-peptides, neuropeptides, ornithine peptides, phenylalanyl-lysine peptides, polypeptides
- (¹²⁵I-labelled), “facteur thymique serique”, G. Auger, D. Blanot, E. Bricas, J.-M. Pléau, M. Dardenne and J.-F. Bach, 331
- , structural similarities among biologically active peptides, H. Jörnvall, V. Mutt and M. Persson, 475
- , high performance liquid chromatography, G. Braunitzer, P. Rücknagel and W. Oberthür, 485
- , N^α-glycosylgastrin-related, A. Previero, G. Mourier, J.-P. Bali, M.F. Lignon and L. Moroder, 813
- , influence of peptide side chain on binding parameters of an intercalating agent, J.-P. Hélichart, J.-L. Bernier and J.-P. Cateau, 835
- , uremic toxin, G. Bovermann, H. Rautenstrauch, G. Seybold and G. Jung, 1187
- , decapeptide as spermatozoal antigen, A. B. Czuppon and L. Mettler, 1465
- Peptide separation**, high performance liquid chromatography, R. Geiger, R. Hell and H. Fritz, 527
- Peptide synthesis**, amino-protecting groups, E. Wünsch, L. Moroder, R. Nyfeler and E. Jaeger, 197
- , in solution, M. Casaretto, W. Danho, R.-D. Hesch and H. Zahn, 407
- , unsymmetrical disulfides, E. Wünsch and S. Romani, 449
- , liquid-phase method, B. Hemmasi, W. Stüber and E. Bayer, 701
- , norleucine-8 analogue of somatostatin-28, L. Moroder, E. Wünsch, N. Vaysse and A. Ribet, 1247
- , [D-Arg^{B22}]insulin, R. Knorr, W. Danho, E.E. Büllsbach, H.-G. Gattner, H. Zahn, G.L. King and C.R. Kahn, 1449
- (solid phase), decapeptide as spermatozoal antigen, A. B. Czuppon and L. Mettler, 1465
- , [perornithine]thynnine fragments, F. Marchiori, G. Borin, D. Stivanello, V. Moretto and G. Chessa, 1483
- Performic acid**, somatotropin activity, M. Schleyer, H. Etzrodt, T. J. Trah and K.-H. Voigt, 1111
- Periodate oxidation**, sialic acids, A.K. Shukla and R. Schauer, 255
- Periportal zone** (rat liver acinus), hexokinase and glucokinase distribution, W. Fischer, M. Ick and N.R. Katz, 375
- Perivenous zone** (rat liver acinus), hexokinase and glucokinase distribution, W. Fischer, M. Ick and N.R. Katz, 375
- Perornithine protamines**, synthesis of [perornithine]-thynnine fragments, F. Marchiori, G. Borin, D. Stivanello, V. Moretto and G. Chessa, 1483
- Peroxidase** (EC 1.11.1.7), separation from other leukocyte enzymes, S. Engelbrecht, E. Pieper, H.W. Macartney, W. Rautenberg, H.R. Wenzel and Tschesche, 305
- Peroxisomes**, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 968
- Phasianus colchicus colchicus** (pheasant), amino acid sequence of hemoglobins, G. Braunitzer and J. Godovac, 229
- Pheasant**, s. *Phasianus colchicus colchicus*
- Phenylacetic acid**, s. 3,4-dimethoxyphenylacetic acid
- Phenylalanyl-lysine peptides** (α- and ε-substituted), enzymatic cleavage, A. Plessing, G. Siebert, J.H. Wissler, A. J. Puigserver and P. Pfaender, 279
- Phenylalanyl-tRNA synthetase** (EC 6.1.1.20), from several sources, relationship, H.-J. Gabius, W. Freist and F. Cramer, 1241
- , from cytoplasm and mitochondria (compared), H.J. Gabius and F. Cramer, 1473

- (2R)-Phenyllactate**, stereospecific water elimination, C. Pitsch and H. Simon, 1253
- Phosphate**, effect on 3-hydroxy-3-methylglutaryl-CoA reductase, G. Gil, V.E. Calvet, A. Ferrer and F.G. Hegardt, 1217
- Phosphatides**, s. bis(monoacylglycero)phosphate, 2-lyso-phosphatidylcholin
- Phosphatidylcholines**, azido fatty acid-substituted, W. Stoffel, K.-P. Salm and M. Müller, 1
- Phosphoglycerate**, s. 2,3-bisphosphoglycerate
- Phospholipids**, glial cells, H.K. Illig, B. Witter, J. Gunawan, P. Ahrens and H. Debusch, 709
 –, chloroquine treatment, A. Harder and H. Debusch, 717
- Phosphorylation**, s.a. dephosphorylation
 –, lysosomal enzymes, A. Waheed, A. Hasilik, M. Cantz and K. v. Figura, 169
 –, of enzymes, G. Gil, V.E. Calvet, A. Ferrer and F.G. Hegardt, 1217
- Photoaffinity labelling**, ecdysteroid receptors, M. Londershausen, P. Kuppert and K.-D. Spindler, 797
- Photocrosslinking**, s. crosslinking (photochemical)
- Photo-label**, vasopressin analoga, F. Fahrenholz, H.S. Husseini, J.L. Morgat and K.-H. Thierauch, 1415
- Photosynthesis**, bacteria and higher plants, O. Klein and R.J. Porra, 551
- Phthalein derivatives**, s. sulfobromophthalein
- Plasma kallikrein (EC 3.4.21.34)**, rat uterus homogenate, M. Marin-Grez, G. Schaechtelin and K. Hermann, 1359
- Plasmalogene**, metabolism in glial cells, H.K. Illig, B. Witter, J. Gunawan, P. Ahrens and H. Debusch, 709
- Plasmin (EC 3.4.21.7)**, fibronectin fragments, H. Richter and H. Hörmann, 351
- Platelets**, s. thrombocytes
- Polyadenylate**, protein complex, A. Bernd, R.K. Zahn, A. Maidhof and W.E.G. Müller, 221
- Polyadenylation**, of RNA in vitro, K.P. Schäfer, 33
- Poly[α -N ^{β} -(2-hydroxyethyl)-DL-asparagine, β -N ^{α} -(2-hydroxyethyl)-DL-asparagine]**, soluble carrier, M. Havranová, D. Čechová, V. Saudek, M. Metaločá and J. Drobník, 295
- Polymorphism**, hemoglobin α -chain, G. Mazur and G. Braunitzer, 59
- Polypeptide composition**, cytochrome *c* oxidase, J. Jarausch and B. Kadenbach, 1133
- Polypeptides**, s.a. lipopolypeptides
 –, separation and purification of strongly hydrophobic polypeptides, W. Stoffel, W. Schröder, H. Hillen and R. Deutzmann, 1117
 – (hydrophobic), separation and purification, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- Polyribosomes**, polyadenylate · protein complex, A. Bernd, R.K. Zahn, A. Maidhof and W.E.G. Müller, 221
 –, vimentin-type intermediate filaments, P. Traub and W.J. Nelson, 1177
- Polysaccharides**, s.a. antistreptococcal group A polysaccharide antibody light chain, lipopolysaccharides
 –, binding to core protein, T. Stein, R. Keller, H.W. Stuhlsatz, H. Greiling, E. Ohst, E. Müller and H.-D. Scharf, 825
- Polysomes**, s. polyribosomes,
- Ponosterone A**, embryonic development of a crab, F. Lachaise and J.A. Hoffmann, 1059
- Pore glass (controlled)**, chromatography, R. Kleine and U. Kettmann, 843
- Primary culture**, glial cells, H.K. Illig, B. Witter, J. Gunawan, P. Ahrens and H. Debusch, 709
- Primary structure**, s. amino acid sequence
- Processing**, of RNA in vitro, K.P. Schäfer, 33
 –, acrylsulfatase A, A. Waheed, A. Hasilik and K. v. Figura, 425
- Proliferation**, s. granulocyte colony-stimulating factor
- Promyelocytes (human leukemic)**, proteolytic activities, M. Kidron, D.B. Friedman, M. Mayer, Y. Klemens and E. Fibach, 865
- Propionyl-CoA**, enzymatic preparation of (3*S*)-citryl-CoA, G. Löhlein and H. Eggerer, 1103
- Prostaglandin E₁**, temperature-induced membrane lipid phase transition and adenylate cyclase, J. Mruk, A. Bakardjiev and W. Burgermeister, 745
- Protamines**, synthesis of [perornithine]thynnine fragments, F. Marchiori, G. Borin, D. Stivanello, V. Moretto and G. Chessa, 1483
- Proteases**, s.a. anionic protease, cationic protease
 – (human granulocytes), coagulation factors IX and X, J. Kárpáti, K. Váradi and S. Elödi, 521
 – (rat myofibrils), inhibition, M. Dudai, M. Mayer and M. Kidron, 651
 –, microbial, R. Klein and U. Kettmann, 843
- Protease inhibitors**, captopril, L. Schack and T. Dietl, 107
 –, on leukocytes, L. Veselský, D. Čechová, V. Hruban and J. Klauudy, 113
 –, serine proteases, M. Muramatu, T. Satoh, Y. Yanagimoto, Y. Kanamoto, I. Katsuyama, M. Kanemoto and K. Taguchi, 203
 –, rat skeletal muscle, M. Dudai, M. Mayer and M. Kidron, 651
 –, promyelocytes, M. Kidron, D.B. Friedman, M. Mayer, Y. Klemens and E. Fibach, 865
- Protein A-gold technique**, kallikrein localization, M. Amouric, P. Lechene de la Porte and C. Figarella, 515
- α_1 -Proteinase inhibitor**, lung secretions, R.A. Stockeley, S.C. Afford and D. Burnett, 387

- , elastase, W. Hornebeck and H.P. Schnebli, 455
- , urine of pregnant women, B.-M. Jönsson, C. Löffler and K. Ohlsson, 1167
- (human) interaction with chymotrypsinogen A, H. Löbermann, F. Lottspeich, W. Bode and R. Huber, 1377
- Proteinase inhibitors**, s.a. α -cysteine proteinase inhibitor
- , α -macroglobulins, L.P. Nelles and H.P. Schnebli, 677
- Proteinases**, s.a. aspartic proteinases, serine proteinases
- , autolysis studies, T. Lah and V. Turk, 247
- , and peptidases, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 976
- , contaminant in α_1 -proteinase inhibitor preparations, H. Löbermann, F. Lottspeich, W. Bode and R. Huber, 1377
- Protein CM-2** (from *Bitis arietans* venom), amino acid sequence, F.J. Joubert, T. Haylett, D.J. Strydom and N. Taljaard, 1087
- Proteins**, s.a. apoprotein, Bence-Jones protein, copper protein complex, core protein, flavoprotein, lipoprotein, membrane protein, proteolipid apoprotein, respiratory proteins
- , inter-protein dependence during assembly of ribosomal 50 S subunits, R. Röhl, H.E. Roth and K.H. Nierhaus, 143
- , cortisol binding, J. Voigt and C.E. Sekeris, 159
- , complex with polyadenylate on mRNA, A. Bernd, R.K. Zahn, A. Maidhof and W.E.G. Müller, 211
- , amatoxin binding, O.G. Brodner, M. Sabbagh and T. Wieland, 273
- , retinoic acid binding, B. Gmeiner and G. Zerlauth, 337
- , high-performance liquid chromatography, G. Braunitzer, P. Rücknagel and W. Oberthür, 485
- (particle-bound), papaverine degradation, B. Hauer, K. Haase-Aschoff and F. Lingens, 499
- , membrane-bound, B. Železná and D. Čechová, 757
- , modern methods in analytical protein chemistry, 40th Conference of the Gesellschaft für Biologische Chemie, 1003
- , high-performance liquid chromatography, M. Kehl, F. Lottspeich and A. Henschel, 1501
- Protein synthesis** (chemical), s.a. peptide synthesis
- , introduction of the *S-tert*-butylthio protecting group, E. Wunsch, L. Moroder and S. Romani, 1461
- Proteokeratan sulfate** (bovine), linkage region between polysaccharide and protein, T. Stein, R. Keller, H.W. Stuhlsatz, H. Greiling, E. Ohst, E. Müller and H.-D. Scharf, 825
- Proteolipid apoprotein** (lipophilin), amino acid sequence of an *N*-terminal fragment, W. Stoffel, H. Hillen, W. Schroeder and R. Deutzmann, 855
- (lipophilin), amino acid sequence of proteolytic fragments, W. Stoffel, W. Schröder, H. Hillen and R. Deutzmann, 1117
- (lipophilin), partial amino acid sequence, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- Proteolysis**, α_1 -proteinase inhibitor, R.A. Stockley, S.C. Afford and D. Burnett, 387
- Proteolytic activity**, maturation of promyelocytes, M. Kidron, D.B. Friedman, M. Mayer, Y. Klemens and E. Fibach, 865
- Proteolytic cleavage**, proteolipid apoprotein, W. Stoffel, W. Schröder, H. Hillen and R. Deutzmann, 1117
- Pseudomonas spec.***, 4-chlorophenylacetic acid, A. Markus, U. Klages and F. Lingens, 431
- Pteridines**, s.a. dihydrobiopterine, tetrahydrobiopterine
- , allograft rejection, D. Fuchs, A. Hausen, C. Huber, R. Margreiter, G. Reibnegger, M. Spielberger and H. Wachter, 661
- Puff adder**, s. *Bitis arietans*
- Pyrenedecanoic acid**, excimer formation, J. Mruk, A. Bakardjiev and W. Burgermeister, 745
- Pyrophosphate**, effect on 3-hydroxy-3-methylglutaryl-CoA reductase, G. Gil, V.E. Calvet, A. Ferrer and F.G. Hegardt, 1217
- Quaternary structure**, hemocyanins, J. Markl, H. Decker, B. Linzen, W.G. Schutter and E.F.J. van Bruggen, 73
- , urokinase W. A. Günzler, G.J. Steffens, F. Ötting, G. Buse and L. Flohé, 133
- Quinoline**, tryptophan degradation, B. Hauer and F. Lingens, 507
- Radicals (OH[•])** ubisemiquinone-dependent reaction, H. Nohl, W. Jordan and D. Hegner, 599
- Radioactive labelling**, ¹²⁵I-labelled “facteur thymique serique”, G. Auger, D. Blanot, E. Bricas, J.-M. Pleau, M. Dardenne and J.-F. Bach, 331
- Radioactivity tracing**, [³H]amatoxin, O.G. Brodner, M. Sabbagh and T. Wieland, 273
- Radioligand assay**, somatotropin activity, M. Schleyer, H. Etzrodt, T.J. Trah and K.-H. Voigt, 1111
- Radioimmunoassay**, somatotropin activity, M. Schleyer, H. Etzrodt, T.J. Trah and K.-H. Voigt, 1111
- Radioimmunoassay**, tissue kallikrein, E. Fink and M. Schleuning, 1331
- Radioiodination**, vegetalizing inducer protein, K. Asahi, M. Asashima, H.-P. Geithe, J. Born, H. Tiedemann and H. Tiedemann, 563

- Reaction mechanism**, enoate reductase, M. Bühler and H. Simon, 609
- Reassociation**, lactate dehydrogenase subunits, R. Hermann, R. Rudolph and R. Jaenicke, 1259
- Receptor binding insulin**, A. Schüttler and D. Brandenburg, 317
- , insulin analogues, R. Geiger, K. Geisen and H.-D. Summ, 1231
- Receptors**, glucagon, O. Sonne, U.D. Larsen and J. Markussen, 95
- , conformational adjustment of insulin, D. Saunders and K. Freude, 655
- , ecdysteroid, M. Londershausen, P. Kuppert and K.-D. Spindler, 797
- Reduction** (stereospecific), oxo groups of oxocholanic acids, M. S. Anwer and D. Hegner, 731
- Reductive methylation**, tritium labelling, K. Asahi, M. Asashima, H.-P. Geithe, J. Born, H. Tiedemann and H. Tiedeman, 563
- Renal clearance**, excretion of tissue kallikrein, E. Fink and M. Schleuning, 1331
- Respiratory proteins**, spider hemocyanins, J. Markl, H. Decker, B. Linzen, W.G. Schutter and E.F.J. van Bruggen, 73
- Respiration** (in high altitude), hemoglobin of geese, W. Oberthür, G. Braunitzer and I. Würdinger, 581
- Restriction**, s. DNA restriction
- Reticulocytes** (rabbit), liver steatosis, C.L. Balduini, F. Sinigaglia, E. Ascari, U. Magrini, C. Seppi and C. Balduini, 1341
- Retinoic acid**, alkaline phosphatase, B. Gmeiner and G. Zerlauth, 337
- Retroviruses**, and embryogenesis, R. Jaenisch, 1267
- Reversed-phase high-pressure liquid chromatography**, reduced biopterins, M. Bräutigam, R. Dreesen and H. Herken, 341
- , pteridine levels, D. Fuchs, A. Hausen, C. Huber, R. Margreiter, G. Reibnegger, M. Spielberger and H. Wachter, 661
- , tetrahydrobiopterin determination, M. Bräutigam and R. Dreesen, 1203
- Rhein**, electron transport particles, P. Egerer, M. Bühler and H. Simon, 627
- Rhinoceros** (white rhinoceros, s. *Ceratotherium simum*)
- Ribonucleic acids**, s.a. messenger RNA
- , in vitro synthesis and processing, K.P. Schäfer, 33
- , influence of nucleosides on RNA labelling with $^{32}\text{P}_i$, C. Scholtissek, D. Evans and H. Bürger, 1389
- Ribosomes**, s.a. Polyribosomes
- (*E. coli*), 50S reconstitution, R. Röhl, H.E. Roth and K.H. Nierhaus, 143
- Rousettus aegyptiacus** (egyptian fruit bat), amino acid sequence of hemoglobin, T. Kleinschmidt and G. Braunitzer, 1209
- Salicylate**, s. diiodosalicylate
- Seminal protease inhibitors**, on leukocytes, L. Veselský, D. Čechová, V. Hruban and J. Klaudy, 113
- Serine proteinases**, acrosin, B. Železná and D. Čechová, 757
- , low-molecular mass urokinase from human urine, G.J. Steffens, W.A. Günzler, F. Ötting, E. Frankus and L. Flohé, 1043
- , high-molecular mass urokinase from human urine, W.A. Günzler, G.J. Steffens, F. Ötting, S.-M.A. Kim, E. Frankus and L. Flohé, 1155
- Serum** (human), α -cysteine proteinase inhibitor, K. Minakata, M. Asano, T. Sato and N. Harada, 493
- Sheeps**, s. *Ovis ammon*
- Shemin's pathway**, biosynthesis of chlorophyll, O. Klein and R.J. Porra, 551
- Sialic acids**, s.a. 9(8)-O-acetylated sialic acids
- , fluorimetric determination, A.K. Shukla and R. Schauer, 255
- , rabbit reticulocytes during liver steatosis, C.L. Balduini, F. Sinigaglia, E. Ascari, U. Magrini, C. Seppi and C. Balduini, 1341
- Sialidase** (EC 3.2.1.18), (human liver), solubilization and affinity chromatography, J.-C. Michalski, A.P. Corfield and R. Schauer, 1097
- Skeletal muscle** (rat), protease inhibitor activity, M. Dudai, M. Mayer and M. Kidron, 651
- Skeletal muscle myosin** (chicken), amino acid sequence of L-1 light chain, T. Umegane, T. Maita and G. Matsuda, 1321
- Skin**, s. fibroblasts, hypodermis
- Snakes**, s. *Bitis arietans* (puff adder)
- Snake venom** (from *Bitis arietans*), protein CM-2, F.J. Joubert, T. Haylett, D.J. Strydom and N. Taljaard, 1087
- Solid-phase synthesis**, s. peptide synthesis
- Somatostatin-28**, synthesis of norleucine-8 analogue, L. Moroder, E. Wünsch, N. Vaysse and A. Ribet, 1247
- Somatotropin**, (porcine), heterogeneity, M. Schleyer, T. Trah and I. Schleyer, 179
- (human), disulfide bridges, M. Schleyer, H. Etzrodt, T.J. Trah and K.-H. Voigt, 1111
- Sperm** (boar), two active forms of acrosin, B. Železná and D. Čechová, 757
- Spermatozoal autolysis**, decapeptide as spermatozoal antigen, A.B. Czuppon and L. Mettlet, 1465
- Sphingomyelins**, azido fatty acid-substituted, W. Stoffel, K.-P. Salm and M. Müller, 1
- Spiders** (tarantula) s. *Eurypelma californicum*
- Steatosis** (rabbit liver), anomalous erythrocytes, C.L. Balduini, F. Sinigaglia, E. Ascari, U. Magrini, C. Seppi and C. Balduini, 1341

- Stereochemistry**, enoate reductase, M. Bühler and H. Simon, 609
- , (2*R*,3*S*)-2,3-dimethylmalate-lyase reaction, G. Löhlein and H. Eggerer, 1103
- , water elimination from (2*R*)-phenyllactate, C. Pitsch and H. Simon, 1253
- Stereospecificity**, reduction of oxo groups of oxocholanic acids, M.S. Anwer and D. Hegner, 731
- Steroid derivatives**, immunogenicity, D. Berg, H.-H. Warnecke and E. Kuss, 737
- Steroid hormones**, drug disposition, M. Wenzel, G. Schachschneider, M. Schneider and R. Herken, 693
- Streptococcus**, s. anti-streptococcal group A polysaccharide antibody light chain
- Structure-activity relationship**, [D-Arg^{B22}]insulin, R. Knorr, W. Danho, E.E. Büllsbach, H.-G. Gattner, H. Zahn, G.L. King and C.R. Kahn, 1449
- Structure-function relationship**, biologically active peptides, H. Jörnvall, V. Mutt and M. Persson, 475
- Subcellular system**, RNA in vitro synthesis and processing, K.P. Schäfer, 33
- Suberic acid**, s. [1,6- α -aminosuberic acid, 8-arginine]-vasopressin
- Submandibular gland** (equine), mucin-specific sialidase, J.-C. Michalski, A.P. Corfield and R. Schauer, 1097
- Substrate specificity**, enoate reductase, M. Bühler and H. Simon, 609
- Subunit assembly**, hemocyanins, J. Markl, H. Decker, B. Linzen, W.G. Schutter and E.F.J. van Bruggen, 73
- Sulfobromophthalein**, uptake into hepatocytes, L.R. Schwarz, 1225
- Sulfhydryl bonds**, s. disulfide bonds, disulfide bridges, disulfides, thiol protection
- SV40 T-Antigen**, related protein, J. Horst, E. Jacob, C. Weckler and W. Deppert, 445
- Swan** (mute swan), s. *Cygnus olor*
- T-2**, s. toxin T-2
- T-Antigen**, s. SV40 T-antigen
- Tarantula**, s. *Eurypelma californicum*
- Temperature**, lipid-phase transition, J. Mruk, A. Bakardjiev and W. Burgermeister, 745
- Teratocarcinoma cells** (human), linkage monosaccharides of glycopeptides, M.-L. Rasilo and O. Renkonen, 89
- Tetrahydrobiopterine**, determination, M. Bräutigam, R. Dreesen and H. Herken, 341
- , determination in biological tissues, M. Bräutigam and R. Dreesen, 1203
- Thermitase**, s. *Thermoactinomyces vulgaris* alkaline proteinase
- Thermoactinomyces vulgaris** alkaline proteinase, separation from anionic protease, R. Kleine and U. Kettmann, 843
- Thermostability**, microbial proteases, R. Kleine and U. Kettmann, 843
- 1-Thiohydrazine-1,2-dicarboxylic acid derivatives**, disulfide synthesis, E. Wünsch and S. Romani, 449
- Thiol protection**, introduction of the *S-tert*-butylthio-protecting group, E. Wünsch, L. Moroder and S. Romani, 1461
- Thrombocytes** (human), lipoproteins, E. Koller, F. Koller and W. Doleschel, 395
- (human), prostaglandin action, J. Mruk, A. Bakardjiev and W. Burgermeister, 745
- Thynnine**, synthesis of fragments of [perornithine]-thynnine, F. Marchiori, G. Borin, D. Stivanello, V. Moretto and G. Chessa, 1483
- Tibia**, assay for somatotropin activity, M. Schleyer, H. Etzrodt, T.J. Trah and K.-H. Voigt, 1111
- Tissue** (biological), tetrahydrobiopterin determination, M. Bräutigam and R. Dreesen, 1203
- Tissue kallikrein** (EC 3.4.21.35), (hog pancreas), blood pressure, L. Schack and T. Dietl, 107
- (human, pancreatic), immunocytochemical localization, M. Amouric, P. Lechene de la Porte and C. Figarella, 515
- (human urinary and pancreatic), comparison, E. Fink, M. Amouric, R. Geiger and C. Figarella, 819
- , excretion from blood into urine, E. Fink and M. Schleuning, 1331
- Tissue specificity**, cytochrome c oxidase, J. Jarausch and B. Kadenbach, 1133
- T-Lymphocytes**, alloantigen-induced proliferation, D. Fuchs, A. Hausen, C. Huber, R. Margreiter, G. Reibnegger, M. Spielberger and H. Wachter, 661
- Toxins**, s. a. snake venom, uremic toxins
- Toxin T-2**, micro enzyme immunoassay, H. Peters, M.P. Dierich and K. Dose, 1437
- Tracing**, s. radioactivity tracing
- Transacylation**, acyl-chymotrypsin, V. Kasche and R. Zöllner, 531
- Transformation**, SV40 gene fragment, J. Horst, E. Jacob, C. Weckler and W. Deppert, 445
- Transglutaminase**, s. glutaminyl-peptide γ -glutamyltransferase
- Translation**, and posttranslational events, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 871
- Transport**, in normal and malignant cells, Joint meeting of the nordic biochemical societies and the Gesellschaft für Biologische Chemie, 894

- , -molecular biology of, 39th Conference of the Gesellschaft für Biologische Chemie, 1409
- Trichothecenes**, detection of toxin T-2, H. Peters, M.P. Dierich and K. Dose, 1437
- Tris(hydroxymethyl)methylamine**, acyl-chymotrypsin, V. Kasche and R. Zöllner, 531
- Tritiation**, vasopressin analoga, F. Fahrenholz, H.S. Hussein, J.L. Morgat and K.-H. Thierauch, 1415
- Tritium labelling**, vegetalizing inducer protein, K. Asahi, M. Asashima, H.-P. Geithe, J. Born, H. Tiedemann and H. Tiedemann, 563
- Triton X-100**, resistant residual cell structures, P. Traub and W.J. Nelson, 1177
- Trypsin (EC 3.4.21.4)**, complex with α_2 -macroglobulin, K. Ohlsson, A. Polling and P. Stenberg, 213
- , inhibitor in skeletal muscle, M. Dudai, M. Mayer and M. Kidron, 651
- , complex with α_2 -macroglobulin, H.J. Schramm and W. Schramm, 803
- Trypsin-kallikrein inhibitor**, binding to soluble carrier polymers, M. Havranová, D. Čechová, V. Saudek, M. Metalová and J. Drobník, 295
- Trypsin inhibitor** (urine of pregnant women), granulocyte elastase, B.-M. Jönsson, C. Löffler and K. Ohlsson, 1167
- Tryptophan**, active site of hemocyanins, H.-J. Schneider, U. Illig, E. Müller, B. Linzen, F. Lottspeich and A. Henschen, 487
- Tryptophan (D- and L-)**, in pos. A1 of an insulin analogue, R. Geiger, K. Geisen and H.-D. Summ, 1231
- Tryptophan cleavage**, proteolipid apoprotein, W. Stoffel, W. Schröder, H. Hillen and R. Deutzmann, 1117
- , lipophilin, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- Tryptophan fragments**, proteolipid apoprotein, W. Stoffel, H. Hillen, W. Schroeder and R. Deutzmann, 855
- Tryptophyl bonds**, cleavage, R. Biewald and G. Buse, 1141
- Tumors**, s. ascites tumor cells, Ehrlich ascites tumor, Lewis lung tumor, malignant cells, teratocarcinoma cells
- Tyrosine aminotransferase (EC 2.6.1.5)**, chloramphenicol degradation products, H.G. Beschle, R. Süßmuth and F. Lingens, 439
- Ubisemiquinone**, radical formation, H. Nohl, W. Jordan and D. Hegner, 599
- Uremic toxins**, oligopeptides, G. Bovermann, H. Rautenstrauch, G. Seybold and G. Jung, 1187
- Urine** (human) comparison of urinary and pancreatic kallikrein, E. Fink, M. Amouric, R. Geiger and C. Figarella, 819
- , (human), low-molecular mass urokinase, G.J. Steffens, W.A. Günzler, F. Ötting, E. Frankus and L. Flohé, 1043
- , (human), high-molecular mass urokinase, W.A. Günzler, G.J. Steffens, F. Ötting, S.-M.A. Kim, E. Frankus and L. Flohé, 1155
- , (pregnant women), trypsin inhibitor, B.-M. Jönsson, C. Löffler and K. Ohlsson, 1167
- , (dog), excretion of tissue kallikrein, E. Fink and M. Schleuning, 1331
- Urokinase (EC 3.4.21.31)**, (human), structural relationships, W.A. Günzler, G.J. Steffens, F. Ötting, G. Buse and L. Flohé, 133
- , (low-molecular mass from human urine), complete amino acid sequence, G.J. Steffens, W.A. Günzler, F. Ötting, E. Frankus and L. Flohé, 1043
- , (high-molecular mass from human urine), amino acid sequence of A chain, W.A. Günzler, G.J. Steffens, F. Ötting, S.-M.A. Kim, E. Frankus and L. Flohé, 1155
- Uterus** (rat), kininogenase activity, M. Marin-Grez, G. Schaechtelin and K. Hermann, 1359
- Vasopressin**, synthesis of tritiated reactive analoga, F. Fahrenholz, H.S. Hussein, J.L. Morgat and K.-H. Thierauch, 1415
- Vegetalizing inducer protein**, radioactive labelling, K. Asahi, M. Asashima, H.-P. Geithe, J. Born, H. Tiedemann and H. Tiedemann, 563
- Venom**, s. snake venom
- Vimentin** (intermediate filaments) polyribosomes, P. Traub and W.J. Nelson, 1177
- Virus**, s. retroviruses, influenza virus
- Virus RNA**, influence of nucleosides on labelling with ³²Pi, C. Scholtissek, D. Evans and H. Bürger, 1389
- Water**, stereospecific elimination from (2R)-phenyl-lactate, C. Pitsch and H. Simón, 1253
- Wheat germ**, amatoxin-binding protein, O.G. Brodner, M. Sabbagh and T. Wieland, 273
- White matter** (bovine brain), partial amino acid sequence of proteolipid apoprotein, W. Stoffel, H. Hillen, W. Schröder and R. Deutzmann, 1397
- Zebra** (mountain zebra), s. *Equus zebra*
- Zona pellucida** (porcine), antigens, J. Dietl, A. Czuppon and L. Mettler, 381
- Zonation**, s. metabolic zonation

Autorenverzeichnis

Die mit * versehenen Seitenzahlen beziehen sich auf Kurzreferate von Tagungen und Konferenzen

- Achstetter, T.**, O. Emter, C. Ehmann and D.H. Wolf, New proteinases in yeast: Studies on regulation and purification 976*
- Aebersold, R.** s. H. Herbst
- Afford, S.C.** s. R.A. Stockley
- Afting, E.-G.** s. J. Frey
- Agarwal, D.P.** s. B. Ziemsen
- Ahrens, P.** s. H.K. Illig
- Akerboom, T.P.M.**, M. Bilzer and H. Sies, The hepatic disposition of glutathione S-conjugates and taurocholate in the perfused rat liver under the influence of the glutathione redox state 963*
- Akerboom, T.P.M.** s. R. Brigelius
- Alexson, S.**, H. Shio and P.B. Lazarow, Intraperoxisomal localisation of β -oxidation enzymes in rat liver 968*
- Almås, I.**, B. Singh and B. Borrebaek, The action of vasopressin and calcium on palmitate metabolism in hepatocytes and isolated mitochondria from rat liver 909*
- Alonso, S.** s. M.E. Buckingham
- Altendorf, K.** s. E. Schneider
- Altendorf, K.** s. K. Steffens
- Altendorf, K.** s. L. Wiczorek
- Althaus, H.H.** s. P. J. Gebicke-Härter
- Amnéus, H.** s. P.F. Zipfel
- Amory, A.** s. A. Goffeau
- Amouric, M.**, P. Lechene de la Porte and C. Figarella, Immunocytochemical localization of pancreatic kallikrein in human acinar cells 515
- Amouric, M.** s. E. Fink
- Anders, F.**, Genes for neoplasia and cell differentiation in *Xiphophorus* 123*
- Andersen, J.P.** s. J.V. Møller
- Andres, K.H.** s. Ch.R. Schätz
- Angel, I.**, A. Fleißner and R. Seifert, Synthese und Aufnahme von γ -Aminobutyrat (Gaba) in synaptische Vesikel 1295*
- Anner, B.M.**, Ion transport in Na,K-ATPase liposomes 465*
- Anwer, M.S.** and D. Hegner, Stereospecific reduction of 3- and 7-oxo groups of oxocholanic acids in isolated perfused rat liver 731
- Appel, B.**, L. Cooley and D. Söll, The 5'-terminus of mature histidine tRNA species is formed by post-transcriptional nucleotide addition 871*
- Appel, B.** s. P. Bringmann
- Aquila, H.**, W. Bogner and M. Klingenberg, ADP/ATP-Translocator from beef heart mitochondria – amino acid sequence and surface labeling 894*
- Aquila, H.**, D. Misra, M. Eulitz and M. Klingenberg, Complete amino acid sequence of the ADP/ATP carrier from beef heart mitochondria 345
- Arad, T.** s. K.R. Leonard
- Arendes, J.** and A. Sugino, In vitro replication of yeast 2- μ m plasmid DNA: Single-stranded DNA-binding protein restores the cdc8 defect 922*
- Arndt, R.** s. H. E. Schlaak
- Arnold, H.-H.** s. A. Ogilvie
- Arnold, M.** s. R. Neumeier
- Asahi, K.**, M. Asashima, H.-P. Geithe, J. Born, H. Tiedemann and H. Tiedemann, Radioiodination with 125 I and reductive methylation with tritium of a vegetalizing inducer protein: Specific radio-activities and effect on biological activity 563
- Asano, M.** s. K. Minakata
- Asashima, M.** s. K. Asahi
- Ascari, E.** s. C.L. Balduini
- Åström, S.** s. M. Norell
- Auger, G.**, D. Blanot, E. Bricas, J.-M. Pléau, M. Dardenne and J.-F. Bach, Synthesis of an immunogenic conjugate and of two 125 I-labelled derivatives of the "facteur thymique sérique" 331
- Bach, J.-F.** s. G. Auger
- Bachmann, B.**, R. Hofmann and H. Follmann, Koordination der Desoxyribonucleotid-Biosynthese während des Zellzyklus 952*
- Bachmann, M.** s. M. Geisert
- Baese, H.-J.** s. R. Gehrmann
- Baese, H.-J.** s. H. Iwan
- Bäuerlein, E.**, H. J. Skrzipezyk and B. Küchler, Inhibition of H^{\oplus} -driven ATP synthesis by [3 H-2,3]propylhydroxylamine in $TF_1 F_0$ -liposomes and chloroplasts 471*
- Bäuerlein, E.**, H. J. Skrzipezyk and B. Küchler, [2,3- 3 H]-Propylhydroxylamine, a trapping reagent for esters and anhydrides, inhibits H^{\oplus} -driven ATP synthesis in $TF_1 \cdot F_0$ -liposomes 540*
- Bäumert, H.G.** and H. Fasold, A study of sarcoplasmic reticulum Ca^{2+} -ATPase from rabbit muscle using different nucleotide analogs 944*
- Bahr-Lindström, H.** von s. H. Jörnvall
- Bakardjiev, A.** s. J. Mruk
- Bald, R.** s. P. Bringmann
- Balduini, C.L.**, F. Sinigaglia, E. Ascari, U. Magrini, C. Seppi and C. Balduini, Anomalous erythrocytes produced by rabbits with liver damage 1341

- Balduini, C. s. C.L. Balduini
 Bali, J.-P. s. A. Previero
 Bali, J.-P. s. E. Wünsch
 Ballard, F. J., Effects of growth factors on protein turnover in cultured cells 977*
 Balkau, D. s. R. Niemann
 Balks, J. s. K. Beckh
 Bandini, G. s. J. Verdenhalven
 Barde, Y.-A., D. Edgar and H. Thoenen, Purification of a new neurotrophic factor from mammalian brain 1295*
 Bargetzi, J.-P. s. L. Juillerat-Jeanneret
 Barkholt, V. s. T.E. Jessen
 Barnhoorn, M. G. s. A. Tulp
 Barth, A. s. G. Fischer
 Barth, A. s. Hj. Matthies
 Barth, A. s. K. Neubert
 Barth, C.A. s. M. Pfeuffer
 Barth, C.A. s. M. de Vrese
 Bartholmes, P., T. Seifert and R. Jaenicke, Reversible denaturation and dissociation of *E. coli* tryptophan synthase β_2 -subunit induced by high hydrostatic pressure 986*
 Bauer, Ch., L. Recktenwald, R. Tauber, R. Bauer, C. Orfanos and W. Reutter, Disturbance of glycoprotein metabolism in psoriatic skin 1023*
 Bauer, H., The dualism of expression of *onc*-genes: Transformation versus differentiation 122*
 Bauer, H. s. L. Khoury
 Bauer, R. s. Ch. Bauer
 Bauer, U. und K. Brand, Glucose- und Ketonkörperstoffwechsel in Synaptosomen, isoliert aus Rattenhirnrinde 1296
 Baumkötter, J. and M. Cantz, Human fibroblast ganglioside sialidase: inhibition by glycosaminoglycans 1023*
 Bause, E., Epoxyalkyl peptide derivatives as active site directed inhibitors of asparagine-*N*-glycosyltransferases 1024*
 Bause, E. s. H. Hettkamp
 Bause, E. s. T. Müller
 Bautz, E.K.F. s. U. Walldorf
 Bayer, E. s. B. Hemmasi
 Bechtel, W.D. and H.A. Ensinger, Brotizolam binding to benzodiazepine and γ -aminobutyric acid receptors 1296*
 Bechtel, W.D. s. A. Haggag
 Beck, K. and R. Peters, Translation diffusion in lipid monolayers at the air/water interface 894*
 Becker, W.F. s. G. von Jagow
 Beckh, K., H. Hartmann, J. Balks and K. Jungermann, Regulation of the glycogen degradation in rat liver by α -sympathetic hepatic nerves 1290*
 Beckh, S. s. W. Seifert
 Beck, van W.P. s. A. Tulp
 Behnel, H. J., Comparative studies on protein synthesis and heatshock puffing activity in larval salivary glands of *Drosophila melanogaster* treated with chloramphenicol 923*
 Behrendt, N., B. Foltmann and P.P. Clausen, Pepstatin-dextran-peroxidase conjugate: A selective marker for aspartic proteases in active conformation 977*
 Bereiter-Hahn, J. s. B.M. Heil
 Béress, L. und J. Zwick, Palytoxin als neues Werkzeug für die Membranforschung 1284*
 Béress, L. s. M. Rack
 Berg, D., H.-H. Warnecke and E. Kuss, Synthesis of immunogenic C-6 derivatives of 2-methoxyestrone and 2-methoxyestradiol-17 β and characterization of the corresponding antisera 737
 Berge, R.K., L. Hossöy and M. Farstad, Influence of dietary status on some hepatic enzymes, CoASH and long-chain Acyl-CoA in rats 969*
 Bergh, M.L.E. s. D.H. van den Eijnden
 Bergmann, W. s. V. Dressler
 Bergseth, S. s. K. Saarem
 Berlet, H.H. und G. Schulz, Isolierung des Myelin-basischen Proteins aus menschlichem Gehirn 1297*
 Bernd, A., R.K. Zahn, A. Maidhof and W.E.G. Müller, Analysis of polyadenylate-protein complex of polysomal messenger RNA from mouse L cells 221
 Berndt, J. s. M. Boll
 Berndt, J. s. J.-S. Jenke
 Bernhardt, J. and E. Neumann, Gating properties of single acetylcholine receptor channels from flux analysis 1297*
 Bernheimer, H., H. Budka und P. Müller, Vermehrung von Immunglobulinen (Ig) im Gehirn bei Adrenoleukodystrophie, einer Entmarkungserkrankung genetisch-metabolischer Ätiologie 1293*
 Bernier, J.-L. s. J.-P. Hénichart
 Bertram, S. s. R. Wagner
 Beschle, H.G., R. Süßmuth and F. Lingens, Conversion of chloramphenicol degradation products by tyrosine aminotransferase from flavobacteria 439
 Beschle, H.G., R. Süßmuth and F. Lingens, Eigenschaften von aromatischen Aminosäure-Aminotransferasen aus zwei Chloramphenicol-resistenten Flavobakterien 1365
 Bessler, W.G., R.B. Johnson, K. Wiesmüller and G. Jung, B-Lymphocyte mitogenicity in vitro of a synthetic lipopeptide fragment derived from bacterial lipoprotein 767
 Bethge, N. s. F. Diel
 Betz, H., D. Graham, F. Pfeiffer and H. Rehm, Synaptic membrane proteins of the vertebrate central nervous system 1285*
 Betz, H., D. Graham and H.A. Rehm, Identification of polypeptides associated with a putative neuronal nicotinic acetylcholine receptor 1298*
 Betz, H. s. F. Pfeiffer

- Betz, H. s. H. A. Rehm
 Bickel-Sandkötter, S. s. H. Strotmann
 Biewald, R. and G. Buse, Studies on cytochrome *c* oxidase, IX. The primary structure of polypeptide VIa 1141
 Bilzer, M. s. T. P. M. Akerboom
 Bjarnason, J. B. and J. W. Fox, Proteolytic specificity and cobalt exchange of hemorrhagic toxin e, a zinc protease isolated from the western diamondback rattlesnake (*Crotalus atrox*) venom 978*
 Bjerrum, O. J., Membrane antigens. Electroimmunochemical analysis 1004*
 Bjerrum, O. J. s. M. Wilken
 Björkhem, I. s. F. Kase
 Blanken, W. M., G. J. M. Hooghwinkel and D. H. van den Eijnden, Biosynthesis of blood group II substances. Specificity of bovine colostrum galactosyltransferase 1024*
 Blanot, D. s. G. Auger
 Blegg, H. S., S. B. Mortensen and M. Kilian, Isolation and properties of an immunoglobulin A1-degrading protease from *Haemophilus influenzae*, serotype b 978*
 Bockemühl, S. s. B. Meier
 Bode, J. s. M. M. Gómez-Lira
 Bode, W. s. A. Henschen
 Bode, W. s. H. Löbermann
 Bodenmüller, H., H. C. Schaller und C. J. P. Grimmelikhuijzen, Immunologische Nachweismethoden für den Kopfaktivator 1298*
 Boehm, B., H. Krippner and D. Drahovsky, Interaction of circulating immunoglobulins with double-stranded DNA: Structural and nucleotide sequence specificity 987*
 Böhm, J. s. E. Pöschl
 Boehm, T. L. J. and D. Drahovsky, Digestion of DNA in agarose with restriction enzymes: a new analytical approach allowing two-dimensional analysis of enzymatic DNA methylation of eukaryotic genomes 923*
 Boehm, T. L. J. and D. Drahovsky, Effects of various chemical carcinogens on enzymatic DNA methylation in eukaryotic cells 987*
 Boehm, T. L. J. s. G. Pfeifer
 Böhmerová, E. s. L. Kováč
 Böttger, M. s. R. Lindigkeit
 Bøg-Hansen, J. C. and J. Hau, Affinity electrophoresis with special reference to glycoproteins 1005*
 Bogner, W. s. H. Aquila
 Boisen, S., Inhibitors of microbial, animal and human proteases in the barley grain 978*
 Boiteux, A., The glycolytic oscillator: model for the cellular clock? 535*
 Boiteux, A., Glycolysis in fertilized eggs of *Paracentrotus lividus* 540*
 Boiteux, A. and H.-G. Busse, Network analysis of glycolysis 541*
 Boiteux, A. s. E. M. Chance
 Boiteux, A. s. M. Markus
 Bolkenius, F. N. s. N. Seiler
 Boll, M., E. Brückner and J. Berndt, Age-related differences in dietary regulation of lipogenic enzymes in rat liver 103
 Bonhoeffer, F., Cell recognition of axonal growth cones in vitro 127*
 Bonifer, C. s. A. E. Sippel
 Bonting, S. L. and J. J. H. H. M. de Pont, Comparative aspects of structure and mechanism of Na,K-ATPase and gastric K,H-ATPase 465*
 Boos, K.-S. and E. Schlimme, A new model for mitochondrial carrier-mediated ADP, ATP transport 909*
 Boos, K.-S. s. E. Schlimme
 Bordas, J. s. H.-J. Hartmann
 Bordier, C. s. J. Stadler
 Borin, G. s. F. Marchiori
 Born, J. s. K. Asahi
 Bornemann, S. s. W. Michels
 Borrebaek, B. s. I. Almås
 Borrebaek, B. s. B. Singh
 Bosca, L. s. P. A. Lazo
 Boustead, C. s. V. Witzemann
 Bovermann, G., H. Rautenstrauch, G. Seybold und G. Jung, Isolierung, Strukturaufklärung und Synthese eines Hexapeptids aus dem Hämodialysat urämischer Patienten 1187
 Bøyum, A., Separation of mononuclear cells, granulocytes and monocytes with Nycodens, a new medium 999*
 Bräutigam, M. and R. Dreesen, Determination of *L-erythro*-tetrahydrobiopterin in biological tissues by high pressure liquid chromatography and electrochemical detection 1203
 Bräutigam, M., R. Dreesen and H. Herken, Determination of reduced biopterins by high pressure liquid chromatography and subsequent electrochemical detection 341
 Brand, K. and H. Schweiger, Interaction between oxidative decarboxylation of branched-chain α -oxo acids and oxidative phosphorylation in rat liver mitochondria 547*
 Brand, K. s. U. Bauer
 Brand, K. s. W. Demmer
 Brandenburg, D. s. C. Diaconescu
 Brandenburg, D. s. A. Schüttler
 Braun, D. G. s. H. Herbst
 Braunitzer, G. and J. Godovac, Hemoglobins, XLV. The amino acid sequence of pheasant (*Phasianus colchicus*) hemoglobins 229
 Braunitzer, G., W. Jelkmann, A. Stangl, B. Schrank und C. Krombach, Hämoglobine, XLVIII: Die primäre Struktur des Hämoglobins des indischen Elefanten (*Elephas maximus*, Proboscidea): $\beta 2 = \text{Asn}$ 683

- Braunitzer, G., P. Rücknagel and W. Oberthür, Einfache Reinigung von Acetonitril für die Hochdruckflüssigkeitschromatographie (HPLC) von Peptiden und Proteinen 485
- Braunitzer, G. s. T. Kleinschmidt
- Braunitzer, G. s. G. Mazur
- Braunitzer, G. s. W. Oberthür
- Brause, U. s. T.O. Kleine
- Bremer, J., The function of peroxisomes in the shortening of carboxylic acids 969*
- Bremer, J. s. H. Lund
- Bremer, J. s. B. Singh
- Brendel, V., E.P. Pashnina and E.N. Trifonov, Prokaryotic transcription terminator structure: Dinucleotide distribution matrix and consensus sequences 923*
- Brennecke, M. and K. Resch, Phosphatidylcholine and phosphatidylinositol show a different activation pattern of their turnover rates of unsaturated fatty acid moieties in plasma membranes of concanavalin A-stimulated thymocytes 894*
- Bricas, E. s. G. Auger
- Brigelius, R., T.P.M. Akerboom, C. Muckel and H. Sies, Glutathione in hepatic mixed disulfides and the influence of 'oxidative stress' 964*
- Brigelius, R. s. H. Sies
- Bringmann, P., R. Reuter, J. Rinke, B. Appel, R. Bald and R. Lührmann, 5'-Terminal caps of snRNAs are available for reaction with m₂^{2,7}G-specific antibody in isolated snRNPs 924*
- Brinkmann, K. s. M. Hoffmans
- Brinkmann, K. s. K.-A. Rinast
- Bro, B. s. J. Carlsen
- Brodner, O.G., M. Sabbagh und Th. Wieland, Isolierung und Charakterisierung eines Amatoin-bindenden Proteins aus Weizenkeimen 273
- Brosius, B., W. Hillen and D. Riesner, Thermodynamics of nucleic acids entrapped in reversephase evaporation vesicles 987*
- Brossmer, R., A. Bünsch, H. Mack, U. Rose, B. Schüll and J. Villalva, Synthesis and biological properties of novel sialic acids and related compounds 1016*
- Brossmer, R. s. G. Keilich
- Brossmer, R. s. D. Ziegler
- Brückner, E. s. M. Boll
- Brüning, G. s. H. Rommelspacher
- Bruggen, E.F. J. van s. J. Markl
- Brummer, W. s. H.-A. Fabricius
- Bruns, W. s. H. Dinter
- Bruns, W. s. U. Mayr
- Brust, R., Structural studies on chromatin by viscosity measurements 924*
- Brust, R. s. H. Notbohm
- Buchner, K. und D.G. Weiss, Retrograder axonaler Transport in C-Fasern des Nervus olfactorius 1298*
- Buckingham, M.E., A. Minty, B. Robert, M. Caravatti, S. Alonso, G. Bugaisky, A. Cohen, P. Daubas and A. Weydert, The expression of myosin and actin genes during skeletal muscle myogenesis 121*
- Buddecke, E. s. R. Niemann
- Budka, H. s. H. Bernheimer
- Büchsel, R., W. Kreisel, E. Löhle, J. Schölmerich, W. Reutter, W. Gerok and E. Köttgen, Vitamin A - deficiency impairs the glycosylation of dipeptidyl peptidase IV isolated from rat liver plasma membrane 1025*
- Büchsel, R. s. W. Kreisel
- Bühler, M. and H. Simon, On the kinetics and mechanism of enoate reductase 609
- Bühler, M. s. P. Egerer
- Büllesbach, E.E. s. R. Knorr
- Bünsch, A. s. R. Brossmer
- Bürger, H. s. C. Scholtissek
- Büther, H. and W. Thiemann, The role of glutathione in the mammalian metabolism of bromoform by the liver monooxygenase system 964*
- Bugaisky, G. s. M.E. Buckingham
- Bunte, T. s. K. Moelling
- Burckhardt, G. s. W. Kramer
- Burgermeister, W. s. J. Mruk
- Burnett, D. s. R.A. Stockley
- Buscher, H.-P. s. G. Fricker
- Buse, E. und H. Matthaei, Zur morphologischen Typisierung cerebellärer Neuronen, die sich ohne direkten Zellkontakt in Kultur differenzieren 1299*
- Buse, G. s. R. Biewald
- Buse, G. s. W.A. Günzler
- Busse, H.-G. s. A. Boiteux
- Busse, H.-G. s. J. Das
- Butz, U. s. B. Wurster
- Cadenas, E., H. Graf, V. Ullrich and H. Sies, Oxene donors yield low-level chemiluminescence with liver microsomes and isolated cytochrome P-450 971*
- Cadenas, E. s. H. Sies
- Calabrese, L. s. B. Meier
- Calas, A. s. H.G. Hartwig
- Calvet, V.E. s. G. Gil
- Cantz, M. s. J. Baumkötter
- Cantz, M. s. K. Mendla
- Cantz, M. s. A. Waheed
- Carafoli, E., The calcium-pumping ATPase of plasma membrane 461*
- Caravatti, M. s. M.E. Buckingham
- Carbone, E., E. Wanke, G. Prestipino, L.D. Possani and A. Maelicke, Selective action of purified scorpion neurotoxins on the ionic currents of the squid giant axon 1299*
- Carlquist, M. s. H. Jörnvall

- Carlsen, J., K. Christiansen and B. Bro, Purification of microvillus membrane vesicles 895*
- Carlsen, J. s. K. Christiansen
- Carrillo, N. s. R. Wagner
- Casaretto, M., W. Danho, R.-D. Hesch und H. Zahn, Synthese von zwei medianen Segmenten des humanen Parathyrens 407
- Catteau, J.-P. s. J.-P. Hénichart
- Čechová, D. s. M. Havranová
- Čechová, D. s. L. Veselský
- Čechová, D. s. B. Železná
- Cervenka, J. s. H. Osmundsen
- Chance, E.M., B. Hess and A. Boiteux, Pattern formation in glycolysis 541*
- Chang, J. Y. s. H. Herbst
- Changeux, J.-P., Regulation of synapse formation in the development of the neuromuscular junction 128*
- Chanpu, S. s. D. Werner
- Charlier, J. s. E. Gerlo
- Chessa, G. s. F. Marchiori
- Christiansen, E.N. s. M. S. Thomassen
- Christiansen, K. and J. Carlsen, Reconstitution of protein into lipid vesicles using natural detergents 895*
- Christiansen, K. s. J. Carlsen
- Christiansen, N. and J. Carlsen, Reconstitution of a protein into lipid vesicles using natural detergents 895*
- Cichutek, K., H. Twifler, K. Gersonde and H. Witzel, Studies on the purple beef spleen phosphatase 958*
- Clark, B.F.C. s. F. Wikman
- Clausen, P.P. s. N. Behrendt
- Cohen, A. s. M.E. Buckingham
- Cohn, W., F. Loechleiter and F. Weber, Influence of vitamin A deficiency on serum lipoproteins in rats 948*
- Collard, J.G. s. A. Tulp
- Collins, J. s. H. Dinter
- Collins, J. s. U. Mayr
- Conradt, H. s. V. Eschenfelder
- Cooley, L. s. B. Appel
- Corfield, A.P. s. J.-C. Michalski
- Cornelius, G. s. M.G. Vicker
- Cramer, F. s. U. Englisch
- Cramer, F. s. H. J. Gabius
- Cramer, F. s. S. Peters
- Cramer, F. s. R. Schröder
- Cramer, F. s. H. Sternbach
- Csordas, A. s. P. Loidl
- Csordas, A. s. I. Multhaup
- Czech, J. s. K.-D. Jany
- Czuppon, A.B., Masking of an embryonal antigen (F9) by sialic acid(s) on the human spermatozoal membrane 1025*
- Czuppon, A. B. and L. Mettler, Chemical synthesis of a decapeptide eliciting characteristics of a human spermatozoal antigen 1465
- Czuppon, A. s. J. Dietl
- Dahlmann, B., L. Kuehn and H. Reinauer, Susceptibility of muscle cytosolic proteins to muscle alkaline proteinase (chymase) 979*
- Dahlmann, N., Human deoxythymidine-triphosphate nucleotidohydrolase. Purification and properties of a new enzyme 959*
- Danho, W. s. M. Casaretto
- Danho, W. s. R. Knorr
- Danielsen, E. M., O. Norén and H. Sjöström, Biosynthesis of intestinal microvillar proteins 871*
- Dardenne, M. s. G. Auger
- Das, J., H.-G. Busse and B.H. Havsteen, Long-period glycolytic oscillations 952*
- Datema, R., P.A. Romero, G. Legler and R.T. Schwarz, Interference with protein glycosylation and glycoprotein processing 1026*
- Daubas, P. s. M.E. Buckingham
- Debuch, H. s. M. Fissenewert
- Debuch, H. s. A. Harder
- Debuch, H. s. H.K. Illig
- Debuch, H. s. G. Pakalapati
- Decken, A. von der s. M. Klaude
- Decken, A. von der s. M. Norell
- Decker, H. s. J. Markl
- Decker, K. s. A. Hinkkanen
- Degn, H., Insights in biological oscillators through model systems 952*
- Dell, A. s. H. Egge
- Demisch, L., Aktivierung und Hemmung von Amin-Oxidase-Aktivität in Abhängigkeit von Calcium 1291*
- Demmer, W. and K. Brand, Processing and degradation of methionine-enkephalin by rat brain cortical synaptosomes 1300*
- Dencher, N.A. s. M. Rehorek
- Depka, M. v. s. B. Kemper
- Deppert, W. s. J. Horst
- Derichs, H., A. Gehrman, E.W. Fünfgeld and G. Ulmar, Untersuchungen zu Hämoto- und Hepatotoxizität des Neuroleptikums Clozapin 1300*
- Derichs, H. s. A. Gehrman
- Deuticke, B. s. V. Dressler
- Deutzmann, R. s. W. Stoffel
- Diaconescu, C., D. Saunders, H.-G. Gattner and D. Brandenburg, [Leu^{B24}]- and [Leu^{B25}]Insulins are not antagonists of lipogenesis in adipocytes 187
- Dianoux, A.-C. s. P.V. Vignais
- Dielh, V. s. U. Schwab
- Diel, F. and N. Bethge, Differential effects of somatostatin on immediate anaphylactic reactions in the rat 1292*
- Dierich, M.P. s. H. Peters
- Dietl, J., A. Czuppon and L. Mettler, Solubilization of four porcine zona pellucida antigens by lithium 3,5-diiodosalicylate 381
- Dietl, T. s. L. Schack

- Digweed, M. and V.A. Erdmann, Structural and functional implications of base transition in RNA 872*
- Dimke, B. s. E. Schlimme
- Dimroth, P., Na⁺ Transport by oxaloacetate decarboxylase as a new type of energy transduction 910*
- Dimroth, P. s. W. Hilpert
- Dimroth, P. s. J. Schulze
- Dinter, H., H. Hauser, W. Bruns, G. Gross and J. Collins, Expression and induction of the human interferon β gene in mouse cells 985*
- Dittmer, J. s. P.F. Zipfel
- Doenecke, D., Comparison of nucleosomes from developing and mature chicken or duck red blood cells 925*
- Dörmer, P. s. K. Pachmann
- Dörner, M. s. W.E. Merz
- Doleschel, W. s. E. Koller
- Dolhofer, R., E.A. Siess and O.H. Wieland, Inactivation of bovine kidney β -N-acetyl-D-glucosaminidase by nonenzymatic glucosylation 1427
- Domagk, G.F. s. H. Gültekin
- Domsch, C. s. G. Mersmann
- Donner, B. s. M.G. Vicker
- Donner, P. s. K. Moelling
- Dose, K. s. H. Peters
- Dose, K. s. H.-J. Schäfer
- Drahovsky, D. s. B. Boehm
- Drahovsky, D. s. T.L.J. Boehm
- Drahovsky, D. s. G. Pfeifer
- Dreesen, R. s. M. Bräutigam
- Dressler, V., W. Bergmann, C.W.M. Haest and B. Deuticke, Transbilayer mobility of phospholipids in the erythrocyte membrane 896*
- Dressler, V. s. C.W.M. Haest
- Driesen, W. s. W. Heller
- Drobník, J. s. M. Havranová
- Dudai, M., M. Mayer and M. Kidron, Protease inhibitor activity in rat skeletal muscle 651
- Dufour, J.-P. s. A. Goffeau
- Dupont, Y., Conformational transitions of the Ca²⁺-ATPase of sarcoplasmic reticulum 462*
- Dworniczak, B. s. O. Pong
- Eckes, B. and M. Schwochau, Organisation of the mitochondrial DNA in *Drosophila hydei* and *D. melanogaster* 925*
- Eckes, B. s. M. Schwochau
- Eckstein, H., H. Zheng and H. Schott, Synthesis of immobilized model peptides of ribosomal protein and their interactions with oligonucleotides 925*
- Eder, J., J.-P. Kremer and H. Rembold, Respiration is limited by cytochrome c in *Apis mellifera* 987*
- Edgar, D. s. Y.-A. Barde
- Egerer, P., M. Bühler and H. Simon, Rhein as an electron acceptor for various flavoproteins and for electron transport particles 627
- Egert, G. s. H. Kratzin
- Egert, G. s. C.-y. Yang
- EGGE, H., A. Dell, H. von Nicolai and J. Peter-Katalinić, Fucose-containing oligosaccharides from human milk 1026*
- Egge, H. s. M. Schlüter
- Eggerer, H. s. G. Löhlein
- Ehmann, C. s. T. Achstetter
- Ehnholm, C. s. M. Jokinen
- Ehrhardt, V., Effect of transmembrane proton gradient on Na⁺-dependent amino acid transport and tetraphenylphosphonium⁺ accumulation in hepatocytes in primary culture 896*
- Eibl, H. s. M. Engelhard
- Eignebrodt, E. s. P. Fister
- Eijnden, D.H. van den, D.H. Joziase, M.L.E. Bergh, W.E.C.M. Schiphorst and P.L. Koppen, Occurrence and specificities of sialyltransferases and their role in glycoprotein biosynthesis 1020*
- Eijnden, D.H. van den s. W.M. Blanken
- Eiklid, E. and S. Olsnes, Activity of shigella cytotoxin 897*
- Elödi, S. s. J. Kárpáti
- Emter, O. s. T. Achstetter
- Engberg, J. s. H. Nielsen
- Engel, W.D. s. G. von Jagow
- Engelbrecht, S., E. Pieper, H.W. Macartney, W. Rautenberg, H.R. Wenzel and H. Tschesche, Separation of the human leucocyte enzymes alanine aminopeptidase, cathepsin G, collagenase, elastase and myeloperoxidase 305
- Engelhard, M., H. Eibl and B. Hess, Renaturation of bacteriorhodopsin fragments with synthetic and native lipids 910*
- Engelhard, M. and B. Hess, Studies on active-site peptide analogues of bacteriorhodopsin 542*
- Engelhard, M. s. R. Gregory
- Englisch, U., von der Haar, F., J. Schischkoff and F. Cramer, Isolation of mitochondrial leucyl-tRNA synthetase from *Neurospora crassa* 872*
- Ensinger, H.A. s. W.D. Bechtel
- Erdmann, V.A. s. M. Digweed
- Erdmann, V.A. s. I. Kumagai
- Erdmann, V.A. s. K.R. Leonard
- Erdmann, V.A. s. T. Pieler
- Erdmann, V.A. s. H. Schmiady
- Erikson, E. s. R.L. Erikson
- Erikson, R.L., T.M. Gilmer, D. Shealy, J. Spivack, E. Erikson and J. Maller, Protein kinase encoded by avian sarcoma virus 873*
- Ernster, L., Mitochondrial ATPase: Structure, function, regulation 911*
- Erusalimsky, J. s. C.W.M. Haest
- Eschenfelder, V. and H. Conradt, On the specificity of neuraminidases: Synthesis of 5-N-acetyl-2-deoxy-2-dicarboxymethyl- α -D-neuraminic acid and its interaction with *Vibrio cholerae* neuraminidase 1027*

- Eschrich, K. s. E. Hofmann
 Etzrodt, H. s. M. Schleyer
 Eulitz, M. and R. P. Linke, Primary structure of the variable part of an amyloidogenic Bence-Jones protein (Mev.): An unusual insertion in the third hyper-variable region of a human κ -immunoglobulin light chain 1347
 Eulitz, M. s. H. Aquila
 Evans, D. s. C. Scholtissek
- Fabricius, H.-A.**, E. Köttgen, W. Brummer and R. Stahn, A serine protease regulates T lymphocyte activation 979*
- Fabricius, H.A. s. E. Köttgen
 Fahrenholz, F., H. S. Husseini, J. L. Morgat und K.-H. Thierauch, Tritium-markierte reaktive Analoga des [1,6- α -Aminosuberinsäure, 8-Arginin]Vasopressins (Desamino-dicarba-[8-Arginin]vasopressin). Synthese und Eigenschaften 1415
 Falk, K.-E., P.-Å. Joval and P. Winyard, Micellar systems for high-resolution proton magnetic resonance spectroscopy of glycosphingolipids 1027*
- Farstad, M. s. R.K. Berge
 Fasold, H. s. H.G. Bäumer
 Fassold, H. s. R. Gregory
 Fautz, E. s. K. Hahlbrock
 Feizi, T., Factors influencing the reactivities of monoclonal antibodies with their carbohydrate determinants 1016*
- Feldman, J.F. s. R. Schulz
 Feller, A.C., E. Heymann, R. Mentlein and M.R. Parwaresch, Dipeptidyl peptidase IV as a marker enzyme for the plasma membrane of human T μ /T-helper lymphocytes 980*
- Feraudi, M. and H. Weicker, Cell organization as reflected by tissue metabolite concentrations in vivo 988*
- Ferrer, A. s. G. Gil
 Fibach, E. s. M. Kidron
 Figarella, C. s. M. Amouric
 Figarella, C. s. E. Fink
 Figura, K. von s. V. Gieselmann
 Figura, K. von s. A. Hasilik
 Figura, K. von s. R. Pohlmann
 Figura, K. von s. F. Steckel
 Figura, K. von s. A. Waheed
 Fillingame, R.H., Proton-translocating sector of the H⁺-ATPase of *Escherichia coli* 468*
- Fink, E., M. Amouric, R. Geiger and C. Figarella, Comparison of immunological and enzymatic properties of human urinary and pancreatic kallikrein 819
 Fink, E. and M. Schleuning, Studies on the excretion of tissue kallikrein from blood into the urine 1331
 Fink, H. J. s. W. Seifert
 Fischer, G., J. Heins and A. Barth, The conformation of the peptide bond between the P₁- and P₂-positions is important for catalytic activity of some proline-specific proteases 981*
- Fischer, W., M. Ick and N.R. Katz, Reciprocal distribution of hexokinase and glucokinase in the periportal and perivenous zone of the rat liver acinus 375
 Fisseneuert, M. und H. Debuch, Phospholipidstoffwechsel an Gliazellkulturen 1301*
- Fister, P., E. Eigenbrodt, M. Reinacher, P. Presek and W. Schoner, Phosphorylation in vivo of chicken liver pyruvate kinase type M₂ 873*
- Flake, B. and W. Wesemann, 5-Hydroxytryptamine uptake and storage by organelles 1301*
- Fleischer, S. s. W. Trommer
 Fleißner, A. s. I. Angel
 Flockerzi, V. s. F. Hofmann
 Flohé, L., W.A. Günzler, G. J. Steffens, F. Ötting and E. Frankus, Complete amino acid sequence of urokinase forms: Structural basis for the conversion of high into low molecular mass urokinase 980*
- Flohé, L. s. W.A. Günzler
 Flohé, L. s. G. J. Steffens
 Förster, M., F. Kopp, H. Reinauer and W. Staib, Application of the two-phase-system "aqueous solution/Triton-X 114" in protein chemistry: extraction of hydrophylic proteins by varyin ionic strength and the use of dense sucrose solutions 1010*
- Follmann, H. s. B. Bachmann
 Foltmann, B. s. N. Behrendt
 Ford, T.C. s. D. Rickwood
 Fox, J.W. s. J.B. Bjarnason
 Frankus, E. s. L. Flohé
 Frankus, E. s. W.A. Günzler
 Frankus, E. s. G. J. Steffens
 Franz, A., P. Nebinger and E. Werries, The physiological role of β -N-acetyl-D-glucosaminidase secreted by *Entamoeba histolytica* 959*
- Freimüller, B. s. C. Siepl
 Freist, W. s. H.-J. Gabius
 Freist, W. s. E. Gerlo
 Freitag, H. and W. Neupert, Biosynthesis and post-translational assembly of the porin of the outer mitochondrial membrane of *Neurospora crassa* 873*
- Freude, K. s. D. Saunders
 Frey, J. and E.-G. Afting, Receptor mediated uptake of glycoproteins by human fibroblasts 1027*
- Fricker, G., W. Kramer, H.-P. Buscher, W. Gerok and G. Kurz, Identification of the bile salt transport system in isolated intact hepatocytes by photoaffinity labelling 897*
- Friedman, D.B. s. M. Kidron
 Friedrich, R. s. M. Schlüter
 Fritsch, K.-G.E., Phenothiazines and tricyclic antidepressants have no effect on the flavoenzyme glutathione reductase 1302*
- Fritz, H. s. R. Geiger
 Fritz, H.-J. s. B. Kemper

- Fritzsch, G. and H. Koepsell, (Na⁺+K⁺)-ATPase: Evidence for active and inactive enzyme states with slow interconversion 466*
- Fritzsch, G. and H. Koepsell, Active and inactive states of (Na⁺+K⁺)-ATPase: A perturbative treatment of inactivation kinetics 897*
- Fritzsche, T.M. s. W. Trommer
- Fröhlich, Th., H. Gutfreund, R.H. Schirmer and R.S. Goody, The kinetic properties of adenylate kinase. A cellbiological interpretation 542*
- Fröschle, M. s. W. Ulmer
- Fuchs, D., A. Hausen, C. Huber, R. Margreiter, G. Reibnegger, M. Spielberger und H. Wachter, Pteridinausscheidung als Marker für alloantigen-induzierte Lymphozytenproliferation 661
- Fuchs, E., The effects of polyamines on in vitro protein synthesis with bacteriophage T7 DNA as template 874*
- Füchtbauer, E.-M., I. Stuhlfauth and H. Jockusch, Histochemische und proteinchemische Vergleiche an neuromuskulären Mutanten der Maus 1302*
- Füchtbauer, E.-M. s. H. Jockusch
- Fünfgeld, E.W. s. H. Derichs
- Fünfgeld, E.W. s. A. Gehrman
- Gabel, C. s. S. Kornfeld**
- Gabius, H.-J. and F. Cramer, Phenylalanyl-tRNA synthetase from cytoplasm and mitochondria of yeast and hen liver: Comparison of their structural and catalytic properties 1473
- Gabius, H.-J., W. Freist and F. Cramer, Phenylalanyl-tRNA synthetases from hen liver cytoplasm and mitochondria, yeast cytoplasm and mitochondria, and from *Escherichia coli*: Substrate specificity relationship with regard to ATP analogs 1241
- Gabius, H.-J., S. Goldbach, G. Graupner, S. Rehm and F. Cramer, Aminoacyl-tRNA synthetases in ageing and leukemia (EC 6.1.1) 874*
- Gabius, H.-J., N. Piel, H. Kratzin and F. Cramer, Fungal and animal mitochondrial and cytoplasmic phenylalanyl-tRNA synthetases: Are they identical homologous or analogous proteins? 874*
- Gabius, H.-J. s. R. Schröder
- Gärtner, A., K.-H. Sellinger and U. Weser, Human erythrocyte Cu₂(Haem₆)₂-protein 959*
- Gahmberg, C.G., Surface glycoproteins of normal and malignant human hematopoietic cells 1017*
- Gahmberg, C.G. s. M. Jokinen
- Gardemann, A., M. Stitt and H.W. Heldt, Regulation of ribulose 5-phosphate kinase by stromal metabolites 988*
- Gargyan, J., D. Kuschnitz, H. Schlüter, P. Klein and Z. Imre, A log time scale transient recorder averager 548*
- Gattner, H.-G. s. C. Diaconescu
- Gattner, H.-G. s. R. Knorr
- Gattner, H.-G. s. V.K. Naithani
- Gatz, C. and W. Hillen, Quantitative investigation of TET repressor – tet operator interaction 989*
- Gebhardt, R. s. K. Valentin
- Gebicke-Härter, P. J., H.H. Althaus, I. Rittner and V. Neuhoff, Morphological and biochemical properties of cultured oligodendrocytes bulk isolated from the pig brain 1302*
- Gehrmann, A., H. Derichs, E.W. Fünfgeld and G. Ulmar, Biochemische und klinische Neuroleptika-Begleiterscheinungen bei Langzeittherapie 1303*
- Gehrmann, A. s. H. Derichs
- Gehrmann, R., H.-J. Baese and B. Havsteen, Isolierung und Charakterisierung einer Protease aus *Pseudomonas maltophilia* 981*
- Geiger, R., K. Geisen and H.-D. Summ, Austausch von A1-Glycin in Rinderinsulin gegen L- und D-Tryptophan 1231
- Geiger, R., R. Hell and H. Fritz, Determination of bradykinin, kallidin and Met-Lys-bradykinin by high performance liquid chromatography 527
- Geiger, R. s. E. Fink
- Geiger, T. s. V. Gross
- Geis, A. and M. Teuber, Polyethylene glycol-mediated transfection of lactic streptococcal protoplasts 989*
- Geisen, K. s. R. Geiger
- Geisert, M., W.E.G. Müller, R.K. Zahn, A. Maidhof, M. Bachmann and H. Umezawa, Additive effects of bleomycin and pepleomycin on cell growth and degradation of DNA 926*
- Geisert, M., D. Weinblum and E. Oswald, Resolution of density gradient profiles from eukaryotic DNA by numerical analysis 926*
- Geisler, C. s. M. Wilken
- Geithe, H.-P. s. K. Asahi
- Gerdes, J. s. U. Schwab
- Gerhard, M. s. G. Keilich
- Gerisch, G., Dynamics of cyclic AMP signal generation and cell development in *Dictyostelium discoideum* 535*
- Gerisch, G., Signal transduction in chemotaxis of amoeboid cells 938*
- Gerisch, G. s. J. Stadler
- Gerlach, U. s. R. Neumeier
- Gerlo, E., W. Freist and J. Charlier, Arginyl-tRNA synthetase from *Escherichia coli* K₁₂: Specificity with regard to ATP analogs and their magnesium complexes 365
- Gerok, W. s. R. Büchsl
- Gerok, W. s. G. Fricker
- Gerok, W. s. E. Köttgen
- Gerok, W. s. W. Kreisel
- Gersonde, K. s. K. Cichutek
- Geyer, H. s. M. Schlüter
- Geyer, R. s. M. Schlüter

- Ghraf, R. s. C. Hiemke
- Gieselmann, V. and K. von Figura, Purification of acid phosphatase from human placenta 875*
- Gieselmann, V., A. Hasilik and K. von Figura, Biosynthesis and transport of cathepsin D in human fibroblasts 875*
- Gieselmann, V. s. A. Hasilik
- Gil, G., V.E. Calvet, A. Ferrer and F.G. Hegardt, Inactivation and reactivation of rat liver 3-hydroxy-3-methylglutaryl-CoA-reductase phosphatases: Effect of phosphate, pyrophosphate and divalent cations 1217
- Gillissen, D. s. E. Wünsch
- Gilmer, T.M. s. R.L. Erikson
- Glendinning, K. s. R. Neumeier
- Gmeiner, B. and G. Zerlauth, Enhanced binding of retinoic acid to its cellular binding protein in Lewis lung tumor cytosol by alkaline phosphatase treatment 337
- Godovac, J. s. G. Braunitzer
- Godovac-Zimmermann, J. s. W. Oberthür
- Godwin, E. s. E. R. Schmidt
- Goedde, H.W. s. B. Ziemsen
- Göhler, D. s. R. Niemann
- Göringer, U. s. R. Wagner
- Götz, H. s. H. Kratzin
- Götz, H. s. C.-y. Yang
- Goffeau, A., A. Amory, J.-P. Dufour and A. Villalobo, The proton-translocating ATPase of the plasma membrane in the yeast *Schizosaccharomyces pombe* 468*
- Goldammer, E. v. s. H.R. Wenzel
- Goldbach, S. s. H.-J. Gabius
- Goldberg, D. s. S. Kornfeld
- Goldfarb, V. s. D. Gradmann
- Golf, S. and V. Graef, Affinity labeling of rat liver microsomal NADH 5 α -reductase with the nucleoside analogue 5'-(4-fluorosulfonylbenzoyl)adenosine 944*
- Golf, S. and V. Graef, Diurnal variations of phosphatase activity in rat liver microsomes 953*
- Gómez-Lira, M.M., H. Schröter and J. Bode, Nucleosomal particles relax their structure as histones become hyperacetylated 927*
- Goody, R.S., The interaction between myosin, actin and nucleotides 460*
- Goody, R.S. s. Th. Fröhlich
- Gordon, P.B. and P.O. Seglen, Electroporation: A method for the introduction of small molecules into cells, applied to the study of autophagy in isolated rat hepatocytes 898*
- Gottwik, M., H. Renner and J.H. Wissler, Biochemical neovascularization of muscles by leukocyte-derived polypeptide effectors: Morphogenesis and turnover of blood vessel patterns with active hemodynamics in vivo 938*
- Gradmann, D., V. Goldfarb and J. Tittor, Electrogenic Cl⁻ pump in acetabularia: Attempts of biochemical identification (ATPase) and reaction kinetic analysis of physical phenomena 912*
- Gradmann, D. s. J. Tittor
- Graef, V. s. S. Golf
- Gräsbeck, R. s. R. Majuri
- Grätz, R. s. H. Kröger
- Graf, H. and V. Ullrich, Prostacyclin synthase as a cytochrome P-450 enzyme 972*
- Graf, H. s. E. Cadenas
- Graf, H. s. B. Lukas
- Graf, H. s. S. Wolbert-Rack
- Graham, D. s. H. Betz
- Graham, D. s. F. Pfeiffer
- Graham, J. and S. Wagner, Subfractionation of rat liver endoplasmic reticulum in iodinated density gradient media 1000*
- Grahn, H. s. H. Kröger
- Graupner, G. s. H.-J. Gabius
- Graw, J. and K.H. Summer, Glutathione, glutathione-dependent and glycolytic enzymes in a dominant cataract in the mouse 965*
- Gregory, R., M. Engelhard, D. Recktenwald, E. Fassold, B. Pevec and B. Hess, Subunit chemistry of yeast F₁-ATPase 469*
- Greiling, H. s. T. Stein
- Greiser-Wilke, I. s. K. Moelling
- Grenner, G., Principles and applications of homogeneous and heterogeneous enzyme immunoassays 1005*
- Greve, H. De s. J. Schell
- Grimmelikhuijzen, C.J.P. s. H. Bodenmüller
- Gross, V., T. Geiger, T.-A. Tran-Thi and P.C. Heinrich, Biosynthesis and secretion of α -1-antitrypsin in rat hepatocyte primary cultures 1022*
- Gross, G. s. H. Dinter
- Gross, G. s. U. Mayr
- Gross, G. s. M.L. Rao
- Grothaus, W., E. Wörner and E. Riedel, Vergleichende Untersuchung der Bindung von Neuropharmaka an subzellulären Säugerhirnfraktionen 1303*
- Gröbner, P. and P. Loidl, Regulation of dTMP-synthesizing enzymes during the life cycle of *Physarum polycephalum* 953*
- Gröbner, P. s. P. Loidl
- Grünhagen, H.H. s. M. Rack
- Grünwald, J. s. A. Schmidt
- Grünwald, S. s. G. Pfeifer
- Grunicke, H. s. I. Multhaup
- Gültekin, H. and G.F. Domagk, An acidic, γ -carboxyglutamate-containing protein from beef brain 941*
- Günther, T. s. L. Khoury
- Günzler, W.A., G.J. Steffens, F. Ötting, G. Buse and L. Flohé, Structural relationship between human high and low molecular mass urokinase 133
- Günzler, W.A., G.J. Steffens, F. Ötting, S.-M.A. Kim, E. Frankus and L. Flohé, The primary structure of high molecular mass urokinase from human urine:

- The complete amino acid sequence of the A chain 1155
- Günzler, W.A. s. L. Flohé
- Günzler, W.A. s. G. J. Steffens
- Güth, K. and H. J. Kuhn, Aspects of the actomyosin interaction and ATPase in the contracting muscle 459*
- Güth, K. s. H. J. Kuhn
- Gunawan, J. s. H. K. Illig
- Gutfreund, H. s. Th. Fröhlich
- Gutschker-Gdaniec, G., M. Sander-Wewer, P. Roggentin, R. Hobrecht and R. Schauer, An efficient method for the isolation of sialidase from *Clostridium perfringens* 1028*
- Gutschker-Gdaniec, G. s. P. Roggentin
- Haar, F. von der** s. U. Englisch
- Haar, F. von der s. S. Peters
- Haase-Aschoff, K. s. B. Hauer
- Hadjianghelu, A. s. G. Weitzel
- Haest, C.W.M., J. Erusalimsky, V. Dressler and G. Plasa, Stabilization of asymmetric arrangement of phospholipids of erythrocyte membranes by skeletal proteins 898*
- Haest, C.W.M. s. V. Dressler
- Hagemeister, H. s. M. Pfeuffer
- Hagenbüchle, O. s. P. K. Wellauer
- Haggag, A., W. D. Bechtel and J. Mierau, The effect of tricyclic antidepressants and α_2 -agonists on synaptosomal [3 H]noradrenaline release 1304*
- Hahlbrock, K., F. Kreuzaler, H. Ragg, E. Fautz and D. N. Kuhn, Regulation of flavonoid and phytoalexin accumulation through mRNA and enzyme induction in cultured plant cells 121*
- Hansen, U.P., P. Keunecke, J. Martens and I. Kronberg, Kinetic Studies of control of transport activity by cell metabolism 899*
- Hansen, U.P. s. J. Tittor
- Harada, N. s. K. Minakata
- Hardeland, R. s. H. F. Krug
- Hardeland, R. s. W. Volkmandt
- Harder, A. and H. Debuch, Effect of chloroquine treatment on the different phospholipid species of rat liver lysosomes 717
- Harisch, G. and H. J. Thissen, The glutathione status of the rat liver after partial hepatectomy 965*
- Harper, G.P. and H. Thoenen, Nerve growth factor from bovine seminal plasma: Purification and characterization 1304*
- Hartl, F.-U. s. W. W. Just
- Hartmann, H. s. K. Beckh
- Hartmann, H.-J., J. Bordas, M.H. J. Koch and U. Weser, X-ray absorption spectroscopy and extended X-ray absorption fine structure (EXAFS) analysis of yeast Cu-thioein 989*
- Hartmann, H.-J. s. A. Ludány
- Hartrodt, B. s. Hj. Matthies
- Hartrodt, B. s. K. Neubert
- Hartwig, H.G. and A. Calas, Light-dependent uptake and retention of tritiated deoxyglucose by photo-neuroendocrine cells and systems 953*
- Hasselbach, W., Energy coupling in sarcoplasmic reticulum- Ca^{2+} -transport 461*
- Hasilik, A., R. Pohlmann, V. Gieselmann, S. Tümmers, M. Zühlsdorf and K. von Figura, Glycosylation and transport of lysosomal enzymes 1018*
- Hasilik, A. s. V. Gieselmann
- Hasilik, A. s. R. Pohlmann
- Hasilik, A. s. F. Steckel
- Hasilik, A. s. A. Waheed
- Hau, J. s. J. C. Bøg-Hansen
- Hauer, B., K. Haase-Aschoff and F. Lingens, Papaverine degradation with papaverine mutants of a *Nocardia* sp. 499
- Hauer, B. and F. Lingens, Tryptophan metabolism by a papaverine-degrading *Nocardia* sp. 507
- Hauptlorenz, S., A. Loidl and B. Puschendorf, The acetylation pattern of histones in adult and regenerating rat liver 927*
- Haurand, M. and V. Ullrich, Isolation and characterization of thromboxane synthase as a cytochrome P-450 enzyme 972*
- Hausen, A. s. D. Fuchs
- Hausner, H. s. H. Dinter
- Hauser, H. s. U. Mayr
- Havranová, M., D. Čechová, V. Saudek, M. Metalová and J. Drobník, A high molecular mass derivative of trypsin-kallikrein inhibitor for potential medical use. II. Study of inhibitory activity 295
- Havsteen, B.H., Remote entry control at catalytic site. Parameters of specific molecular switch in chymotrypsin 981*
- Havsteen, B.H. s. J. Das
- Havsteen, B. s. R. Gehrmann
- Havsteen, B. s. H. Iwan
- Havsteen, B. s. H. Lüddens
- Havsteen, B. s. K. Westerbrink
- Haylett, T. s. F. J. Joubert
- Hebisch, S., S. Soboll, M. Schwenen and H. Sies, Subcellular distribution of high-energy phosphates in different types of skeletal muscle of the rat 912*
- Hegardt, F.G. s. G. Gil
- Hegner, D. s. M.S. Anwer
- Hegner, D. s. H. Nohl
- Heider, I. s. R. Rudolph
- Heil, B.M., J. Bereiter-Hahn and G. Zimmer, NADH, Flavoprotein and 2-[4-(Dimethylamino)styryl]-1-methylpyridinium iodide (DASPMI) fluorescence at the surface of the isolated working rat heart 912*
- Heinlein, U.A.O. s. W. Wille

- Heinrich, P.C., K. Schneider, W. Northemann and E. Schmelzer, Immunological methods for the detection of proteins synthesized in cell-free systems, in rat hepatocytes and in *E. coli* cells transformed with recombinant DNA 1006*
- Heinrich, P.C. s. V. Gross
- Heinrich, P.C. s. A. Villringer
- Heinrich, U. s. D.W. Lübbers
- Heins, J. s. G. Fischer
- Hekim, N. s. P.I. Szendro
- Heldt, H.W. s. A. Gardemann
- Hell, R. s. R. Geiger
- Heller, W., W. Driesen, R. Schneider and R. Trapp, Cerebral and hepatic metabolism following experimental unilateral carotid ligation 1294*
- Heller, W. s. G.U. Wollmann
- Helliger, W., J. Leiter and B. Puschendorf, The acetylation pattern of histones in induced friend erythroleukemia cells F4N 927*
- Hellmann, K.P. s. H. Sternbach
- Hemmasi, B., W. Stüber and E. Bayer, Syntheses of 4-[*N*-(*tert*-butoxycarbonyl)aminoacyloxymethyl]-3-nitrobenzoic acids for use in the liquid-phase peptide synthesis 701
- Hempel, K. und E. Mayer, Lokalisierung der Proteine im Myelin peripherer Nerven 1305*
- Hempel, V. s. G.U. Wollmann
- Hénichart, J.-P., J.-L. Bernier and J.-P. Catteau, Interaction of 4-(9-acridinylamino)aniline and derivatives with DNA. Influence of a lysylglycyl side chain on the binding capacity 835
- Hennig, B. s. B. Schmidt
- Henschen, A., M. Kehl and F. Lottspeich, On the biosynthesis of fibrinogen in heterozygous cases of genetically abnormal fibrinogen: The absence of hybrid molecules 876*
- Henschen, A., C. Southan, M. Kehl and W. Bode, On the specificity of thrombin: Evidence for the selective cleavage of a histidyl bond 982*
- Henschen, A. s. M. Kehl
- Henschen, A. s. H.-J. Schneider
- Henschen, A. s. J. Stadler
- Hensel, R. and U. Mayr, Comparative studies on the primary structure of bacterial L-lactate-dehydrogenase 1011*
- Heppelmann, B. and H. Rahmann, Changes in the glycoconjugate metabolism of the fish brain after adequate sensory stimulations. A deoxyglucose study 1028*
- Herbert, M. s. I. Krüger
- Herbst, H., J.Y. Chang, R. Aebersold and D.G. Braun, Murine V_K25 isotype sequence: Monoclonal antibody 2S1.3 specific for the group A streptococcal polysaccharide 1069
- Herbold, U., H. Neufang, H. Müller and K. Knobloch, On the subunit composition of the coupling factor-ATPases F₁ from *Rhodospseudomonas palustris* and *Rhodospseudomonas sphaeroides* 913*
- Herbold, U. s. K. Knobloch
- Herbold, U. s. H. Müller
- Herbold, U. s. H. Neufang
- Herken, H. s. M. Bräutigam
- Herken, R. s. M. Wenzel
- Hermann, K. s. M. Marin-Grez
- Hermann, R., R. Rudolph and R. Jaenicke, The use of subunit hybridization to monitor the reassociation of porcine lactate dehydrogenase after acid dissociation 1259
- Hernalsteens, J.P. s. J. Schell
- Hernanto, A.-R. s. G.U. Wollmann
- Herrchen, M. and G. Legler, Charge distribution at the active site of β -D-galactosidase from *Escherichia coli* 1029*
- Herrlich, P. s. H. J. Rahmsdorf
- Herrnstadt, C. s. M. Schwochau
- Hesch, R.-D. s. M. Casaretto
- Hess, B. s. E.M. Chance
- Hess, B. s. M. Engelhard
- Hess, B. s. R. Gregory
- Hess, B. s. D. Kuschmitz
- Hess, B. s. J. Watters
- Hess, G.P., Can the acetylcholine receptor control the transfer of signals between cells of the nervous system? 899*
- Hettkamp, H., E. Bause and G. Legler, Calf liver microsomal glucosidases: characterisation and inhibition by various inhibitors 1019*
- Heymann, E. s. A.C. Feller
- Heymann, St. s. R. Lindigkeit
- Heymann, E. s. R. Mentlein
- Heymann, E. s. M. Suttorp
- Heyn, M.P. s. M. Rehorek
- Hiemke, C. and R. Ghraf, Thiol methyltransferase in rat brain 1305*
- Hilbig, R., Anagenetic changes of neuronal gangliosides in phylogeny 1029*
- Hilf, G., W.E. Merz and W. Schmidt, Biosynthesis and secretion of chorionadotropin in placental tissue culture 1030*
- Hilgenfeldt, U., Microheterogeneity of rat angiotensinogen 1030*
- Hillen, W. s. B. Brosius
- Hillen, W. s. C. Gatz
- Hillen, W. s. G. Klock
- Hillen, W. s. K. Schollmeier
- Hillen, H. s. W. Stoffel
- Hillen, W. s. B. Unger
- Hilpert, W. and P. Dimroth, Methylmalonyl-CoA decarboxylase is a new vectorial catalyst-converting decarboxylation energy into α Na⁺ gradient 913*
- Hilschmann, N. s. H. Kratzin
- Hilschmann, N. s. C.-y. Yang

- Hinkkanen, A., J. Nowack, R. Maas and K. Decker, A rapid purification of the flavoproteins 6-hydroxy-D-nicotine oxidase and 6-hydroxy-L-nicotine oxidase from arthrobacter oxidans using ω -aminoalkylated agaroses 990*
- Hinz, H.-J. and E. Moses, Stability of native and modified basic pancreas trypsin inhibitor 982*
- Hinz, H.-J. s. A. Seidl
- Hobrecht, R. s. G. Gutschker-Gdaniec
- Hobrecht, R. s. P. Roggentin
- Höfer, M. s. F.R. Nassar
- Höök, M., Structure and function of cell surface heparan sulfate proteoglycans 1021*
- Hörmann, H. s. H. Richter
- Hoffmann, J. s. D.W. Lübbers
- Hoffmann, J.A. s. F. Lachaise
- Hoffmann, M. and K. Brinkmann, The circadian rhythm of extracellular pH in stationary cultures of *Chlamydomonas reinhardtii* 954*
- Hofmann, E., K. Eschrich and W. Schellenberger, Regulation der Glykolyse (Probleme – Lösungswege – offene Fragen) 537*
- Hofmann, F. and V. Flockerzi, Phosphorylation of cGMP-dependent protein kinase affects of the activation of the enzyme by cAMP 939*
- Hofmann, H. s. G. Steger
- Hofmann, R. s. B. Bachmann
- Hofmann, W. s. R. Tauber
- Hollenberg, C.P. s. R. Roggenkamp
- Holmes, K.C., The structure of actin and myosin 459*
- Holsters, M. s. J. Schell
- Hooghwinkel, G. J.M. s. W.M. Blanken
- Hoppe, J., Topography of the F_0 -subunits in the ATP synthase from *E. coli* 468*
- Hornebeck, W. and H.P. Schnebli, Effect of different elastase inhibitors on leukocyte elastase pre-adsorbed to elastin 455
- Hornig, H. and R. Lührmann, Two-base pair codon-anticodon interaction at the ribosomal A-site is sufficient to hydrolyse GTP from [aminoacyl-tRNA \times EF-Tu \times GTP] complexes but results in abortive aminoacyl-tRNA binding 876*
- Hornig, H. and R. Lührmann, A-site-active antibiotics can modulate aminoacyl-tRNA binding by adding or removing increments of stabilizing energy due to reinforcement or disruption of A-site/aminoacyl-tRNA interactions 877*
- Horst, J., E. Jacob, C. Weckler and W. Deppert, Production of a T-antigen related protein in mammalian cells after stable transformation with a cloned SV40 gene fragment 445
- Hosöy, L. s. R.K. Berge
- Hotlund, J., T. Kristensen, A.C. Østvold and S.G. Laland, ADP-ribosylation in permeable metaphase HeLaS3 cells 928*
- Hotlund, J. s. T. Lund
- Hovemann, B., Vitellogenin genes in *Drosophila melanogaster* 928*
- Hovemann, B. s. U. Walldorf
- Howard, R. J. s. R. Schauer
- Hruban, V. s. L. Veselský
- Huber, C. s. D. Fuchs
- Huber, R. s. H. Löbermann
- Hucho, F. s. J. Verdenhalven
- Hucho, F. s. P. Muhm
- Hüther, G., U. Sprotte, K. Schott and V. Neuhoff, Regulation of the free amino acid pool of the developing brain 1306*
- Hunsmann, G. s. M. Schlüter
- Husseini, H.S. s. F. Fahrenholz
- Huth, W. and R. Menke, Mitochondrial acetyl-CoA acetyltransferase: Initial rate kinetics in the presence of the product CoASH reveal intermediary plateau regions 944*
- Huth, W. s. L. Quandt
- Huttner, W.B. and R.W.H. Lee, Protein sulphation on tyrosine residues 877*
- Huttner, W.B. s. R.W.H. Lee
- Huybrechts, G. s. D.A. Vanden Berge
- Ick, M. s. W. Fischer
- Illig, H.K., B. Witter, J. Gunawan, P. Ahrens and H. Debuch, Phospholipid metabolism of glial cell primary cultures, IV. Metabolism of 1-Alkenyl-sn-glycero-3-phosphoethanolamine between 1 and 20 hours incubation 709
- Illig, U. s. H.-J. Schneider
- Imre, Z. s. J. Gargyan
- Isenberg, G. s. M.W. Kilimann
- Israelewski, N. s. E.R. Schmidt
- Iwan, H., H.-J. Baese und B. Havsteen, Eine modifizierte Boyden-Kammer zur Mikrobestimmung der Chemokinese von Granulozyten 939*
- Jacob, E. s. J. Horst
- Jaeger, E. s. E. Wünsch
- Jaenicke, L. s. T. Müller
- Jaenicke, R. s. P. Bartholmes
- Jaenicke, R. s. R. Hermann
- Jaenisch, R., Retroviruses and embryogenesis (7th Adolf Butenandt lecture) 1267
- Jagow, G. von, W.F. Becker and W.D. Engel, Characterization of a new reaction site of cytochrome *b* 539*
- Jagow, G. von and W.D. Engel, New inhibitors acting at energy conversion site 2 914*
- Jakobs, K.H. and G. Schultze, Occurrence of an inhibitory guanine nucleotide-binding regulatory component of the adenylate cyclase system in cyc^- variants of S49 lymphoma cells 1306*

- Jany, K.-D., J. Czeck and G. Pfeleiderer, Aminopeptidase M in the sequence analysis of peptides and proteins 1009*
- Jany, K.-D. s. W. Ulmer
- Jarausch, J. and B. Kadenbach, Tissue-specificity overrides species-specificity in cytochrome c oxidase polypeptides as demonstrated by immunodetection on nitrocellulose 914*
- Jarausch, J. and B. Kadenbach, Tissue-specificity overrides species-specificity in cytoplasmic cytochrome c oxidase polypeptides 1133
- Jeck, R., Isolierung der NAD⁺-kinase aus Hühnerleber 945*
- Jeckel, D., H.-G. Müller and H. Schimassek, Mechanism of inhibition of glutathione reductase by Zn²⁺ 945*
- Jelkmann, W. s. G. Braunitzer
- Jenke, J.-S., M. Löwel and J. Berndt, Effect of dietary lipids on the activity of 3-hydroxy-3-methylglutaryl-CoA reductase in rat liver 725
- Jensch, F. s. B. Kemper
- Jessen, T.E., V. Barkholt and K.G. Welinder, An alternative pathway hemolytic assay of complement component C3 1011*
- Jockusch, H., Studies on mouse mutants affected in neuro-muscular interactions 129*
- Jockusch, H., G. Mehrke und E.-M. Füchtbauer, Histochemische und Isoenzym-Analyse von Skelett- und Herzmuskeltransplanten 1294*
- Jockusch, H. s. E.-M. Füchtbauer
- Jönsson, B.-M., C. Löffler and K. Ohlsson, Human granulocyte elastase is inhibited by the urinary trypsin inhibitor 1167
- Jörnvall, H., N. Kalkkinen, J. Luka, R. Kaiser, M. Carlquist and H. von Bahr-Lindström, Protein studies as important tools in amplifying different characterizations of biologically active macromolecules 1003*
- Jörnvall, H., V. Mutt and M. Persson, Structural similarities among gastrointestinal hormones and related active peptides 475
- Johnson, R.B. s. W.G. Bessler
- Jokinen, M., V. Väisänen, T.K. Korhonen, N. Kalkkinen, C.G. Gahmberg and C. Ehnholm, A blood group M specific haemagglutinin in pyelonephritogenic *Escherichia coli* 1030*
- Jong, W.W. de s. T. Kleinschmidt
- Jordan, W. s. H. Nohl
- Jørgensen, P.L., Protein structure and conformations of pure membrane-bound Na, K-ATPase 464*
- Jørgensen, P.L., Protein conformations and cation translocation by pure Na, K-ATPase from mammalian kidney 900*
- Jørgensen, P.L. s. J.V. Møller
- Joubert, F.J., T. Haylett, D.J. Strydom and N. Taljaard, Snake venom: Protein CM-2 from *Bitis arietans* (Puff adder) venom 1087
- Joval, P.-Å. s. K.-E. Falk
- Joziase, D.H. s. D.H. van den Eijnden
- Juillerat-Jeanneret, L., M. Roth and J.-P. Bargetzi, Some properties of porcine carboxypeptidase N 51
- Jung, G. s. W.G. Bessler
- Jung, G. s. G. Bovermann
- Jungblut, P.W. s. P.I. Szendro
- Junge, W. s. H.-W. Trissl
- Junge, W. s. R. Wagner
- Jungermann, K. s. K. Beckh
- Jungwirth, C. s. J. Rösel
- Just, W.W., Synthesis and application of non-commercial carrier ampholytes for isoelectric focusing and for chromatofocusing 1011*
- Just, W.W. and F.-U. Hartl, Peroxisomal β -oxidation in isolated rat liver parenchymal cells 970*
- Kadenbach, B.**, Occurrence of tissue-specific isoenzymes of cytochrome c oxidase in higher animals 915*
- Kadenbach, B. s. J. Jarausch
- Kagawa, Y. s. H.-J. Schäfer
- Kahn, C.R. s. R. Knorr
- Kaiser, R. s. H. Jörnvall
- Kajander, E.O. and R.-L. Pajula, Effect of erythro-9-(2-hydroxy-3-nonyl)adenine on the metabolism of adenosine in rat liver extracts 990*
- Kalkkinen, N. s. H. Jörnvall
- Kalkkinen, N. s. M. Jokinen
- Kalsbeek, R. s. F. Steckel
- Kamerling, J.P., Modern approaches to the structural analysis of carbohydrate chains in glycoconjugates 1015*
- Kamerling, J.P. s. U. Nöhle
- Kanemoto, M. s. M. Muramatu
- Kanamoto, Y. s. M. Muramatu
- Kárpáti, J., K. Váradi and S. Elődi, Effect of granulocyte proteases on human coagulation factors IX and X. The protective effect of calcium 521
- Kasche, V. and R. Zöllner, Tris(hydroxymethyl)methylamine is acylated when it reacts with acyl-chymotrypsin 531
- Kasche, V. s. P.F. Zipfel
- Kase, F., I. Björkhem and J.I. Pedersen, Conversion of 3 α , 7 α , 12 α -trihydroxy-5 β -cholestanic acid into cholic acid by rat liver peroxisomes 970*
- Katsuyama, I. s. M. Muramatu
- Katz, N. and U. Müller-Eberhard, Secretion of hemopexin in primary cultures of rabbit hepatocytes during inhibition of glycosylation 878*
- Katz, N.R. s. W. Fischer
- Kaufmann, W. s. M. Pfeuffer
- Kehl, M., F. Lottspeich and A. Henschen, High-performance liquid chromatography of proteins as applied to fibrinogen chains 1501
- Kehl, M. s. A. Henschen

- Keilich, G. and R. Brossmer, Circular dichroism – a tool to study the structure of sialic acid 1031*
- Keilich, G., D. Ziegler, M. Gerhard and R. Brossmer, Studies on the structure of the carbohydrate units in *Collocalia mucin* 1032*
- Keilich, G. s. D. Ziegler
- Kehl, M. s. A. Henschen
- Keller, K. s. K. Lange
- Keller, R. s. T. Stein
- Kemper, B., F. Jensch, H.-J. Fritz and M. v. Depka, Cleavage of hairpins by T4-induced endonuclease VII 929*
- Kenny, A. J., Endopeptidases in brush borders and synaptic membranes 983*
- Kersten, H., Involvement of tRNAs and the modified nucleoside queuosine in cell development and differentiation 123*
- Kersten, H. s. G. Ott
- Kersten, H. s. H. Richter
- Kersten, H. s. E. Schachner
- Keszthelyi, L. s. P. Ormos
- Kettmann, U. s. R. Kleine
- Keuncke, P. s. U. P. Hansen
- Khoury, L., H. Bauer and T. Günther, Mg Transport across erythrocyte membranes 900*
- Kidron, M., D. B. Friedman, M. Mayer, Y. Klemes and E. Fibach, Changes in proteolytic activities of human leukemic promyelocytes (HL-60 cells) during maturation 865
- Kidron, M. s. M. Dudai
- Kilian, M. s. H. S. Bleeg
- Kilimann, M. W. und G. Isenberg, Die Isolierung und Charakterisierung von „Capping Protein“ – ein Actin regulierendes Protein aus Rinderhirn 1286*
- Kim, S.-M. A. s. W. A. Günzler
- Kindl, H. s. C. Kruse
- Kindler, A., R. Minwegen and M. F. Rajewsky, Possible cell type- and developmental stage-dependence of transformation probability in prenatal rat brain exposed to the carcinogen ethylnitrosourea. I. Cell surface-directed monoclonal antibodies for identification and separation of neural cell subpopulations 1306*
- King, G. L. s. R. Knorr
- Kinnunen, P. K. J., P. Vainio and J. A. Virtanen, Regulation of the catalytic activity of lipoprotein lipase 949*
- Kinnunen, P. K. J. s. T. Thuren
- Kinnunen, P. K. J. s. P. Vainio
- Kirchner, H. s. U. Schwab
- Kivirikko, K. I., Post-translational modifications in the biosynthesis of collagen 878*
- Klages, W. s. A. Markus
- Klaude, M. and A. von der Decken, Transcription activity of liver chromatin after administration of dimethylnitrosamine to mice 929*
- Klaudy, J. s. L. Veselský
- Klein, G. s. P. V. Vignais
- Klein, O. and R. J. Porra, The participation of the Shemin and C₅ pathways in 5-aminolaevulinic acid and chlorophyll formation in higher plants and facultative photosynthetic bacteria 551
- Klein, P. s. J. Gargyan
- Kleine, R. and U. Kettmann, Separation and comparative characterization of the cationic protease and anionic protease from the culture medium of *Thermoactinomyces vulgaris* 843
- Kleine, T. O., Indication for a ventricular-lumbar concentration gradient for enkephalins in human cerebrospinal fluid 1307*
- Kleine, T. O., U. Brause and M. Tlatlik, Determination of metabolites of catecholamine and indolamine transmitters in human urine by high performance liquid chromatography and gas chromatography, comparison of both methods 1307*
- Kleinschmidt, T. und G. Braunitzer, Die Primärstruktur der γ -Ketten der fötalen Hämoglobine von Schaf (*Ovis ammon*) und Ziege (*Capra aegagrus*), *Artiodactyla* 789
- Kleinschmidt, T. und G. Braunitzer, Die Primärstruktur des Hämoglobins vom Ägyptischen Flughund (*Rousettus aegyptiacus*, Chiroptera) 1209
- Kleinschmidt, T., W. W. de Jong und G. Braunitzer, Hämoglobine, XLVI: Die Primärstruktur der α -Ketten des Hämoglobins vom Gürteltier (*Dasypus novemcinctus*, Edentata) 239
- Kleinschmidt, T., W. de Jong und G. Braunitzer, The primary structure of the α -chain of armadillo (*Dasypus novemcinctus*) hemoglobin 543*
- Klemes, Y. s. M. Kidron
- Klingenberg, M., Nucleotide-binding protein from brown fat mitochondria 915*
- Klingenberg, M. s. H. Aquila
- Klink, F., H. Schümann and A. Thomsen, Archaeobacterial elongation factor 1 (EF-1) is closer related to eukaryotic EF-1 than to eubacterial EF-T_u as revealed by hybrid polyphenylalanine synthesis systems mixed from the three kingdoms of organisms 878*
- Klink, F. s. D. Uschtrin
- Klock, G. and W. Hillen, Purification of the TET repressor from the transposon Tn 10 991*
- Klose, J., High resolution two-dimensional electrophoresis of proteins – method and application 1004*
- Kluge, F. s. E. Kötting
- Klumpp, S. and J. E. Schultz, Adenylate cyclase and guanylate cyclase in cilia from *Paramecium tetraurelia* 1308*
- Knobloch, K., U. Herbold, H. Neufang and H. Müller, A loosely bound F₁-ATPase in *Rhodospseudomonas palustris* 916*
- Knobloch, K. s. U. Herbold

- Knobloch, K. s. H. Müller
Knobloch, K. s. H. Neufang
Knöchel, W., Regulation of gene expression during embryonic development 132*
Knorr, R., W. Danho, E. E. Büllesbach, H.-G. Gattner, H. Zahn, G. L. King and C. R. Kahn, [B22-D-Arginine]Insulin: Synthesis and biological properties 1449
Knust, E. s. M. Schwochau
Kobus, S. s. O. Pongs
Koch, M. H. J. s. H.-J. Hartmann
Koch, N. s. H. J. Rahmsdorf
Koch, W. s. M. Schlüter
Kölbl, S. s. H. Kratzin
Kölbl, S. s. C.-y. Yang
Koepsell, H. s. G. Fritsch
Köttgen, E., H. A. Fabricius, F. Kluge, B. Volk and W. Gerok, Gluten – a lectin-like protein with binding properties for mannose-rich glycoproteins 1018*
Köttgen, E. s. R. Büchsel
Köttgen, E. s. H.-A. Fabricius
Kohler, K. s. H. Mägdefrau
Kolassa, N. s. J. Suko
Koller, E., F. Koller and W. Doleschel, Specific binding sites on human blood platelets for plasma lipoproteins 395
Koller, F. s. E. Koller
Koob, R. s. C. Woenckhaus
Kopp, F. s. M. Förster
Koppen, P. L. s. D. H. van den Eijnden
Korhonen, T. K. s. M. Jokinen
Kornfeld, S., M. Reitman, A. Varki, D. Goldberg and C. Gabel, Biosynthesis of lysosomal enzyme oligosaccharide units 1019*
Kostka, G. s. A. Schweiger
Kouri, T. and E. Vuorio, Plasma membrane glycoproteins of synovial fibroblasts cultures from rheumatoid arthritis patients 1033*
Kouvonen, I. s. R. Majuri
Kováč, L. and E. Böhmerová, The nature of aerobic glycolysis in yeast 539*
Kraayenhof, R. s. G. Zimmer
Kramer, W., G. Burckhardt, F. A. Wilson and G. Kurz, Identification of components of the bile salt transport system in small intestine by photoaffinity labelling 901*
Kramer, W. s. G. Fricker
Kratzin, H., C.-y. Yang, H. Götz, F. P. Thinner, T. Kruse, G. Egert, E. Pauly, S. Kölbl and N. Hilschmann, High performance liquid chromatography of peptides and proteins – micropreparative separations in the primary structure analysis of proteins 1007*
Kratzin, H. s. H.-J. Gabius
Kratzin, H. s. C.-y. Yang
Krauth-Siegel, R. L. s. F. Lederbogen
Kreickmann, H. s. W. Schoner
Kreisel, W., R. Büchsel, B. Volk, W. Reutter and W. Gerok, Influence of liver regeneration on the turnover of fucose, mannose and polypeptide chain of dipeptidyl peptidase IV isolated from rat liver plasma membrane 1033*
Kreisel, W. s. R. Büchsel
Kremer, J.-P. s. J. Eder
Kreutzberg, G. W. s. C. A. Lucas
Kreutzberg, G. W. s. M. Reddington
Kreutzfeldt, C., Translation in a cell-free yeast system 879*
Kreuzaler, F. s. K. Hahlbrock
Krippner, H. s. B. Boehm
Kristensen, T. s. J. Hotlund
Kröger, H., R. Grätz, H. Grahn and H. Wohlert, Influence of azacytidine on the induction of tyrosine aminotransferase 930*
Kroll, W. and Fr. Schneider, Growth and energy metabolism of Ehrlich ascites tumor cells in the presence of oligomycin 946*
Krombach, C. s. G. Braunitzer
Kronberg, I. s. U. P. Hansen
Krüger, I., M. Herbert and C. Schnarrenberger, Immunochemical comparison of the aldolases and glucose-phosphate isomerases from spinach leaves and some other organisms 1012*
Krüger, S. s. R. Pohlmann
Krug, H. F. and R. Hardeland, Diurnal rhythmicity of hepatic protein synthesis: Cytosolic regulation in an invitro system 954*
Kruse, C. and H. Kindl, Biosynthesis of microbody enzymes: Oligomerization of de novo synthesized malate synthase 879*
Kruse, H. s. W. Schill
Kruse, T. s. H. Kratzin
Kruse, T. s. C.-y. Yang
Küchler, B. s. E. Bäuerlein
Kühl, P. W., Partitioning of β -adrenergic agents into micelles 991*
Kühn, B. s. A. Villringer
Kuehn, L. s. B. Dahlmann
Kuhn, D. N. s. K. Hahlbrock
Kuhn, H. J. and K. Güth, The effect of ATP on cross-bridge kinetics in insect flight muscle 460*
Kuhn, H. J. s. K. Güth
Kumagai, I., T. Pieler, A. R. Subramanian and V. A. Erdmann, Nucleotide sequence and secondary structure analysis of spinach chloroplast 4.5S RNA 880*
Kunze, U. s. H.-W. Trissl
Kuppert, P. s. M. Londershausen
Kurz, G. s. G. Fricker
Kurz, G. s. W. Kramer
Kuschmitz, D., Chemical basis for the generation of ion gradients 537

- Kuschmitz, D. and R. Müller, *Trans-cis* isomerisation of the retinal chromophore and charge displacements during the photocycle of bacteriorhodopsin 543*
- Kuschmitz, D., J. Watters and B. Hess, On the control of the photocycle of bacteriorhodopsin 916*
- Kuschmitz, D. s. J. Gargyan
- Kuschmitz, D. s. J. Watters
- Kuss, E. s. D. Berg
- Lachaise, F. and J. A. Hoffmann, Ecdysteroids and embryonic development in the shore crab, *Carcinus maenas* 1059
- Lah, T. and V. Turk, Autolysis studies of cathepsin D 247
- Laland, S.G. s. J. Hotlund
- Laland, S.G. s. T. Lund
- Landauer, P., K.-P. Rueß and M. Liefländer, Hydrophobic and non-hydrophobic globular forms of acetylcholinesterase of bovine caudate nucleus 1308*
- Lange, K. and K. Keller, Schnelle endogene Regulation des Glucosetransports in Kulturzellen 1290*
- Lange, R.H. and H.-P. Richter, A highly successful lipoprotein architecture occurring in yolk-platelets of lower vertebrates 949*
- Larsen, K., B. Svensson and I. Svendsen, Partial amino acid sequence of cyanogen bromide fragments of the fungal glycoprotein, glucoamylase from *Aspergillus niger* 1033*
- Larsen, U.D. s. O. Sonne
- Lauffer, L. s. P. Muhn
- Lazarow, P.B. s. S. Alexson
- Lazo, P.A. and L. Bosca, Mitochondrial membrane-bound hexokinase of ascites tumor cells. Functional implications of lysine residues studied by modification with imidoesters 635
- Lebuhn, R. s. H. Paulsen
- Lechene de la Porte, P. s. M. Amouric
- Lederbogen, F., R.L. Krauth-Siegel, G.E. Schulz and R.H. Schirmer, Inhibitors of human glutathione reductase, an enzyme of known threedimensional structure 966*
- Lee, K.S. s. M. Reddington
- Lee, R.W.H., S.B. Por and W.B. Huttner, Protein sulphation on tyrosine residues, studied in neuronal systems 1289*
- Lec, R.W.H. s. W.B. Huttner
- Leemans, J. s. J. Schell
- Legler, G. s. R. Datema
- Legler, G. s. M. Herrchen
- Legler, G. s. H. Hettkamp
- Lehle, L., Structure and biosynthesis of yeast glycoproteins 1019*
- Leiter, J. s. W. Helliger
- Lemke, H. s. H. Lüddens
- Lemke, H. s. U. Schwab
- Lentzen, H. and J. Palenker, Enkephalin degradation by glial cells (primary astrocytes) 1309*
- Lentzen, H. s. J. Palenker
- Leonard, K.R., T. Arad, B. Tesche, V.A. Erdmann, H.G. Wittmann and A.E. Yonath, Crystallization, electron microscopy and three-dimensional reconstructions studies of ribosomal subunits 880*
- Liefländer, M. s. P. Landauer
- Lindemann, H., Studies on the reaction products of cyclophosphamide (endoxan) with DNA in vitro 930*
- Linder, S. s. N.R. Ringertz
- Linder, D. s. M. Schlüter
- Lindigkeit, R., St. Heymann, G. Schmidt, C.-U. v. Mickwitz, Th. v. Zglinicki and M. Böttger, Structural and biochemical characterization of decondensed chromatin 930*
- Lindner, E. s. H. Metzger
- Lindy, S. s. T. Sorsa
- Lingens, F. s. H.G. Beschle
- Lingens, F. s. B. Hauer
- Lingens, F. s. A. Markus
- Lignon, M.F. s. A. Previero
- Linington, C. and T.V. Waehneltdt, Perturbation of the in vitro assembly of peripheral nervous system myelin by monensin 881*
- Linke, R.P. s. M. Eulitz
- Linzen, B. s. J. Markl
- Linzen, B. s. H.-J. Schneider
- Little, C. s. R.L. Olsen
- Löbermann, H., F. Lottspeich, W. Bode and R. Huber, Interaction of human α_1 -proteinase inhibitor with chymotrypsinogen A and crystallization of a proteolytically modified α_1 -proteinase inhibitor 1377
- Loechleiter, F. s. W. Cohn
- Löffler, C. s. B.-M. Jönsson
- Löffler, H.-G. and F. Schneider, What may be the real physiological function of aminoacylase (EC 3.5.1.14) in the kidney? 960*
- Löhle, E. s. R. Büchsel
- Löhlein, G. and H. Eggerer, Nicotinic acid metabolism: Stereochemical course of the (2R, 3S)-2,3-dimethylmalate lyase reaction 1103
- Löwel, M. s. J.-S. Jenke
- Logemann, E. and J.H. Wissler, Humoral polypeptide mediators of inflammation (leukorecruitin, anaphylatoxin, cocytotaxin): Homogeneity criteria and separation of identified nutrition pollutants as companion products present in blood 939*
- Loidl, A. s. S. Hauptlorenz
- Loidl, P., P. Gröbner, A. Csordas and B. Puschendorf, Cell cycle perturbations by short-chain fatty acids in *Physarum polycephalum* 954*
- Loidl, P. s. P. Gröbner

- Londershausen, M., P. Kuppert and K.-D. Spindler, Ecdysteroid receptors: A comparison of cytoplasmic and nuclear receptors from crayfish hypodermis 797
- Lorez, H. P. s. U. Otten
- Lorenz, S. s. H. Schmiady
- Lottspeich, F. s. A. Henschen
- Lottspeich, F. s. M. Kehl
- Lottspeich, F. s. H. Löbermann
- Lottspeich, F. s. H.-J. Schneider
- Lottspeich, F. s. J. Stadler
- Løvstad, R. A., Inhibition of copper-induced hemolysis by ceruloplasmin, apoceruloplasmin and asialoceruloplasmin 922*
- Lozano, G. and P. K. Müller, Collagen type I mRNA level in dematosporaxis 931*
- Lozano, G. s. E. Pöschl
- Lubberding, H. J. s. G. Zimmer
- Lucas, C. A. and G. W. Kreutzberg, Regulation of acetylcholinesterase release from nerve cells 1309*
- Ludány, A., H.-J. Hartmann and U. Weser, Circular dichroism of gold(I)-metallothioein 992*
- Lübbers, D. W., U. Heinrich and J. Hoffmann, Quantitative analysis of reflection spectra on the perfused brain in different states of oxygen supply 543*
- Lübbers, D. W. s. K. Zierold
- Lücken, U. s. G. Schäfer
- Lüddens, H., H. Lemke and B. Havsteen, Studies on the porcine adrenal ACTH receptor 942*
- Lührmann, R. s. P. Bringmann
- Lührmann, R. s. H. Hornig
- Luka, J. s. H. Jörnval
- Lukas, B., H. Graf and V. Ullrich, Metabolism of 7-ethoxycoumarin 973*
- Lund, H. and J. Bremer, Carnitine acetyltransferase. Effect of malonyl-CoA, fasting and clofibrate feeding in different rat and rabbit tissues 970*
- Lund, T., J. Hotlund and S. G. Laland, Phosphorylation of HMG 14 and 17 in metaphase and interphase HeLaS3 cells 931*
- Luterbacher, S. s. H. J. Schatzmann
- Maas, R. s. A. Hinkkanen**
- Macartney, H. W. s. S. Engelbrecht
- Macartney, H. W. s. H. Tschesche
- Mack, H. s. R. Brossmer
- Mägdefrau, H., R. Runzler, K. Kohler and D. G. Weiss, Rapid axoplasmic transport of metabolically inert low molecular mass substances 1310*
- Maelicke, A. and D. Watters, On the organization of ligand binding and antigenic sites at the acetylcholine receptor 1283*
- Maelicke, A. s. E. Carbone
- Männlein, E. s. G. Ott
- Magnusson, S. and B. Símónarson, The digestion of protein substrates by pepsin 983*
- Magrini, U. s. C. L. Balduini
- Maidhof, A. s. A. Bernd
- Maidhof, A. s. M. Geisert
- Maita, T. s. T. Umegane
- Majuri, R., I. Kouvonon and R. Gräsbeck, Isolation and partial characterization of the pig intestinal haem receptor 901*
- Malcovati, M. and G. Valentini, Exploring an allosteric enzyme: the fructose 1,6-bisphosphate-activated pyruvate kinase from *E. coli* 544*
- Maller, J. s. R. L. Erikson
- Mallick, U. s. H. J. Rahmsdorf
- Mannervik, B., Glutathione conjugation in the biotransformation of xenobiotics 966*
- Marchiori, F., G. Borin, D. Stivanello, V. Moretto and G. Chessa, Protamines, V. Synthesis of three fragments spanning the entire sequence of [perornithine]-thynnine Z1 1483
- Margreiter, R. s. D. Fuchs
- Marin-Grez, M., G. Schaechtelin and K. Hermann, Kininogenase activity in rat uterus homogenates 1359
- Markl, J., H. Decker, B. Linzen, W. G. Schutter and E. F. J. van Bruggen, Hemocyanins in spiders, XV. The role of the individual subunits in the assembly of *Eurypelma* hemocyanin 73
- Markus, A., W. Klages und F. Lingens, Mikrobieller Abbau von 4-Chlorphenylelessigsäure. Chemische Synthese von 3-Chlor-4-hydroxy-, 4-Chlor-3-hydroxy- und 4-Chlor-2-hydroxyphenylelessigsäure 431
- Markus, M., A. Boiteux and Th. Plessner, Kinetics of pyruvate kinase: determination of 17 molecular parameters by successive linearization of the concerted model 544*
- Markus, M. s. Th. Plessner
- Markussen, J. s. O. Sonne
- Marnhoorn, M. G. s. A. Tulp
- Marquardt, H. s. A. Ogilvie
- Martens, J. s. U. P. Hansen
- Martensen, H. J. s. J. Tittor
- Matsuda, G. s. T. Umegane
- Matthaei, H. s. E. Buse
- Matthaei, H. s. J. Wildmann
- Matthies, H. J., H.-L. Rührich, B. Hartrodt, K. Neubert, H. Stark and A. Barth, Structural modifications of β -casomorphin-5: Synthesis and pharmacology 942*
- Matthies, H. J. s. K. Neubert
- Maurer, H. R. s. R. Neumeier
- Mayer, E. s. K. Hempel
- Mayer, M. s. M. Dudai
- Mayer, M. s. M. Kidron
- Mayr, U., G. Gross, H. Hauser, W. Bruns and J. Collins, On the nature and coinduction of two genes in the neighbourhood of the human interferon β gene 985*
- Mayr, U. s. R. Hensel
- Mazur, G. und G. Braunitzer, Hämoglobine, XLIV: *Perissodactyla*: Die Sequenz der Hämoglobine von

- Wildesel (*Equus hemionus kulan*) und Zebra (*Equus zebra*) 59
- Mazur, G., G. Braunitzer und P.G. Wright, Die Primärstruktur des Hämoglobins vom Breitmaulnashorn (*Ceratotherium simum*, Perissodactyla): β 2 Glu 1077
- McIntyre, J.O. s. W. Trommer
- Mechler, B., M. Müller, H. Müller, F. Meussdoerffer and D.H. Wolf, In vivo biosynthesis of vacuolar proteinases in wild-type and proteinase mutants of *Saccharomyces cerevisiae* 881*
- Mecke, D. s. K. Valentin
- Mehrke, G. s. H. Jockusch
- Meier, B., S. Bockemühl, L. Calabrese and G. Rotilio, Evidence that superoxide dismutase inside intact bacteria has a different form to the isolated enzyme 960*
- Melchers, F., Cellular and molecular requirements for collaboration of T and B cells 902*
- Mendla, K. and M. Cantz, Oligosaccharide sialidase of pig kidney: some properties 1034*
- Menke, R. s. W. Huth
- Mentlein, R. and E. Heymann, Inhibition of fibrin polymerization by dipeptidyl peptidase IV 984*
- Mentlein, R. s. A.C. Feller
- Mentlein, R. s. M. Suttrop
- Mergenhausen, D., Genetic characterization of a short-period clock mutant of *Chlamydomonas reinhardtii* 955*
- Mergenhausen, D. s. O. Mittelsten Scheid
- Mersmann, G. and C. Domsch, Factors affecting the separation of lysosomes from fibroblasts by Percoll gradient centrifugation 1034*
- Mersmann, G. s. C. Noeske
- Mersmann, G. s. C. Ziegler
- Merz, R. and Fr. Schneider, Growth characteristics of the S-compartment of the cell cycle of Ehrlich ascites tumor cells after deprivation of oxygen 955*
- Merz, W.E. and M. Dörner, Investigations on choriogonadotropin chemically modified by iodination 1034*
- Merz, W.E. s. G. Hilf
- Metalová, M. s. M. Havranová
- Mettler, L. s. A.B. Czuppon
- Mettler, L. s. J. Dietl
- Metz, P. s. W. Stoffel
- Metzger, H. and E. Lindner, Forskolin-dependent activation of an adenylate cyclase of rat heart membranes leads to an inhibition of a membrane-bound Na,K-ATPase 466*
- Meuel, B. s. H. Notbohm
- Meussdoerffer, F. s. B. Mechler
- Meves, H. s. M. Rack
- Meyer, H.H.D. s. P.I. Szendro
- Michalski, J.-C., A.P. Corfield and R. Schauer, Solubilization and affinity chromatography of a sialidase from human liver 1097
- Michel, R. and G. Wegener, Metabolic effects of anoxia in the central nervous system of the locust (*Locusta migratoria*) 1310*
- Michels, W., S. Bornemann and E. Schlimme, Syntheses of 5'-capped 2'.5'-oligoadenylates and their catabolic properties in rat liver nuclei 985*
- Mickwitz, C.-U. v. s. R. Lindigkeit
- Mierau, J. s. A. Haggag
- Minakata, K., M. Asano, T. Sato and N. Harada, Assay of α -cysteine proteinase inhibitor in serum or plasma 493
- Minty, A. s. M.E. Buckingham
- Minwegen, R. s. A. Kindler
- Misra, D. s. H. Aquila
- Mitchell, P., Enzymes and porters as molecular machines 916*
- Mittelsten Scheid, O. and D. Mergenhausen, Zoospore liberation in a cell-cycle mutant of *Chlamydomonas reinhardtii* 956*
- Miyake, A., Conjugation in ciliates: A model system for biochemistry of morphogenesis and differentiation 130*
- Möbius, D. s. W. Probst
- Moelling, K., P. Donner, M.-K. Owada, I. Greiser-Wilke and T. Bunte, Biochemical characterization of transformation-specific proteins of acute avian leukemia and sarcoma viruses 882*
- Møller, J.V., J.P. Andersen and P.L. Jørgensen, Functional significance of quaternary organization of sarcoplasmic reticulum Ca²⁺-ATPase 462*
- Montagu, M. van s. J. Schell
- Moretto, V. s. F. Marchiori
- Morgat, J.L. s. F. Fahrenholz
- Moroder, L., E. Wünsch, N. Vaysse and A. Ribet, Synthesis of [8-norleucine]somatostatin-28 1247
- Moroder, L. s. A. Previero
- Moroder, L. s. E. Wünsch
- Morris, St. J. s. Th. Chr. Südhof
- Mortensen, S.B. s. H.S. Bleeg
- Moses, E. s. H.-J. Hinz
- Mourier, G. s. A. Previero
- Mruk, J., A. Bakardjiev and W. Burgermeister, Prostaglandin E₁ action on adenylate cyclase activity and membrane lipids in platelets 745
- Muckel, C. s. R. Brigelius
- Mühleisen, M., W. Probst and H. Rahmann, Calcium-ion binding to liposomes composed of neutral and negatively charged lipids 1310*
- Mühlradt, P.F., Altered cell surface glycosphingolipids of murine lymphocytes belonging to different differentiation pathways 129*
- Müller, E. s. H.-J. Schneider
- Müller, E. s. T. Stein
- Müller, H., H. Neufang, U. Herbold and K. Knobloch, Purification and properties of the coupling factor-

- ATPases F₁ from *Rhodopseudomonas palustris* and *Rhodopseudomonas sphaeroides* 917*
- Müller, H. s. U. Herbold
- Müller, H. s. K. Knobloch
- Müller, H. s. B. Mechler
- Müller, H. s. H. Neufang
- Müller, H.-G. s. D. Jeckel
- Müller, H.W. s. W. Seifert
- Müller, K.-H. and Th. Plessner, Confidence regions for the rate constants in a two-exponential model 545*
- Müller, M. s. B. Mechler
- Müller, M. s. W. Stoffel
- Müller, M. s. D. Werner
- Müller, M. J. s. A. Thomsen
- Müller, P. s. H. Bernheimer
- Müller, P.K. s. G. Lozano
- Müller, P.K. s. E. Pöschl
- Müller, P.K. s. M. Wiestner
- Müller, R. s. D. Kuschnitz
- Müller, T., E. Bause and L. Jaenicke, Formation of lipid-linked mannosyl oligosaccharides in *Volvox carteri* 1035*
- Müller, W.E., β -Carbolines as ligands of the benzodiazepine receptor 1284*
- Müller, W.E. s. S.A. C. Schläfer
- Müller, W.E.G. s. A. Bernd
- Müller, W.E.G. s. M. Geisert
- Müller, W.H. s. C. Siepl
- Müller-Enoch, D., The nature of the modified type II (reverse Type I)-spectral change induced by numerous substrates of the cytochrome P-450-containing monooxygenase-system in liver microsomes 973*
- Muhn, P. and F. Hucho, Covalent labeling of the acetylcholine receptor from torpedo electric tissue with the channel blocker [³H]triphenylmethylphosphonium by UV irradiation 902*
- Muhn, P., L. Lauffer and F. Hucho, [³H]Methyltriphenylphosphonium as a reversible and irreversible ligand for the ion channel of the nicotinic acetylcholine receptor 1311*
- Muller-Eberhard, V. s. N. Katz
- Multhaup, I., A. Csordas, H. Grunicke, R. Pfister and B. Puschendorf, The true acetylation pattern of histones in Ehrlich ascites tumor cells 931*
- Muramatu, M., T. Satoh, Y. Yanagimoto, Y. Kanamoto, I. Katsuyama, M. Kanamoto and K. Taguchi, Inhibitory effects of aryl *trans*-4-(aminomethyl)cyclohexanecarboxylate and aryl *trans*-4-(guanidinomethyl)cyclohexanecarboxylate on serine proteases and their antiallergic effects 203
- Muscholl, E. and F.-J. Spira, Kinetik der durch elektrische Feldreizung des Herzens hervorgerufenen Freisetzung von Noradrenalin und Dopamin- β -Monooxygenase 1312*
- Mutt, V. s. H. Jörnvall
- Naithani, V.K. and H.-G. Gattner, Preparation and properties of citraconyl-insulins 1443
- Nassar, F.R. and M. Höfer, Anaerobic active transport of D-glucose analogues in *Schizosaccharomyces pombe* (972h⁻) 902*
- Nastainczyk, W., L. Vittozzi and V. Ullrich, Microsomal target proteins for metabolically activated carbon tetrachloride 974*
- Nebinger, P. s. A. Franz
- Nelles, L.P. and H.P. Schnebli, Subunit structure of the rat α -macroglobulin proteinase inhibitors 677
- Nelson, W.J. s. P. Traub
- Neubert, K. s. Hj. Matthies
- Neufang, H., H. Müller, U. Herbold and K. Knobloch, Quantitation of bacteriochlorophyll in chromatophore suspensions from purple bacteria at 375 nm 917*
- Neuhoff, V. s. P.J. Gebicke-Härter
- Neufang, H. s. U. Herbold
- Neuhoff, V. s. G. Hüther
- Neufang, H. s. K. Knobloch
- Neufang, H. s. H. Müller
- Neumann, E. s. J. Bernhardt
- Neumeier, R. and H.R. Maurer, Isolation of a high molecular mass granulocyte colony stimulating factor from bovine lung conditioned medium 1493
- Neumeier, R., H.R. Maurer, M. Arnold, U. Gerlach, K. Glendinning, H. Renner and J.H. Wissler, Identification of two granulocyte/macrophage colony-stimulating factors from porcine leukocyte cultures 193
- Neupert, W. s. H. Freitag
- Neupert, W. s. B. Schmidt
- Nicolai, H. von s. H. Egge
- Nicolis, G., Non-equilibrium transitions: a mechanism of evolution of complex systems 536*
- Nielsen, H. and J. Engberg, Genetic analysis of the *rdaA* - Locus in *Tetrahymena pigmentosa* 932*
- Niemann, H., Biosynthesis of a viral glycoprotein carrying exclusively O-glycosidic carbohydrate-protein linkages 1016*
- Niemann, R., D. Balkau, D. Göhler and E. Buddecke, Separation and characterization of chondroitin sulfotransferase and N-desulfoheparan sulfate sulfotransferase from calf arterial tissue 1035*
- Niemann, R. and E. Buddecke, Substrate specificity and regulation of activity of rat liver β -D-glucuronidase 591
- Nierhaus, K.H. s. R. Röhl
- Nika, H. s. O. Nygård
- Nilsson, L. s. O. Nygård
- Nishimura, S. s. G. Ott
- Nishimura, S. s. E. Schachner
- Nöhle, U., A.K. Shukla, C. Schröder, G. Reuter, J.P. Kamerling, J.F.G. Vliegenthart and R. Schauer,

- Synthesis and natural occurrence of 2-deoxy-2,3-didehydro-*N*-glycoloylneuraminic acid 1036*
- Noeske, C. and G. Mersmann, Partial purification and characterization of β -D-mannosidase from human placenta 1037*
- Nohl, H., W. Jordan and D. Hegner, Mitochondrial formation of OH[•] radicals by an ubisemiquinone-dependent reaction. An alternative pathway of the iron-catalysed Haber-Weiss cycle 599
- Norell, M., S. Aström and A. von der Decken, Nuclear proteins associated with transcriptionally active and inactive chromatin 932*
- Norén, O. s. E. M. Danielsen
- Northemann, W. s. P. C. Heinrich
- Northemann, W. s. A. Villringer
- Norum, K. R. s. M. S. Thomassen
- Notbohm, H., B. Meuel and R. Brust, Assembling of chromatin quaternary structure with increasing ionic strength 933*
- Nowack, J. s. A. Hinkkanen
- Nowock, J. s. A. E. Sippel
- Nyberg, F., A. Wahlström and L. Terenius, Endorphins: a growing family of peptides with opiate activity 942*
- Nyfelner, R. s. E. Wünsch
- Nygård, O. and H. Nika, Protein-RNA interactions at the mammalian ribosomal interface as studied by crosslinking 882*
- Nygård, O., P. Westermann and L. Nilson, Interaction of eukaryotic initiation factors eIF-2 and eIF-3 with 18S ribosomal RNA and its role in factor-40S subunit interaction 883*
- Nygård, O. s. P. Westermann
- Oberthür, W., G. Braunitzer und I. Würdinger, Hämoglobine, XLVII: Das Hämoglobin der Streifengans (*Anser indicus*). Primärstruktur und Physiologie der Atmung, Systematik und Evolution
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- Oberthür, W. s. G. Braunitzer
- Obrocki, J. s. Th. Chr. Südhof
- Oesterhelt, D., Photosynthesis in halobacteria: bacteriorhodopsin and halorhodopsin 538*
- Ötting, F. s. L. Flohé
- Ötting, F. s. W. A. Günzler
- Ötting, F. s. G. J. Steffens
- Oftebro, H. s. K. Saarem
- Ogilvie, A., M. Schrappe, H.-H. Arnold and H. Marquardt, Alterations of glycoprotein pattern during chemically induced malignant transformation and its reversal by 5-bromodeoxyuridine 903*
- Ohlsson, K., A. Polling and P. Stenberg, Glutaminylopeptide γ -glutamyltransferase dependence of the uptake of trypsin- α -macroglobulin complexes by macrophages 213
- Ohlsson, K. s. B.-M. Jönsson
- Ohst, E. s. T. Stein
- Olsen, R. L. and C. Little, Isolation of both myeloperoxidase and eosinophil peroxidase from human white blood cells 960*
- Olsnes, S. s. E. Eiklid
- Olsnes, S. s. K. Sandvig
- Olsnes, S. s. A. Sundan
- Opperdoes, F. R. s. R. D. Walter
- Orfanos, C. s. Ch. Bauer
- Ormos, P., L. Reinisch and L. Keszthelyi, Fast electric response signals in the bacteriorhodopsin photocycle 545*
- Osmundsen, H. and J. Cervenka, Isolation of rat liver peroxisomes by vertical rotor centrifugation using self-generated CDP 545 density gradients 1000*
- Østvold, A. C. s. J. Hotlund
- Oswald, E. s. M. Geisert
- Otten, L. s. J. Schell
- Ott, G., R. Praiser, E. Männlein and H. Kersten, On the mechanism of fine tuning of the translational apparatus involving ribosylthymine in tRNA of eubacteria 884*
- Otten, U. and H. P. Lorez, Nerve growth factor regulates neuropeptide content in primary sensory neurones 1287*
- Otto, M. K., J. Thiele and J. E. Schultz, Biochemical characterization of the calcium channel in the excitable ciliary membrane from *Paramecium* 1312*
- Oude Elferink, R. P. J. s. F. Steckel
- Owada, M.-K. s. K. Moelling
- Pachmann, K., M. Pech and P. Dörmer, Combining microimmunofluorimetry with in situ hybridization. Determination of surface immunoglobulin and its mRNA in the same individual cells 903*
- Pajula, R.-L. s. E. O. Kajander
- Pakalapati, G. and H. Debuch, Studies on the liberation of fatty acids from 2-lysophosphatidylcholine by a liver lysosomal enzyme activity from chloroquine-treated rats 573
- Palenker, J. and H. Lentzen, Enkephalin degradation by neuroblastoma cells (clone N1E-115) 943*
- Palenker, J. s. H. Lentzen
- Pappert, C. and D. Schubert, Stable noncovalent dimers of band 3 protein from erythrocyte membranes solubilized by nonionic detergent as detergent-induced artifacts 904*
- Parawaresch, M. R. s. A. C. Feller
- Park, C.-S. s. R. Tauber
- Pashnina, E. P. s. V. Brendel

- Passing, R. and D. Schubert, The binding of Ca^{2+} to band 3 protein of the human erythrocyte membrane 904*
- Pattus, F. s. P. Vainio
- Patzelt-Wenczler, R. s. W. Schoner
- Paul, J., The human ϵ globin gene: A paradigm for erythroid differentiation 125*
- Pauls, H. s. W. Schoner
- Paulsen, H., R. Lebuhn and H. Tietz, Chemical synthesis on glycoprotein structures 1015*
- Pauly, E. s. H. Kratzin
- Pauly, E. s. C.-y. Yang
- Pech, M. s. K. Pachmann
- Pedersen, J. I., Hepatic mitochondrial cytochrome P-450. Characterization, function and clinical significance 974*
- Pedersen, J. I. s. F. Kase
- Pedersen, J. I. s. K. Saarem
- Persson, M. s. H. Jörnvall
- Peter-Katalinić, J. s. H. Egge
- Peters, H., M. P. Dierich and K. Dose, Enzyme-linked immunosorbent assay for detection of T-2 toxin 1437
- Peters, R., Fluorescence microphotolysis: Diffusion measurements on single cells 904*
- Peters, R. s. K. Beck
- Peters, S., F. von der Haar and F. Cramer, Lactonization of γ -Hydroxyvaline during aminoacylation of tRNA^{Val} from yeast. The mechanism of valyl-tRNA synthetase from yeast 884*
- Petersen, H. U., Mechanism of initiation of protein biosynthesis 885*
- Petersen, H. U. s. F. Wikman
- Petersen, T. E., K. Skorstengaard, P. Sahl, K. Vibe-Pedersen and H. C. Thøgersen, Partial primary structure of bovine plasma fibronectin: Evidence for multiple gene multiplication in its evolution 905*
- Pevec, B. s. R. Gregory
- Pfaender, P. s. A. Plessing
- Pfeifer, G., S. Grünwald, T. L. J. Boehm and D. Dra-hovsky, Isolation and characterization of DNA-methylating enzymes from human placenta 933*
- Pfeiffer, F., D. Graham and H. Betz, Characterization of the affinity purified glycine receptor of rat spinal cord 1312*
- Pfeiffer, F. s. H. Betz
- Pfeiffer, U. s. B. Ziemsen
- Pfeiffer, W., Pheromone binding sites in the antenna of *Antheraea polyphemus* (a big silkworm) 992*
- Pfeuffer, M., C. A. Barth, H. Hagemeister and W. Kaufmann, Influence of dietary changes in lipid and protein on serum lipoproteins in swine 950*
- Pfister, R. s. I. Multhaupt
- Pfleiderer, G. s. K.-D. Jany
- Pfleiderer, G. s. W. Ulmer
- Pflugfelder, G. O. s. J. Sonnenbichler
- Piel, N. s. H.-J. Gabius
- Piel, N. s. R. Schröder
- Pieler, T. and V. A. Erdmann, Ribosomal 5S RNA – A model system for RNA structure and stability 885*
- Pieler, T. s. I. Kumagai
- Pieper, E. s. S. Engelbrecht
- Pires, P. s. J. Suko
- Pitsch, C. and H. Simon, The stereochemical course of the water elimination from (2R)-phenyllactate in the amino acid fermentation of *Clostridium sporogenes* 1253
- Plagens, U. s. D. Werner
- Plank, B. s. J. Suko
- Plasa, G. s. C. W. M. Haest
- Plesner, T. s. M. Wilken
- Plessner, Th. and M. Markus, Minimum energy dissipation in the pyruvate kinase reaction and the thermodynamic efficiency of glycolysis 546*
- Plessner, Th. s. M. Markus
- Plessner, Th. s. K.-H. Müller
- Plessing, A., G. Siebert, J. H. Wissler, A. J. Puigserver and P. Pfaender, Enzymatic cleavage of the ϵ -peptide bond in α - and ϵ -substituted glycyl- and phenylalanyl-lysine peptides 279
- Pléau, J.-M. s. G. Auger
- Pöschl, E., G. Lozano, J. Böhm, C. Sorbas and P. K. Müller, Isolation and partial characterization of genomic clones specific for cartilage 933*
- Pohlmann, R., S. Krüger, A. Hasilik and K. von Figura, Effect of monensin on transport and processing of lysosomal enzymes 886*
- Pohlmann, R. s. A. Hasilik
- Polling, A. s. K. Ohlsson
- Pongs, O., B. Dworniczak, S. Kobus and K. Schaltmann, Regulation of development of salivary glands in 3rd instar *Drosophila melanogaster* larvae by ecdysterone 127*
- Pont, J. J. H. H. M. de s. S. L. Bonting
- Pontz, B. F. and H. Richter, Chemotactic activity of fibronectin-derived fragments in vitro 905*
- Por, S. B. s. R. W. H. Lee
- Porra, R. J. s. O. Klein
- Porsche, E., Kainic acid induced wet dog shakes in rat. The effect of 2-chloroadenosine, methylxanthines and of the new synthetic xanthine HWA 285 1313*
- Port, H. s. P. Wunderwald
- Possani, L. D. s. E. Carbone
- Praisler, R. s. G. Ott
- Preis, P. s. J. Suko
- Presek, P. s. P. Fister
- Prestipino, G. s. E. Carbone
- Previero, A., G. Mourier, J.-P. Bali, M. F. Lignon and L. Moroder, N^{α} -Glycosylgastrin related peptides. Synthesis characterization and biological activity 813
- Probst, W., D. Möbius and H. Rahmann, Surface behaviour of gangliosides at different temperatures 1313*

- Probst, W. s. M. Mühleisen
 Puigserver, A. J. s. A. Plessing
 Puschendorf, B. s. S. Hauptlorenz
 Puschendorf, B. s. W. Helliger
 Puschendorf, B. s. P. Loidl
 Puschendorf, B. s. I. Multhaup
- Quandt, L. and W. Huth, The molecular basis of the charge heterogeneity of mitochondrial acetyl-CoA acetyltransferase 946*
- Rack, M., Effects of some chemical reagents on the voltage-dependent sodium channel of frog nerve fibres 1314*
- Rack, M., H. Meves, L. Béress and H. H. Grünhagen, Synthesis and properties of a toxic, fluorescent derivative of the sea anemone toxin II from *Anemonia sulcata* 993*
- Radola, B. J., High resolution analytical and preparative isoelectric focusing of proteins: principles and strategy 1003*
- Radsak, K., G. Schwarzmann and H. Wiegandt, Studies on the cell association of exogenously added sialoglycolipids 263
- Ragg, H. s. K. Hahlbrock
- Rahmann, H., Distribution and possible functional role of vertebrate brain gangliosides during phylogeny and ontogeny 1021*
- Rahmann, H. s. B. Heppelmann
 Rahmann, H. s. M. Mühleisen
 Rahmann, H. s. W. Probst
- Rahmsdorf, H. J., U. Mallick, P. Herrlich and N. Koch, Arresting replication induces Ia-associated invariant chain synthesis in proliferating B cells 993*
- Rajewsky, M. F. s. A. Kindler
- Randles, J. W. s. G. Steger
- Rao, M. L. und G. Gross, Welche Beziehung besteht zwischen der Bioverfügbarkeit von Neurotransmittervorstufen, Neurotransmitter und hypophysären Hormonen beim Menschen? 1314*
- Rasilo, M.-L. and O. Renkonen, Analysis of linkage monosaccharides in human teratocarcinoma cell glycopeptides: Paper chromatographic separation of *N*-acetylglucosaminitol and *N*-acetylgalactosamininitol 89
- Rathgeber, G. s. H.-J. Schäfer
 Rautenberg, W. s. S. Engelbrecht
 Rautenstrauch, H. s. G. Bovermann
 Recktenwald, D. s. R. Gregory
 Recktenwald, L. s. Ch. Bauer
- Reddington, M., K. S. Lee, P. Schubert and G. W. Kreutzberg, An A₁-adenosine receptor as mediator of the depressive effect of adenosine on synaptic transmission in the rat hippocampus 1285*
- Rehm, H. A. and H. Betz, Specific cytotoxicity and binding of β -bungarotoxin in the chick central nervous system 1315*
- Rehm, H. A. s. H. Betz
 Rehm, S. s. H.-J. Gabius
- Rehorek, M., N. A. Dencher and M. P. Heyn, Fluorescence energy transfer between 1,6-diphenyl-1,3,5-hexatriene and the chromophore of bacteriorhodopsin: determination of the distance of closest approach and effect on fluorescence depolarization 546*
- Reiber, H. und A. Suckling, Immunologische Prozesse und Blut-Liquor-Schrankenstörung bei der Chronisch rezidivierenden experimentellen allergischen Enzephalomyelitis 1294*
- Reibnegger, G. s. D. Fuchs
 Reinacher, M. s. P. Fister
 Reinauer, H. s. B. Dahlmann
 Reinauer, H. s. M. Förster
 Reinisch, L. s. P. Ormos
 Reipen, G. s. R. Roggenkamp
 Reitman, M. s. S. Kornfeld
 Rembold, H. s. J. Eder
 Rempeters, G. and W. Schoner, Imidazole-Cl and Tris-Cl substitute for NaCl in inducing high-affinity AdoPP[NH]P binding to (Na⁺ + K⁺)-ATPase 906*
- Rempeters, G. s. W. Schoner
 Renkonen, O. s. M.-L. Rasilo
 Renner, H. s. M. Gottwik
 Renner, H. s. R. Neumeier
 Rensing, L. s. W. Schill
 Rensing, L. s. R. Schulz
 Rensing, L. s. M. G. Vicker
 Resch, K. s. M. Brennecke
 Reuter, G. s. U. Nöhle
 Reuter, G. s. R. Schauer
 Reuter, R. s. P. Bringmann
 Reutter, W. s. Ch. Bauer
 Reutter, W. s. R. Büchsel
 Reutter, W. s. W. Kreisel
 Reutter, W. s. R. Tauber
 Ribet, A. s. L. Moroder
- Richter, H. and H. Hörmann, Early and late cathepsin D-derived fragments of fibronectin containing the C-terminal interchain disulfide cross-link 351
- Richter, H. and H. Kersten, Function of *E. coli* tRNAs with a heterologous methyl group in homologous protein synthesizing systems 886*
- Richter, H. s. B. F. Pontz
 Richter, H.-P. s. R. H. Lange
- Rickwood, D. and T. C. Ford, Separation of macromolecules and macromolecular complexes 1001*
- Riedel, E. s. W. Grothaus
 Riesner, D. s. B. Brosius
 Riesner, D. s. G. Steger

- Rinast, K.-A. and K. Birkmann, Influence of temperature on the aerobic glycolysis of *Saccharomyces carlsbergiensis*. An approach towards system identification via signal analysis 956*
- Ringertz, N. R., S. Linder and S. Zuckerman, Molecular and cellular aspects on the determination of embryonic cells for tissue-specific differentiation 126*
- Rinke, J. and J. A. Steitz, snRNP particles containing precursor molecules of both human 5SrRNA and tRNAs are recognized by the 'Anti-La' lupus antibodies 934*
- Rinke, J. s. P. Bringmann
- Risse, H. J., H. H. Rössler and A. Zimpfer, The glycosylation of polyisoprenols in *Dictyostelium* membranes 1021*
- Rittner, I. s. P. J. Gebicke-Härter
- Robert, B. s. M. E. Buckingham
- Röhl, R., H. E. Roth and K. H. Nierhaus, Inter-protein dependences during assembly of the 50S subunit from *Escherichia coli* ribosomes 143
- Röhm, K.-H., Improved adsorbents for the affinity chromatography of aminopeptidases 641
- Rösel, J. and C. Jungwirth, Characterization of early virus-specific DNA-binding proteins in poxvirus-infected chick-embryo fibroblasts and inhibition of their synthesis by chicken interferon 986*
- Rösner, H., Changes of ganglioside synthesis in renal ganglion cells and optic lobes of chicken in relation to development of retino-tectal projection 1315*
- Rössler, H. H. s. H. J. Risse
- Roggenkamp, R., G. Reipen and C. P. Hollenberg, Processing of the bacterial secretory β -lactamase in *Saccharomyces cerevisiae* 887*
- Roggentin, P., G. Gutschker-Gdaniec, M. Sander-Wewer, R. Schauer and R. Hobrecht, Sialidase production in different media of *Clostridia* causing myonecrosis 1037*
- Roggentin, P. s. G. Gutschker-Gdaniec
- Rohrer, H. and I. Sommer, Developmental expression of high affinity norepinephrine uptake and nerve growth factor receptors in non-neuronal cells from the chick ciliary ganglion 1286*
- Romani, S. s. E. Wünsch
- Romero, P. A. s. R. Datema
- Rommelspacher, H. und G. Brüning, Zum Wirkungsmechanismus von Tetrahydronorharman 1284*
- Rørtveit, T. s. M. S. Thomassen
- Rose, U. s. R. Brossmer
- Rossi, J. P. F. C. s. H. J. Schatzmann
- Roth, H. E. s. R. Röhl
- Roth, M. s. L. Juillerat-Jeanneret
- Rotilio, G. s. B. Meier
- Rott, R., Determinants of influenza virus pathogenicity (a review) 1273
- Rudolph, R. and I. Heider, Influence of glutathione on protein folding 967*
- Rudolph, R. s. R. Hermann
- Rücknagel, P. s. G. Braunitzer
- Rüdiger, H., Plant lectins and lectin-binding proteins 1017*
- Rueß, K.-P. s. P. Landauer
- Rüthrich, H.-L. s. H. J. Matthies
- Rüthrich, H.-L. s. K. Neubert
- Ruf, H. H., Microsomal electron transport. The rates of the electron transfers to cytochrome P-450 975*
- Runzler, R. s. H. Mägdefrau
- Saarem, K., S. Bergseth, H. Oftebro and J. I. Pedersen, Subcellular localization of vitamin D₃-25-hydroxylase in human liver 975
- Sabbagh, M. s. O. G. Brodner
- Sachs, L., Mosbacher Kolloquium 82; Synchrony of gene expression and regulation of the developmental program in normal and leukemic cells 119*
- Sahl, P. s. T. E. Petersen
- Salm, K.-P. s. W. Stoffel
- Sander-Wewer, M. s. G. Gutschker-Gdaniec
- Sander-Wewer, M. s. P. Roggentin
- Sandvig, K. and S. Olsnes, Entry of the toxic proteins abrin, ricin, modeccin and diphtheria toxin into cells 906*
- Sato, T. s. K. Minakata
- Satoh, T. s. M. Muramatu
- Satre, M. and G. Zaccari, Approach of F₁-ATPase structure by small-angle scattering methods 472*
- Satre, M. s. P. V. Vignais
- Saudek, V. s. M. Havranová
- Saunders, D. and K. Freude, Cross-linked [DAIa^{A1}]-insulins. Evidence for a change in the conformation of the insulin monomer at its receptor 655
- Saunders, D. s. C. Diaconescu
- Schaadt, M. s. U. Schwab
- Schaal, H. s. W. Wille
- Schachner, E., S. Nishimura and H. Kersten, Development of *Dictyostelium discoideum* in the presence and absence of queuine and the queuine family of tRNAs 887*
- Schachschneider, G. s. M. Wenzel
- Schack, L. and T. Dietl, Effect of hog pancreatic kallikrein on blood pressure in rats 107
- Schaechtelin, G. s. M. Marin-Grez
- Schäfer, D. s. K. Zierold
- Schäfer, G., U. Lücken, H. Tiedge and J. Weber, Functional states of mitochondrial ATP-synthetase as probed by nucleotide analogs 470*
- Schäfer, H.-G. s. C. Woenckhaus
- Schäfer, H.-J., P. Scheurich, G. Rathgeber, K. Dose and Y. Kagawa, Photoaffinity labeling and photoaffinity cross-linking of bacterial F₁ATPases 918*

- Schäfer, K. P., RNA Synthesis and processing reactions in a subcellular system from mouse L cells 33
- Schätz, Ch. R., R. W. Veh and K. H. Andres, Acetylcholine and butyrylcholine as pseudoinhibitors in cholinesterase histochemistry 1316*
- Schaller, H. C., Morphogenetic substances and their role in pattern formation in *Hydra* 131*
- Schaller, H. C. s. H. Bodenmüller
- Schaltmann, K. s. O. Pongs
- Scharf, H.-D. s. T. Stein
- Schartau, W. s. G. Tukanits-Stolz
- Schatz, G., Mechanisms of protein import into mitochondria 888*
- Schatzmann, H. J., S. Luterbacher, J. Stieger and J. P. F. C. Rossi, The calcium pump of the human red cell 461*
- Schauer, R., G. Reuter and R. J. Howard, Influence of malaria infection of Rhesus monkeys on erythrocyte membrane sialic acids 1039*
- Schauer, R. s. G. Gutschker-Gdanic
- Schauer, R. s. J.-C. Michalski
- Schauer, R. s. U. Nöhle
- Schauer, R. s. P. Roggentin
- Schauer, R. s. A. K. Shukla
- Schell, J., M. Van Montagu, M. Holsters, J. P. Hernalsteens, H. De Greve, J. Leemans, L. Willmitzer, L. Otten, J. Schröder and G. Schröder, Plant cells transformed by modified Ti-plasmids: A model system to study plant development 122*
- Schellenberger, W. s. E. Hofmann
- Scheurich, P. s. H.-J. Schäfer
- Schibler, U. s. P. K. Wellauer
- Schill, W., A. Wilkens, H. Kruse and L. Rensing, Are different cell cycle models distinguishable by variations of the cell cycle and responses to pulsive perturbations? 956*
- Schimassek, H. s. D. Jeckel
- Schiphorst, W. E. C. M. s. D. H. van den Eijnden
- Schirmer, R. H. and G. E. Schulz, Dinucleotide-binding proteins 547*
- Schirmer, R. H. s. Th. Fröhlich
- Schirmer, R. H. s. F. Lederbogen
- Schischkoff, J. s. U. Englisch
- Schlaak, H. E., D. Uschtrin and R. Arndt, Comparison of the lipolytic activity of unspecific carboxylesterase and lipase 961*
- Schläfer, S. A. C. and W. E. Müller, Drug binding to tyrosine-modified bovine serum albumin 994*
- Schleuning, M. s. E. Fink
- Schleyer, I. s. M. Schleyer
- Schleyer, M., H. Eitzrodt, T. J. Trah and K.-V. Voigt, Dependence of human somatotropin activity on interchain disulfide bridges 1111
- Schleyer, M., T. Trah and I. Schleyer, Heterogeneity of porcine somatotropin 179
- Schlimme, E., K.-S. Boos and B. Dimke, Mitochondrial ADP, ATP transport and F_1 -ATPase: Prevention and abolition of TNP-derivatized substrate analogs-mediated inhibition 919*
- Schlimme, E. s. K.-S. Boos
- Schlimme, E. s. W. Michels
- Schlüter, M., D. Linder, H. Egge, R. Friedrich, R. Geyer, H. Geyer, G. Hunsmann, W. Koch, J. Schneider and S. Stirm, Glycoprotein 69/71 (gp69/71) from Friend Murine Leukemia virus (F-MuLV): Studies on primary structure and glycosylation 1038*
- Schlüter, H. s. J. Gargyan
- Schmelzer, E. s. P. C. Heinrich
- Schmiady, H., B. Tesche, S. Lorenz and V. A. Erdmann, Electron microscopical structure analysis of isolated 50S ribosomal subunits of *E. coli* and *B. stearothermophilus* with respect to 5S RNA 888*
- Schmidt, A. and J. Grünwald, Differences in [35 S]-proteoglycan metabolism of proliferating and resting arterial smooth muscle cells 1039*
- Schmidt, B., B. Hennig, R. Zimmermann and W. Neupert, Biosynthetic pathway of mitochondrial ATPase subunit 9 in *Neurospora crassa* 888*
- Schmidt, E. R., E. Godwin and N. Israelowski, Entering of centromeric repetitive DNA into the nucleolar DNA (NTS) in the course of DNA duplications in *Chironomus thummi* 934*
- Schmidt, G. s. R. Lindigkeit
- Schmidt, R., Zentralnervöse Plastizität bei Lernvorgängen: Untersuchungen zu molekularen Eigenschaften und zur Verteilung beteiligter Proteine 1288*
- Schmidt, W. s. G. Hilf
- Schnarrenberger, C. s. I. Krüger
- Schnebli, H. P. s. W. Hornebeck
- Schnebli, H. P. s. L. P. Nelles
- Schneider, E. and K. Altendorf, H^+ -ATPase of *Escherichia coli*: High-yield preparation and properties of the proton-translocating sector (F_0) 919*
- Schneider, E., K. Steffens and K. Altendorf, ATP Synthetase (F_1F_0) (EC 3.6.1.3) of *Escherichia coli*: New procedures for the isolation of F_0 and its individual subunits 467*
- Schneider, E. s. K. Steffens
- Schneider, F. s. H.-G. Löffler
- Schneider, Fr. s. W. Kroll
- Schneider, Fr. s. R. Merz
- Schneider, H.-J., U. Illig, E. Müller, B. Linzen, F. Lottspeich and A. Henschen, Hemocyanin in spiders, XVII. A presumptive active-site of arthropodan hemocyanins 487
- Schneider, J. s. M. Schlüter
- Schneider, K. s. P. C. Heinrich
- Schneider, K. s. A. Villringer
- Schneider, M. s. M. Wenzel
- Schneider, R. s. W. Heller

- Schöler, H. und H.-P. Vosberg, Die Rolle von Mg²⁺ bei der Relaxation superhelikaler DNA durch die DNA-Topoisomerase I (ω -Enzym) aus *E. coli* 935*
- Schölmerich, J. s. R. Büchsel
- Schollmeier, K. and W. Hillen, Control of expression and genetic organisation of the Tn 10-encoded tetracycline resistance 994*
- Scholtissek, C., D. Evans and H. Bürger, Enhanced labelling of RNA synthesized in nuclei and reduced labelling of RNA synthesized in the cytoplasm by [³²P]orthophosphate in the presence of nucleosides 1389
- Schoner, W., R. Patzelt-Wenczler, G. Rempeters, H. Kreickmann, H. Pauls and E. H. Serpersu, Comparative studies on the ATP binding sites in (Na⁺ + K⁺)-ATPase and Ca²⁺-ATPase by the use of ATP-analogues 463*
- Schoner, W. s. P. Fister
- Schoner, W. s. G. Rempeters
- Schorer, R. s. G. U. Wollmann
- Schott, H. s. H. Eckstein
- Schott, K. s. G. Hüther
- Schramm, H. J. and W. Schramm, Computer averaging of single molecules of α_2 -macroglobulin and the α_2 -macroglobulin/trypsin complex 803
- Schramm, W. s. H. J. Schramm
- Schrank, B. s. G. Braunitzer
- Schrapppe, M. s. A. Ogilvie
- Schrenk, W. J. s. P. Wunderwald
- Schröder, C. s. U. Nöhle
- Schröder, G. s. J. Schell
- Schröder, J. s. J. Schell
- Schröder, R., N. Piel, H.-J. Gabius and F. Cramer, Application of kinetic methods to different problems on aminoacyl-tRNA synthetases 889*
- Schroeder, W. s. W. Stoffel
- Schröter, H. s. M. M. Gómez-Lira
- Schubert, D. s. C. Pappert
- Schubert, D. s. R. Passing
- Schubert, P. s. M. Reddington
- Schüll, B. s. R. Brossmer
- Schumann, H. s. F. Klink
- Schüttler, A. and D. Brandenburg, Preparation and properties of covalently linked insulin dimers 317
- Schultz, G. s. K. H. Jakobs
- Schultz, J. E. s. S. Klumpp
- Schultz, J. E. s. M. K. Otto
- Schulz, G. s. H. H. Berlet
- Schulz, G. E. s. F. Lederbogen
- Schulz, G. E. s. R. H. Schirmer
- Schulz, R., J. F. Feldmann and L. Rensing, Evidence for the involvement of energy metabolism within the circadian clock mechanism of *Neurospora crassa* 957*
- Schulze, J. and P. Dimroth, Citrate transport in *Klebsiella aerogenes* 920*
- Schutter, W. G. s. J. Markl
- Schwab, U., H. Stein, J. Gerdes, H. Lemke, H. Kirchner, M. Schaadt and V. Diehl, Detection of a Hodgkin and Sternberg-Reed cell specific membrane molecule shared with a normal cell population in human lymphatic tissue 907*
- Schwartz, T. W. and H. S. Tager, Posttranslation modification in the biogenesis of peptides in endocrine F-cells of the pancreas 889*
- Schwarz, L. R., Conjugation does not influence initial rates of uptake of sulfobromophthalein into isolated hepatocytes 1225
- Schwarz, R. T. s. R. Datema
- Schwarzmann, G. s. K. Radsak
- Schweiger, A. and G. Kostka, High molecular mass phosphoproteins of the initiation factor eIF-3 are not identical with a 110 kDa polyribosomal phosphoprotein 1012*
- Schweiger, H. s. K. Brand
- Schwenen, M. s. S. Hebisch
- Schwochau, M., C. Herrnstadt and B. Eckes, rDNA intervening sequence is transcribed at a high level in certain X/Y males of *Drosophila hydei* 935*
- Schwochau, M., C. Herrnstadt and E. Knust, Functional role of the Y-chromosome in the meiotic prophase of *Drosophila hydei* 935*
- Schwochau, M. s. B. Eckes
- Seglen, P. O. s. P. B. Gordon
- Seglen, P. O. s. A. E. Solheim
- Seidl, A. and H.-J. Hinz, Energetics of superhelix-unwinding 935*
- Seifert, R. s. I. Angel
- Seifert, T. s. P. Bartholmes
- Seifert, W., H. J. Fink, S. Beckh and H. W. Müller, Zur Entwicklung von Neuronen des Hippocampus in der Zellkultur: Synapsenbildung und Neuron-Glia-Wechselwirkung in chemisch definiertem Medium 1289*
- Seiler, M. und D. G. Weiss, Irreversible Erniedrigung der Transportkapazität des axonalen Transportes durch Nocodazol 1316*
- Seiler, N. and F. N. Bolkenius, The intracellular catabolism of the polyamines spermidine and spermine 961*
- Seipke, G. und D. Tripier, Isolierung und Aminosäuresequenz eines Hormons mit immunotroper Wirkung 940*
- Seitz, H. J. s. A. Thomsen
- Sekeris, C. E. s. J. Voigt
- Sellinger, K.-H. s. A. Gärtner
- Seppi, C. s. C. L. Balduini
- Serpseru, E. H. s. W. Schoner
- Seybold, G. s. G. Bovermann
- Shealy, D. s. R. L. Erikson
- Shio, H. s. S. Alexson
- Shooter, E. M., Nerve growth factor and neuronal differentiation 127*

- Shukla, A. K. and R. Schauer, Fluorimetric determination of unsubstituted and 9(8)-*O*-acetylated sialic acids in erythrocyte membranes 255
- Shukla, A. K. and R. Schauer, High performance liquid chromatography assay of enzymes of the sialic acid metabolism 1039*
- Shukla, A. K. s. U. Nöhle
- Siboska, G. E. s. F. Wikman
- Siebers, A. s. L. Wiczorek
- Siebert, G. s. A. Plessing
- Siepl, C., B. Freimüller and W. H. Müller, Glutamatdehydrogenase- und γ -Glutamyltransferase-Aktivität bei isolierten Hirnzellen in Kultur 1317*
- Sierralta, W. D. and P. I. Szendro, „Cytosol“ is an unreliable source for the quantitation of cytoplasmic estrogen receptor 994*
- Sies, H., R. Brigelius, E. Cadenas and H. Wefers, Redox cycling, mixed disulfide formation and lipid peroxidation in rat liver 547*
- Sies, H. s. T. P. M. Akerboom
- Sies, H. s. R. Brigelius
- Sies, H. s. E. Cadenas
- Sies, H. s. S. Hebisch
- Siess, E. A. s. R. Dolhofer
- Sigrist-Nelson, K., Chloroplast dicyclohexylcarbodiimide-binding protein: Functional, mechanistic and structural implications 469*
- Silson, F. A. s. W. Kramer
- Simon, H. s. M. Bühler
- Simon, H. s. P. Egerer
- Simon, H. s. C. Pitsch
- Simonarson, B. s. S. Magnusson
- Singh, B., J. Bremer and B. Borrebaek, Malonyl-CoA in rat heart, kidney and liver 920*
- Singh, B. s. I. Almås
- Sinigaglia, F. s. C. L. Balduini
- Sippel, A. E., J. Nowock, M. Theisen and C. Bonifer, The gene for chicken lysozyme: Structure and expression of a steroid-regulated gene 120*
- Sjöström, H. s. E. M. Danielsen
- Skorstengaard, K. s. T. E. Petersen
- Skrzypczyk, H. J. s. E. Bäuerlein
- Slater, E. C., ATPase-ATP synthase: Function and regulation of mitochondrial energy transduction 537*
- Soboll, S. s. S. Hebisch
- Söll, D. s. B. Appel
- Soerensen, U. B. s. E. Wünsch
- Solheim, A. E. and P. O. Seglen, Electro-disruption: A new method for cell homogenization 907*
- Sommer, I. s. H. Rohrer
- Sonne, O., U. D. Larsen and J. Markussen, The effect of oxidation of the Met²⁷ residue of [¹²⁵I]monoidoglugagon on receptor-binding affinity 95
- Sonnenbichler, J., G. O. Pflugfelder and I. Zetl, The structure of oligonucleosomes after transcription 938*
- Sorbas, C. s. E. Pöschl
- Sorsa, T., K. Suomalainen and S. Lindy, Latent human collagenase 984*
- Southan, C. s. A. Henschen
- Spielberger, M. s. D. Fuchs
- Spindler, K.-D. s. M. Londershausen
- Spira, F.-J. s. E. Muscholl
- Spivack, J. s. R. L. Erikson
- Sprotte, U. s. G. Hüther
- Srivastava, L. M. s. B. Ziemsen
- Stadler, J., C. Bordier, F. Lottspeich, A. Henschen and G. Gerisch, Improved purification and *N*-terminal amino acid sequence determination of the contact site A glycoprotein of *Dictyostelium discoideum* 771
- Stahn, R. s. H.-A. Fabricius
- Staub, W. s. M. Förster
- Stangl, A. s. G. Braunitzer
- Stark, H. s. Hj. Matthies
- Stark, H. s. K. Neubert
- Steckel, F. and K. von Figura, Arylsulfatase B: Purification from human placenta, preparation of an antiserum and biosynthesis in cultured human fibroblasts 890*
- Steckel, F., A. Waheed, A. Hasilik, K. von Figura, R. P. J. Oude Elferink, R. Kalsbeek and J. M. Tager, Decreased stability of α -D-glucosidase in the adult form of Pompe disease (glycogenosis II) 1040*
- Steffens, G. J., W. A. Günzler, F. Ötting, E. Frankus and L. Flohé, The complete amino acid sequence of low molecular mass urokinase from human urine 1043
- Steffens, G. J. s. L. Flohé
- Steffens, G. J. s. W. A. Günzler
- Steffens, K., E. Schneider and K. Altendorf, H⁺-ATPase of *Escherichia coli*: Amino acid residues involved in the binding of F₁ to F₀ 921*
- Steffens, K. s. E. Schneider
- Steger, G., H. Hofmann, J. W. Randles and D. Riesner, Structure of circular single-stranded RNA: Viroids, viroid-like RNA and RNA with random sequence 995*
- Stein, H. s. U. Schwab
- Stein, T., R. Keller, H. W. Stuhlsatz, H. Greiling, E. Ohst, E. Müller and H.-D. Scharf, Structure of the linkage-region between polysaccharide chain and core protein in bovine corneal proteokeratan sulfate 825
- Steitz, J. A. s. J. Rinke
- Stenberg, P. s. K. Ohlsson
- Sternbach, H., K. P. Hellmann and F. Cramer, ATP(CTP): tRNA Nucleotidyltransferase from yeast affinity labelling of the enzyme with modified substrates 890*
- Stieger, J. s. H. J. Schatzmann
- Stirm, S. s. M. Schlüter
- Stitt, M. s. A. Gardemann
- Stivanello, D. s. F. Marchiori
- Stockley, R. A., S. C. Afford and D. Burnett, The electrophoretic mobility of α_1 -proteinase inhibitor: Effect of proteolysis and cigarette smoke 387

- Stoffel, W., Structure and biosynthesis of human serum high density lipoprotein 950*
- Stoffel, W., H. Hillen, W. Schroeder and R. Deutzmann, Primary structure of the C-terminal cyanogen bromide fragments II, III and IV from brain proteolipid-apoprotein 855
- Stoffel, W., H. Hillen, W. Schroeder and R. Deutzmann, Lipophilin (proteolipid apoprotein) of brain white matter: Purification and amino acid sequence studies of the four tryptophan fragments 1397
- Stoffel, W. and P. Metz, Chemical studies on the structure of human serum high-density lipoprotein (HDL). Photochemical crosslinking of azido-labelled lipids in HDL 19
- Stoffel, W., K.-P. Salm and M. Müller, Syntheses of phosphatidylcholines, sphingomyelins and cholesterol substituted with azido fatty acids. Photocrosslinking with nearest neighbouring lipids in liposomes. Chemical and mass spectroscopic proof 1
- Stoffel, W., W. Schröder, H. Hillen and R. Deutzmann, Analysis of the primary structure of the strongly hydrophobic brain myelin proteolipid apoprotein (lipophilin). Isolation and amino acid sequence determination of proteolytic fragments 1117
- Storkebaum, W. und H. Witzel, Einfluß von zweiwertigen Metallionen auf die Aktivität und die pH-Abhängigkeit der Diisopropylfluorophosphatase 962*
- Strotmann, H. and S. Bickel-Sandkötter, Properties of the active site of chloroplast ATPase 470*
- Strydom, D. J. s. F. J. Joubert
- Stüber, W. s. B. Hemmasi
- Stuhlfauth, I. s. E.-M. Füchtbauer
- Stuhlsatz, H. W. s. T. Stein
- Subramanian, A. R. s. I. Kumagai
- Suckling, A. s. H. Reiber
- Südhof, Th. Chr., Osmometer behaviour of neurosecretory organelles: Biophysical concepts and implications 1317*
- Südhof, Th. Chr. and St. J. Morris, Biophysical aspects of lysis in chromaffin granules 1318*
- Südhof, Th. Chr., J. H. Walker and J. Obrocki, Spectroscopic studies on calelectrin 1319*
- Süssmuth, R. s. H. G. Beschle
- Sugino, A. s. J. Arendes
- Suko, J., B. Plank, P. Preis and N. Kolassa, Phosphorylation of sarcoplasmic reticulum Ca^{2+} -transport ATPase by orthophosphate 463*
- Summ, H.-D. s. R. Geiger
- Summer, K. H. s. J. Graw
- Sundan, A. and S. Olsnes, A hybrid toxin consisting of ricin A chain and diphtheria toxin fragment B 907*
- Suomalainen, K. s. T. Sorsa
- Sutter, A. s. A. Zimmermann
- Suttorp, M., R. Mentlein and E. Heymann, Hydrolysis of natural membrane destabilizing lipoids by liver carboxylesterases 962*
- Svendsen, I. s. K. Larsen
- Svenson, B. s. K. Larsen
- Szendro, P. I., N. Hekim, H. H. D. Meyer and P. W. Jungblut, False and true antibodies against the estradiol receptor 995*
- Szendro, P. I. s. W. D. Sierralta
- Szulmajster, J., Regulation of bacterial sporogenesis 124*
- Tager, H. S.** s. T. W. Schwartz
- Tager, J. M. s. F. Steckel
- Taguchi, K. s. M. Muramatu
- Taljaard, N. s. F. J. Joubert
- Tauber, R., C.-S. Park, W. Hofmann and W. Reutter, Successive degradation of the carbohydrate moieties in five integral glycoproteins isolated from rat liver plasma membrane 1022*
- Tauber, R. s. Ch. Bauer
- Terenius, L. s. F. Nyberg
- Tesche, B. s. K. R. Leonard
- Tesche, B. s. H. Schmiady
- Teuber, M. s. A. Geis
- Thiele, J. s. M. K. Otto
- Theilen, C. s. W. Wille
- Theisen, M. s. A. E. Sippel
- Thiemann, W. s. H. Büther
- Thierach, K.-H. s. F. Fahrenholz
- Thinnes, F. P. s. H. Kratzig
- Thinnes, F. P. s. C.-y. Yang
- Thissen, H. J. s. G. Harisch
- Thoenen, H. s. Y.-A. Barde
- Thoenen, H. s. G. P. Harper
- Thøgersen, H. C. s. K. Vibe-Pedersen
- Thomassen, M. S., T. Rørtveit, E. N. Christiansen and K. R. Norum, The effect of partially hydrogenated dietary oils on content of essential fatty acids and peroxisomal β -oxidation in rat liver 971*
- Thomsen, A., M. J. Müller and H. J. Seitz, Thyroid hormone regulation of rat liver phosphoenolpyruvate carboxykinase 996*
- Thorn, W., Catecholamines in the carotid body, adrenal medulla and heart muscle – hormones or transmitter? 1293*
- Thomsen, A. s. F. Klink
- Thuren, T., J. A. Virtanen and P. K. J. Kinnunen, Hydrolysis of 2-[4-(1-pyrenyl)butanoyl]-1-triacontanoyl-sn-glycero-3-phosphorylcholine by pancreatic phospholipase A_2 996*
- Tiedemann, H., Signals of cell determination in embryogenesis 132*
- Tiedemann, H. s. K. Asahi
- Tiedge, H. s. G. Schäfer
- Tietz, H. s. H. Paulsen
- Tittor, J., U. P. Hansen, D. Gradmann and H. J. Martensen, Non-steady state kinetic behavior of class I

- transport systems observed as "pump capacitance" in electrical impedance of biological membranes 908*
- Tittor, J. s. D. Gradmann
- Tosi, M. s. P.K. Wellauer
- Tlatlik, M. s. T. O. Kleine
- Trah, T.J. s. M. Schleyer
- Tran-Thi, T.-A. s. V. Gross
- Trapp, R. s. W. Heller
- Traub, O. s. K. Willecke
- Traub, P. and W.J. Nelson, Polyribosomes are not associated with vimentin-type intermediate filaments in Ehrlich ascites tumor cells 1177
- Trentham, D.R. and M.R. Webb, Details of the chemistry of ATP-hydrolysis by myosin and actomyosin 460*
- Trifonov, E.N. s. V. Brendel
- Tripier, D. s. G. Seipke
- Trissl, H.-W., U. Kunze and W. Junge, A picosecond-electrical signal from chloroplasts related to primary events of photosynthesis 548*
- Trommer, W., T.M. Fritzsche, J.O. McIntyre and S. Fleischer, Spin-label studies of 3-hydroxybutyrate dehydrogenase, a lipid-requiring enzyme 951*
- Truscheit, E., Microbial α -glucosidase inhibitors: Chemistry, biochemistry and medical applicability 947*
- Tschesche, H. and H.W. Macartney, Human leukocyte collagenase and regulation of activity 968*
- Tschesche, H. s. S. Engelbrecht
- Tschesche, H. s. H.R. Wenzel
- Tümmers, S. s. A. Hasilik
- Tukanits-Stolz, G., W. Schartau und D.G. Weiss, Verteilung endogener Aminosäuren und Amine im Riech- und Sehnerven des Hechtes 1319*
- Tulp, A., J.G. Collard, M.G. Barnhoorn and W.P. van Beek, Separation of cells and cell organelles at weak physical forces in low cost devices 997*
- Turk, V. s. T. Lah
- Twiffler, H. s. K. Cichutek
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- Ulmar, G. s. A. Gehrman
- Ulmer, W., M. Frösche, G. Pfeleiderer and K.-D. Jany, Chemical modification and sequence analysis of glucose dehydrogenase from *Bacillus megaterium* 1013*
- Umegane, T., T. Maita and G. Matsuda, Amino-acid sequence of the L-1 light chain of chicken fast skeletal-muscle myosin 1321
- Umezawa, H. s. M. Geisert
- Unger, B. and W. Hillen, Analysis of TET repressor tet operator interaction by thermal denaturation studies of the complexes 997*
- Uschtrin, D. and F. Klink, In vitro polyphenylalanine synthesis with purified ribosomes and two elongation factors from the archaebacterium *Thermoplasma acidophilum* 891*
- Uschtrin, D. s. H.E. Schlaak
- Väisänen, V. s. M. Jokinen
- Vainio, P., P.K.J. Kinnunen, F. Pattus and R. Verger, Mode of action of lipoprotein lipase on mixed monomolecular films of triacylglycerol/lecithin 951*
- Vainio, P. s. P.K.J. Kinnunen
- Valentini, K., R. Gebhardt and D. Mecke, Regulation of tyrosine aminotransferase activity in primary cultures of rat hepatocytes: Two modes of insulin action? 891*
- Valentini, G. s. M. Malcovati
- Vallejos, R. s. R. Wagner
- Vanden Berghe, D.A. and Huybrechts, New density gradient media and animal RNA-viruses 1001*
- Váradi, K. s. J. Kárpáti
- Varki, A. s. S. Kornfeld
- Vaysse, N. s. L. Moroder
- Veh, R.W. s. Chr. R. Schätz
- Verdenhalven, J., G. Bandini and F. Hucho, Evidence for a membrane bound proteinase in acetylcholine receptor-rich membranes from torpedo electric tissue 1320*
- Verdenhalven, J. and F. Hucho, Affinity iodination of membrane proteins by an α -bungarotoxin-lactoperoxidase conjugate 1283*
- Verger, R. s. P. Vainio
- Veselský, L., D. Čechová, V. Hruban and J. Klauďy, Seminal and colostrum protease inhibitors on leukocytes 113
- Vesterberg, O., Protein quantification with zone immunoelectrophoresis assay 1006*
- Vibe-Pedersen, K. s. T.E. Petersen
- Vicker, G.M., B. Donner, G. Cornelius and L. Rensing, Circadian control of cell cycle events in the dinoflagellate *Gonyaulax polyedra* 957*
- Vignais, P.V., G. Klein, M. Satre and A.-C. Dianoux, Structural and functional studies on the natural mitochondrial adenosinetriphosphate inhibitor 472*
- Villalobo, A. s. A. Goffeau
- Villalva, J. s. R. Brossmer
- Villringer, A., B. Kühn, W. Northemann, K. Schneider and P.C. Heinrich, Inhibition of cell-free protein synthesis by low-molecular mass RNAs from free cytoplasmic RNP particles 891*
- Virtanen, J.A. s. P.K.J. Kinnunen
- Virtanen, J.A. s. T. Thuren
- Vittozzi, L. s. W. Nastainczyk

- Vliegenthart, J. F. G. s. U. Nöhle
- Voigt, J. and C. E. Sekeris, Influence of the adrenal gland on uptake, retention, metabolism and binding to cytoplasmic proteins of [³H]cortisol by the rat liver 159
- Voigt, K.-V. s. M. Schleyer
- Volk, B. s. E. Köttgen
- Volk, B. s. W. Kreisel
- Volkandt, W. and R. Hardeland, Circadian rhythmicity of protein synthesis in *Gonyaulax polyedra* 958*
- Vosberg, H.-P. s. H. Schöler
- Vrese, de M. and C. A. Barth, Influence of lysine on urea synthesis in the isolated perfused liver 998*
- Vuorio, E. s. T. Kouri
- Wachter, E.**, Strategies for solid-phase Edman degradation 1009*
- Wachter, H. s. D. Fuchs
- Waehneltd, T. V. s. C. Linington
- Wagner, R., S. Bertram and U. Göringer, Altered accessibilities of guanosines in *E. coli* tRNA^{Phe} bound to the ribosomal A-site 892*
- Wagner, R., N. Carrillo, W. Junge and R. Vallejos, The terminal elements of the photosynthetic electron transport chain form a large complex which diffuses collectively in the thylakoid membrane 548*
- Wagner, R. and W. Junge, Heat-activated conformational changes of the isolated coupling factor of photophosphorylation 473
- Wagner, S. s. J. Graham
- Waheed, A., A. Hasilik, M. Cantz and K. von Figura, Phosphorylation of lysosomal enzymes in fibroblasts: Marked deficiency of *N*-acetylglucosamine-1-phosphattransferase in fibroblasts of patients with mucopolipidosis III 169
- Waheed, A., A. Hasilik and K. von Figura, Synthesis and processing of arylsulfatase A in human skin fibroblasts 425
- Waheed, A. s. F. Steckel
- Wahlström, A. s. F. Nyberg
- Walker, J. H. s. Th. Chr. Südhof
- Walldorf, U., B. Hovemann and E. K. F. Bautz, Characterization of a gene family with sex-specific regulation 936*
- Walter, R. D. and F. R. Opperdoes, Subcellular distribution of nucleoside-stimulated and suramin-sensitive protein kinases in *Trypanosoma brucei* 963*
- Wanke, E. s. E. Carbone
- Warnecke, H.-H. s. D. Berg
- Watters, D. s. A. Maelicke
- Watters, J., D. Kuschmitz and B. Hess, Coupling of the photocycle and proton current in bacteriorhodopsin: a regulated phenomenon 549*
- Watters, J. s. D. Kuschmitz
- Webb, M. R. s. D. R. Trentham
- Weber, F. s. W. Cohn
- Weber, J. s. G. Schäfer
- Weckler, C. s. J. Horst
- Wefers, H. s. H. Sies
- Wegener, G. s. R. Michel
- Weicker, H. s. M. Feraudi
- Weinblum, D. s. M. Geisert
- Weiss, D. G., Eigenschaften des schnellen axonalen Transportsystems 1288*
- Weiss, D. G. s. K. Buchner
- Weiss, D. G. s. H. Mägdefrau
- Weiss, D. G. s. M. Seiler
- Weiss, D. G. s. G. Tukanits-Stolz
- Weitzel, G. und A. Hadjianghelu, Einfluß von Guanidinverbindungen auf die Glucoseaufnahme in isolierten Fettzellen 45
- Welinder, K. G. s. T. E. Jessen
- Wellauer, P. K., U. Schibler, O. Hagenbüchle, R. A. Young and M. Tosi, Structure and tissue-specific expression of members of the mouse α -amylase multigene family 120*
- Wenzel, H. R., H. Tschesche and E. v. Goldammer, Spin-labelled amino acids, peptides and proteins – synthesis and application 1010*
- Wenzel, H. R. s. S. Engelbrecht
- Wenzel, M., G. Schachschneider, M. Schneider und R. Herken, Einfluß von Sexualhormonen auf die Pharmakaverteilung? Versuche mit Acetylruthenocin bei Ratten und Mäusen 693
- Werner, D., S. Chanpu, U. Plagens and M. Müller, Anchorage of DNA in 'nuclear matrix' 936*
- Wernet, P. s. C.-y. Yang
- Werries, E. s. A. Franz
- Wesemann, W. s. B. Flake
- Weser, U. s. A. Gärtner
- Weser, U. s. H.-J. Hartmann
- Weser, U. s. A. Ludány
- Westerbrink, K. and B. Havsteen, High-resolution two-dimensional electrophoresis of protein fractions from samples of normal human tissue and of tumors. Computer search for novel tumor markers 908*
- Westermann, P. and O. Nygård, Spatial arrangement of the complex between eukaryotic initiation factor eIF-3 and 40S ribosomal subunits. Cross-linking between factor and ribosomal proteins 892*
- Westermann, P. s. O. Nygård
- Weydert, A. s. M. E. Buckingham
- Wieczorek, L., A. Siebers and K. Altendorf, Potassium transport in *Escherichia coli*: Biochemical and genetical characterization of the K^o transport ATPase 466*
- Wiegand, M. s. G. U. Wollmann
- Wiegandt, H. s. K. Radsak
- Wieker, H.-J., Pyruvate kinase – an example for the complexity of regulatory enzymes 536*

- Wieber, H.-J., Fluorescent and binding studies with yeast pyruvate kinase 549*
- Wieland, O.H. s. R. Dolhofer
- Wieland, Th. s. O.G. Brodner
- Wiesmüller, K. s. W.G. Bessler
- Wiesner, H. s. W. Oberthür
- Wiestner, M. and P.K. Müller, Bovine granulos cells synthesize collagens in vitro 998*
- Wikman, F., G.E. Siboska, H.U. Petersen and B.F.C. Clark, Protection of elongator tRNAs against specific ribonuclease digestions 893*
- Wikström, M., Proton translation by cytochrome oxidase 921*
- Wildmann, J. und H. Matthaehi, Struktur analogien zwischen trizyklischen Psychopharmaka und endogenen opioiden Peptiden 1292*
- Wilken, M., O.J. Bjerrum, C. Geisler and T. Plesner, Chronic lymphocytic leukemia lymphocyte antigens 1013*
- Wilken, M., O.J. Bjerrum, C. Geisler and T. Plesner, Microheterogeneity of lymphocyte associated monoclonal immunoglobulin 1014*
- Wilkens, A. s. W. Schill
- Wille, W., H. Schaal, U.A.O. Heinlein und C. Theilen, Biochemisches Parameter der Cerebellum-Entwicklung von normalen und Mutanten-Mäusen in vivo, in vitro und in oculo 1291*
- Willecke, K. and O. Traub, Expression of gap junction protein in different mouse tissues 126*
- Williams, K., Morphogenetic molecules in the multicellular stage of *Dictyostelium discoideum* 130*
- Willmitzer, L. s. J. Schell
- Wilson, F.A. s. W. Kramer
- Wintersberger, U., The yeast mating type system – a model for the regulation of gene expression by the position of a certain gene within the genome? 119*
- Winyard, P. s. K.-E. Falk
- Wissler, J.H., Mediators of inflammation: Chemical signals for differentiation and morphogenesis in tissue regeneration and wound healing 131*
- Wissler, J.H., A novel endogenous mechanism of atherogenesis: The "intravasally leaky tip" as cellular reaction operated by leukocyte-derived mediators of inflammation (angiotropins) 941*
- Wissler, J.H. s. M. Gottwik
- Wissler, J.H. s. E. Logemann
- Wissler, J.H. s. R. Neumeier
- Wissler, J.H. s. A. Plessing
- Witter, B. s. H.K. Illig
- Wittmann, H.G., Bacterial ribosomes 893*
- Wittmann, H.G. s. K.R. Leonard
- Wittmann-Liebold, B., Advanced automatic microsequencing of polypeptides 1007*
- Witzel, H. s. K. Cichutek
- Witzel, H. s. W. Storkebaum
- Witzemann, V. and C. Boustead, The catalytic subunits of the acetylcholinesterase forms from the electric organ of *Torpedo marmorata* shows structural differences 1320*
- Woenckhaus, C., R. Koob und H.-G. Schäfer, Kovalent Fixierung von NAD an Lactat- und Alkohol-Dehydrogenase durch Diazoniumgruppentragende Coenzymverbindungen 947*
- Wörner, E. s. W. Grothaus
- Wohlert, H. s. H. Kröger
- Wolbert-Rack, S., H. Graf and V. Ullrich, Isolation of crosslinked pig liver microsomal monooxygenases by affinity chromatography 976*
- Wolf, D.H. s. T. Achstetter
- Wolf, D.H. s. B. Mechler
- Wollmann, G.U., A.-R. Hernanto, W. Heller, V. Hempel, M. Wiegand and R. Schorer, Fractionation of fresh and fresh frozen plasma proteins by gel chromatography and their immunological detection by laser nephelometry 1014*
- Wollmer, A., CD Spectroscopy and protein conformation 1010*
- Wright, P.G. s. G. Mazur
- Wünsch, E., L. Moroder, D. Gillessen, U.B. Soerensen and J.P. Bali, Biological and immunological properties of human gastrin I analogues 665
- Wünsch, E., L. Moroder, R. Nyfeler and E. Jaeger, (Alkyldithio)carbonyl groups for protection of amino functions in peptide synthesis 197
- Wünsch, E., L. Moroder and S. Romani, 1-(*tert*-Butylthio)-1,2-hydrazinedicarboxylic acid derivatives: New reagents for the introduction of the *S-tert*-butylthio group into cysteine and cysteine derivatives 1461
- Wünsch, E. and S. Romani, A new method for the selective synthesis of unsymmetrical cystine peptides 449
- Wünsch, E. s. L. Moroder
- Würdinger, I. s. W. Oberthür
- Wunderwald, P., W.J. Schrenk and H. Port, Removal of endoproteinasen from biological fluids by sandwich affinity chromatography with α_2 macroglobulin bound to Zn-chelate sepharose 948*
- Wurster, B. and U. Butz, A study on sensing and adaptation in *Dictyostelium discoideum* 550*
- Yanagimoto, Y.** s. M. Muramatu
- C.-y. Yang, H. Kratzin, H. Götz, F.P. Thinnies, T. Kruse, G. Egert, E. Pauly, S. Kölbl, P. Wernet und N. Hilschmann, Primärstruktur menschlicher Histokompatibilitätsantigene der Klasse II. 2. Mitteilung: Aminosäuresequenz der N-terminalen 179 Reste der α -Kette des HLA-Dw2/DR2-Alloantigens 671
- Yang, C.-y. s. H. Kratzin
- Yonath, A.E. s. K.R. Leonard
- Young, R.A. s. P.K. Wellauer

- Zaccà, G. s. M. Satre
Zahn, H. s. M. Casaretto
Zahn, H. s. R. Knorr
Zahn, R.K. s. A. Bernd
Zahn, R.K. s. M. Geisert
Železná, B. and D. Čechová, Boar acrosin. Isolation of two active forms from boar ejaculated sperm 757
Zerlauth, G. s. B. Gmeiner
Zetl, I. s. J. Sonnenbichler
Zglinicki, Th. v. s. R. Lindigkeit
Zheng, H. s. H. Eckstein
Ziegler, C. and G. Mersmann, Studies on the sulfate content of the carbohydrate-protein binding region in keratan sulfate from bovine cornea 1040*
Ziegler, D., G. Keilich and R. Brossmer, Relationship between substrate structure and sialidase action 1041*
Ziegler, D. s. G. Keilich
Ziensen, B., U. Pfeiffer, D.P. Agarwal, L.M. Srivastava and H.W. Goedde, Effect of lithium, imipramine and chlorpromazine on the enzyme phosphatidylethanolamine methyltransferase 998*
Zierold, K., D. Schäfer and D.W. Lübbers, Intracellular localization of diffusible ions in ultrathin cryosections 550*
Zimmer, G., H.J. Lubberding and R. Kraayenhof, Isolation and characterization of the ATPase complex (F_1-F_0) from the *Thermophilic cyanobacterium Synechococcus lividus* 922*
Zimmer, G. s. B.M. Heil
Zimmermann, A. und A. Sutter, Der NGF-Rezeptor und Zell-Zell-Interaktion in sensorischen Ganglien des Hühnchens 1287*
Zimmermann, R. s. B. Schmidt
Zimpfer, A. s. H.J. Risse
Zipfel, P.F., J. Dittmer, V. Kasche and H. Amnéus, DNA turnover in cultured animal cells? 937*
Zöllner R. s. V. Kasche
Zuckerman, S. s. N.R. Ringertz
Zühlsdorf, M. s. A. Hasilik
Zwick, J. s. L. Béress

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