



Vol. 256 No. 5517

August 7, 1975



Macmillan Journals Ltd 1975 Published weekly ISSN 0028-0836 Registered as a newspaper at the British Post Office

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4 Little Essex Street, WC2R 3LF
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Subscription enquiries to: Macmillan Journals Ltd, Brunel Road, Basingstoke, Hants, RG21 2XS Telephone: Basingstoke 29242

	Pi	rice	
	UK		£35
Surface mail	Australia Europe Japan USA		A\$58 £35 Y24,500 US\$95
Airmail (Europe Rest of world	Full Personal	£40 US\$118 US\$103

US Postmaster, please send form 3579 to Nature, 711 National Press Building, Washington DC 20045

Application to mail at second-class postage rate is pending at New York, NY.
US mailing agent is:

Air and Sea Freight Inc., 527 Madison Avenue, New York, NY 10022

Cover picture

Desert locusts settle for the night. See pages 484, 486. Photo: Jean Manuel, FAO Rome.



REVIEW ARTICLE The origin of nuclei and of eukaryotic cells—T. Cavalier-Smith 4. ARTICLES Palaeolithic remains at the Hadar in the Afar region—G. Corvinus Integration of viral genomes—V. M. Zhdanov 4. LETTERS TO NATURE Definition of 'charge on an atom' and nature of the inductive effect— S. M. Dean and W. G. Richards 4. A low velocity zone underlying a fast-spreading rise crest—J. Orcutt, B. Kennett, L. Dorman and W. Prothero Mercury contamination in a 54-m core from lake Huleh—U. M. Cowgill A resonant point absorber of ocean-wave power—K. Budar and J. Falnes Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston Tree remains in southern Pennine peats—J. H. Tallis Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green Development of a desert locust plague—L. V. Bennett Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity—specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Püppel, D. von Cramon and H. Backmund Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma Thymus rudinent of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Kühler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of cat		
REVIEW ARTICLE The origin of nuclei and of eukaryotic cells—T. Cavalier-Smith ARTICLES Palaeolithic remains at the Hadar in the Afar region—G. Corvinus Integration of viral genomes—V. M. Zhdanov LETTERS TO NATURE Definition of 'charge on an atom' and nature of the inductive effect— S. M. Dean and W. G. Richards 4 Alow velocity zone underlying a fast-spreading rise crest—J. Oreutt, B. Kennett, L. Dorman and W. Prothero 4 Aresonant point absorber of ocean-wave power—K. Budar and J. Falnes Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston Tree remains in southern Pennine peats—J. H. Tallis Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green Development of a desert locust plague—L. V. Bennett Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Püppel, D. von Cramon and H. Backmund Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of abult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos finduced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider SRNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D, E. Schumm and T. E. Webb Searly role during chemical evolution for cytochrome P450 in oxygen	Whitlam, Connor and Cameron	447
REVIEW ARTICLE The origin of nuclei and of eukaryotic cells—T. Cavalier-Smith 4. ARTICLES Palaeolithic remains at the Hadar in the Afar region—G. Corvinus ARTICLES Palaeolithic remains at the Hadar in the Afar region—G. Corvinus ARTICLES Definition of viral genomes—V. M. Zhdanov 4. LETTERS TO NATURE Definition of charge on an atom' and nature of the inductive effect—S. M. Dean and W. G. Richards 4. Iow velocity zone underlying a fast-spreading rise crest—J. Orcutt, B. Kennett, L. Dorman and W. Prothero 4. Mercury contamination in a 54-m core from lake Huleh—U. M. Cowgill 4. A resonant point absorber of ocean-wave power—K. Budar and J. Falnes 4. Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook 4. Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 4. Tree remains in southern Pennine peats—J. H. Tallis 4. Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green 4. Development of a desert locust plague—L. V. Bennett 5. Seed-borne microorganisms stimulate seed-corn maggot egg laying— C. J. Eckenode, G. E. Harman and D. R. Webb 5. Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk 6. Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk 6. Eccentricity-specific dissociation of visual functions in patients with lesions of the 6. central visual pathways—E. Pippel, D. von Cramon and H. Backmund 6. Evidence for visual function mediated by anomalous projection in goldfish— 6. D. Yager and S. C. Sharma 7. H. Tlaskalova and H. Vidmarova 7. H. Tlaskalova and H. Vidmarova 8. Videna muscle fibres differentiate in monolayer cultures of adult thymus reticulum— 7. H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman 8. Anturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin 8. Naturally occurring cytotoxic tumour fractive antibodies directed against type C viral envelope antigents—S. E.	INTERNATIONAL NEWS	448
ARTICLES Palaeolithic remains at the Hadar in the Afar region—G. Corvinus Integration of viral genomes—V. M. Zhdanov 4 LETTERS TO NATURE Definition of 'charge on an atom' and nature of the inductive effect—S. M. Dean and W. G. Richards 4 Iow velocity zone underlying a fast-spreading rise crest—J. Orcutt, B. Kennett, L. Dorman and W. Prothero 4 Mercury contamination in a 54-m core from lake Huleh—U. M. Cowgill 4 A resonant point absorber of ocean-wave power—K. Budar and J. Falnes 5 C. M. Malmberg and J. M. Colebrook 4 Anericium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 5 Tree remains in southern Pennine peats—J. H. Tallis 6 Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green 6 Development of a desert locust plague—L. V. Bennett 7 Seed-borne microorganisms stimulate seedcorn maggot egg laying— 6 C. J. Eckenrode, G. E. Harman and D. R. Webb 6 Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk 6 Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pôppel, D. von Cramon and H. Backmund 7 Evidence for visual function mediated by anomalous projection in goldfish— 7 Yager and S. C. Sharma 7 H. Tlaskalova and H. Vidmarova 7 Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— 7 H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman 8 Veridence for visual function mediated by anomalous projection in goldfish— 8 Paterson, UP. Ketelsen and M. Feldman 8 Continuous cultures of fused cells secreting antibody of predefined specificity— 8 G. Köhler and C. Milstein 8 Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin 8 Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin 9 Naturally occurring cytotoxic tumour fractive antibodies directed against type C viral envelope antigents—S. E. Martin	NEWS AND VIEWS	455
ARTICLES Palaeolithic remains at the Hadar in the Afar region—G. Corvinus Integration of viral genomes—V. M. Zhdanov 4 LETTERS TO NATURE Definition of 'charge on an atom' and nature of the inductive effect— S. M. Dean and W. G. Richards 4 low velocity zone underlying a fast-spreading rise crest—J. Orcutt, B. Kennett, L. Dorman and W. Prothero 4 Mercury contamination in a 54-m core from lake Huleh—U. M. Covgill 4 A resonant point absorber of ocean-wave power—K. Budar and J. Falnes 4 A resonant point absorber of ocean-wave power—K. Budar and J. Falnes 4 A resonant point absorber of ocean-wave power—K. Budar and J. Falnes 4 A resonant point absorber of ocean-wave power—K. Budar and J. Falnes 4 A malmberg and J. M. Colebrook 4 Annericium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 4 Tree remains in southern Pennine peats—J. H. Tallis 5 Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green 5 Development of a desert locust plague—L. V. Bennett 5 Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb 6 Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk 6 Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pippel, D. von Cramon and H. Backmund 6 Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma 7 Hymus rudinent of the athymic nude mouse—M. Holub, P. Rossmann, 7 H. Tlaskalova and H. Vidmarova 8 Briated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— 7 H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman 8 Continuous cultures of fused class scretting antibody of predefined specificity— 9 G. Köhler and C. Milstein 1 Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 1 Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 1 Antigen formation in metal contact sensitivity—J. M. Jones an	REVIEW ARTICLE	
Palaeolithic remains at the Hadar in the Afar region—G. Corvinus 4. Integration of viral genomes—V. M. Zhdanov 4. LETTERS TO NATURE Definition of 'charge on an atom' and nature of the inductive effect— S. M. Dean and W. G. Richards 4. A low velocity zone underlying a fast-spreading rise crest—J. Orcutt, B. Kemett, L. Dorman and W. Prothero 4. Mercury contamination in a 54-m core from lake Huleh—U. M. Cowgill 4. A resonant point absorber of ocean-wave power—K. Budar and J. Falnes 4. Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, S4. Malmberg and J. M. Colebrook 4. Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 4. Tree remains in southern Pennine peats—J. H. Tallis 6. Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green 7. Development of a desert locust plague—L. V. Bennett 8. Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb 8. Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk 8. Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund 4. Evidence for visual function mediated by anomalous projection in goldfish— 8. Vager and S. C. Sharma 7. H. Tlaskalova and H. Vidmarava 8. Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— 8. H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman 8. Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— 8. H. Wickernas in metal contact sensitivity—J. M. Jones and H. E. Amos 8. Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schmeider 8. Rate of nucleologenesis as a measure of gene activity—C. de la Torre, 8. M. E. Fernandez-Gomez and G. Gimenez-Martin 9. St. RNA secondary structure—G. E. Fox and C. R. Woese 9. Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restricti	The origin of nuclei and of eukaryotic cells—T. Cavalier-Smith	463
LETTERS TO NATURE Definition of 'charge on an atom' and nature of the inductive effect— S. M. Dean and W. G. Richards A low velocity zone underlying a fast-spreading rise crest—J. Orcutt, B. Kennett, L. Dorman and W. Prothero Mercury contamination in a 54-m core from lake Huleh—U. M. Cowgill 4 resonant point absorber of ocean-wave power—K. Budar and J. Falnes Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston Tree remains in southern Pennine peats—J. H. Tallis Regularities in duration of regional desert locust plague—Z. Waloff and S. M. Green Development of a desert locust plague—L. V. Bennett Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity-specific dissociation of visual functions in patients with esions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma 4. Thaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos finduced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Sarto funcleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimnez-Martin SS RNA secondary structure—G. E. Fox and C.	ARTICLES	
Definition of 'charge on an atom' and nature of the inductive effect— S. M. Dean and W. G. Richards 4 Now velocity zone underlying a fast-spreading rise crest—J. Oreutt, B. Kennett, L. Dorman and W. Prothero 4 Mercury contamination in a 54-m core from lake Huleh—U. M. Cowgill 4 A resonant point absorber of ocean-wave power—K. Budar and J. Falnes 5 Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook 4 Anericium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 5 Tree remains in southern Pennine peats—J. H. Tallis 6 Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green 6 Development of a desert locust plague—L. V. Bennett 7 Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb 7 Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk 7 Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund 7 Evidence for visual function mediated by anomalous projection in goldish— D. Yager and S. C. Sharma 7 H. Tlaskalova and H. Vidmarova 8 Ustriated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman 7 Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein 8 Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin 8 Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 8 Andigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 9 And C. Kersteeg, J. van der Gugten and J. M. van Ree 9 And C. R. Westeeg, J. van der Gugten and J. M. van Ree 9 Start of nucleologenesis as a measure of gene activity—C. de la Torre, 9 M. E. Fernandez-Gomez and G. Gimnerez-Martin 9 Start of plasma fractions from normal and tumour-bearing rats	Palaeolithic remains at the Hadar in the Afar region—G. Corvinus	468
Definition of 'charge on an atom' and nature of the inductive effect— S. M. Dean and W. G. Richards 4 Now velocity zone underlying a fast-spreading rise crest—J. Orcutt, B. Kennett, L. Dorman and W. Prothero 4 Mercury contamination in a 54-m core from lake Huleh—U. M. Cowgill 4 A resonant point absorber of ocean-wave power—K. Budar and J. Falnes 4 Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook 4 Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 4 Tree remains in southern Pennine peats—J. H. Tallis Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green Development of a desert locust plague—L. V. Bennett Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund 4 Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma 4 Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidnarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Annos Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Seate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin SS RNA	Integration of viral genomes—V. M. Zhdanov	47
S. M. Dean and W. G. Richards A low velocity zone underlying a fast-spreading rise crest—J. Orcutt, B. Kennert, L. Dorman and W. Prothero Mercury contamination in a 54-m core from lake Huleh—U. M. Cowgill 4 resonant point absorber of ocean-wave power—K. Budar and J. Falnes 4 Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook 4 Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 4 Tree remains in southern Pennine peats—J. H. Tallis 8 Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green 4 Development of a desert locust plague—L. V. Bennett 8 Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb 5 Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk 6 Eccentricity-specific dissociation of visual functions in patients with lesions of the 6 central visual pathways—E. Pöppel, D. von Cramon and H. Backmund 6 Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma 6 Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova 8 Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman 6 Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein 8 Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral 8 envelope antigents—S. E. Martin and W. J. Martin 8 Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 8 Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 9 Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 9 Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 9 Antigent formation in metal contact sensitivity—J. M. Jones and H. E. Amos 9 Antigent formation in metal contact sensitivity—J. M. Jones and H. E	LETTERS TO NATURE	
B. Kennett, L. Dorman and W. Prothero Mercury contamination in a 54-m core from lake Huleh—U. M. Cowgill 4 A resonant point absorber of ocean-wave power—K. Budar and J. Falnes Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook 4 Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 4 Tree remains in southern Pennine peats—J. H. Tallis 4 Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green Development of a desert locust plague—L. V. Bennett Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum—H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Anduced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernander-Gomez and G. Gimenez-Martin SS RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D, E. Sch	Definition of 'charge on an atom' and nature of the inductive effect— S. M. Dean und W. G. Richards	47:
A resonant point absorber of ocean-wave power—K. Budar and J. Falnes 4. Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook 4. Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 4. Tree remains in southern Pennine peats—J. H. Tallis 4. Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green 4. Development of a desert locust plague—L. V. Bennett 5. Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb 6. Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk 6. Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund 6. Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma 7. Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova 8. Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman 4. Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein 4. Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin 7. Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 7. Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 7. Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 8. Rate of nucleologenesis as a measure of gene activity—C. de la Torre, 8. E. Fernandez-Gomez and G. Gimenez-Martin 5. S. RNA secondary structure—G. E. Fox and C. R. Woese 7. Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb 6. Early role during chemical evolution for cytochrome P450 in oxygen detoxification—R. H	A low velocity zone underlying a fast-spreading rise crest—J. Orcutt, B. Kennett, L. Dorman and W. Prothero	475
Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 4 Tree remains in southern Pennine peats—J. H. Tallis Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green Development of a desert locust plague—L. V. Beunett Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund 4 Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma 1 Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova 4 Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman 4 Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin SS RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D, E. Schumm and T. E. Webb SERIED ST. R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness)	Mercury contamination in a 54-m core from lake Huleh-U. M. Cowgill	470
SA. Malmberg and J. M. Colebrook Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston 4 Tree remains in southern Pennine peats—J. H. Tallis 4 Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green 4 Development of a desert locust plague—L. V. Bennett 5 Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb 5 Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk 6 Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund 6 Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma 6 Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova 6 Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman 6 Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein 7 Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin 8 Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 7 Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree 8 Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin 8 S RNA secondary structure—G. E. Fox and C. R. Woese 9 Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb 5 Early role during chemical evolution for cytochrome P450 in oxygen detoxification—R. H. Wickramasinghe and C. A. Villee 1 Human embryonic haemoglobins including a comparison by homology of the human \(\zeta \) and a chains—H. Kamuzora and H. Lehmann 5 Intracellular killing of Lis	A resonant point absorber of ocean-wave power-K. Budar and J. Falnes	478
Tree remains in southern Pennine peats—J. H. Tallis Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green Development of a desert locust plague—L. V. Bennett Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin SS RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb Searly role during chemical evolution for cytochrome P450 in oxygen detoxification— R. H. Wickremasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human ζ and α chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intr	Climatic reversal in northern North Atlantic—R. R. Dickson, H. H. Lamb, SA. Malmberg and J. M. Colebrook	47
Regularities in duration of regional desert locust plagues—Z. Waloff and S. M. Green Development of a desert locust plague—L. V. Bennett Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrede, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin SS RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D, E. Schumm and T. E. Webb Salty role during chemical evolution for cytochrome P450 in oxygen detoxification— R. H. Wickramasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human \(\frac{1}{2} \) and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness)	Americium 242m in nuclear test debris—V. T. Bowen and H. D. Livingston	48
Development of a desert locust plague—L. V. Bennett Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund 4. Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma 1. Tlaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin SR RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D, E. Schumm and T. E. Webb Salving chemical evolution for cytochrome P450 in oxygen detoxification— R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human \(\frac{1}{2} \) and a chains—H. Kanuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Tree remains in southern Pennine peats—J. H. Tallis	48
Development of a desert locust plague—L. V. Bennett Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund 4. Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma 1. Tlaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin SR RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D, E. Schumm and T. E. Webb Salving chemical evolution for cytochrome P450 in oxygen detoxification— R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human \(\frac{1}{2} \) and a chains—H. Kanuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness		48
C. J. Eckenrode, G. E. Harman and D. R. Webb Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund Evidence for visual function mediated by anomalous projection in goldfish—D. Yager and S. C. Sharma Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum—H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity—G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 4 Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus—D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin SS RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D, E. Schumm and T. E. Webb Early role during chemical evolution for cytochrome P450 in oxygen detoxification—R. H. Wickramasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human \(\zeta \) and a chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Lisa and G. Calabrese (Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Development of a desert locust plague—L. V. Bennett	48
Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund 4 Evidence for visual function mediated by anomalous projection in goldfish—D. Yager and S. C. Sharma 4 Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova 4 Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum—H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman 4 Continuous cultures of fused cells secreting antibody of predefined specificity—G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin 4 Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 4 Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider 5 Regional turnover and synthesis of catecholamines in rat hypothalamus—D. H. G. Versteeg, J. van der Gugten and J. M. van Ree 8 Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernander-Gomez and G. Gimenez-Martin 5 S RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webh 5 Early role during chemical evolution for cytochrome P450 in oxygen detoxification—R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human \(\zeta \) and a chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese (Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Seed-borne microorganisms stimulate seedcorn maggot egg laying— C. J. Eckenrode, G. E. Harman and D. R. Webb	48
Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma 4 Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova 4 Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos finduced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin SS RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webh Sarly role during chemical evolution for cytochrome P450 in oxygen detoxification— R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human ζ and α chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese (Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness)	Defensive stoning by baboons—W. J. Hamilton III, R. E. Buskirk and W. H. Buskirk	48
D. Yager and S. C. Sharma Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin SS RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D, E. Schumm and T. E. Webh Searly role during chemical evolution for cytochrome P450 in oxygen detoxification—R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human ζ and α chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Eccentricity-specific dissociation of visual functions in patients with lesions of the central visual pathways—E. Pöppel, D. von Cramon and H. Backmund	489
H. Tlaskalova and H. Vidmarova Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree SRate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin SS RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webh Searly role during chemical evolution for cytochrome P450 in oxygen detoxification—R. H. Wickramasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human \(\zeta and a chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Evidence for visual function mediated by anomalous projection in goldfish— D. Yager and S. C. Sharma	490
Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin 4. Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin Stan Stan Secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb Starty role during chemical evolution for cytochrome P450 in oxygen detoxification— R. H. Wickramasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human \(\zeta\) and a chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Thymus rudiment of the athymic nude mouse—M. Holub, P. Rossmann, H. Tlaskalova and H. Vidmarova	49
G. Köhler and C. Milstein Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 4 Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider 5 Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree 5 Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin 5 SRNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb 5 Early role during chemical evolution for cytochrome P450 in oxygen detoxification—R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human ζ and α chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese (Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Striated muscle fibres differentiate in monolayer cultures of adult thymus reticulum— H. Wekerle, B. Paterson, UP. Ketelsen and M. Feldman	49
envelope antigents—S. E. Martin and W. J. Martin Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos 4 Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider 5 Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree 5 Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin 5 SR RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb Early role during chemical evolution for cytochrome P450 in oxygen detoxification— R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human \(\zeta and \(\alpha\) chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Continuous cultures of fused cells secreting antibody of predefined specificity— G. Köhler and C. Milstein	49
Induced thermal resistance in HeLa cells—E. W. Gerner and M. J. Schneider Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. R. Woese State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Schumm and T. E. Webs State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Schumm and T. E. Woese State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Calabrese State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Schumm and T. E. Woese State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. R. Woese State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. R. Woese State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. R. Woese State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. R. Woese State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. R. Woese State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. R. Woese State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. R. Woese State of nucleologe	Naturally occurring cytotoxic tumour reactive antibodies directed against type C viral envelope antigents—S. E. Martin and W. J. Martin	49
Regional turnover and synthesis of catecholamines in rat hypothalamus— D. H. G. Versteeg, J. van der Gugten and J. M. van Ree Strate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin Strate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin Strate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin Strate of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb Starly role during chemical evolution for cytochrome P450 in oxygen detoxification— R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human \(\xi \) and \(\alpha \) chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness)	Antigen formation in metal contact sensitivity—J. M. Jones and H. E. Amos	49
D. H. G. Versteeg, J. van der Gugten and J. M. van Ree State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin State of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin State of Nuclear RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb Early role during chemical evolution for cytochrome P450 in oxygen detoxification—R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human \(\xi \) and \(\alpha \) chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness)	Induced thermal resistance in HeLa cells-E. W. Gerner and M. J. Schneider	50
M. E. Fernandez-Gomez and G. Gimenez-Martin SS RNA secondary structure—G. E. Fox and C. R. Woese Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb Early role during chemical evolution for cytochrome P450 in oxygen detoxification—R. H. Wickramasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human ζ and α chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness		50
Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb Early role during chemical evolution for cytochrome P450 in oxygen detoxification—R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human ζ and α chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Rate of nucleologenesis as a measure of gene activity—C. de la Torre, M. E. Fernandez-Gomez and G. Gimenez-Martin	50
nuclear RNA restriction—D, E. Schumm and T. E. Webb Early role during chemical evolution for cytochrome P450 in oxygen detoxification— R. H. Wickromasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human ζ and α chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	5S RNA secondary structure—G. E. Fox and C. R. Woese	50
R. H. Wickramasinghe and C. A. Villee Human embryonic haemoglobins including a comparison by homology of the human ζ and α chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Differential effect of plasma fractions from normal and tumour-bearing rats on nuclear RNA restriction—D. E. Schumm and T. E. Webb	50
human ζ and α chains—H. Kamuzora and H. Lehmann Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese (Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness		50
R. A. Liso and G. Calabrese (Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	Human embryonic haemoglobins including a comparison by homology of the human ζ and α chains—H. Kamuzora and H. Lehmann	51
	Lycorine as an inhibitor of ascorbic acid biosynthesis—O. Arrigoni, R. A. Liso and G. Calabrese	51
	Intracellular killing of Listeria monocytogenes by activated macrophages (Mackaness	¢1

Continuous cultures of fused cells secreting antibody of predefined specificity

The rearranteer of predefined specific antibodies by means of termanent tissue culture cell lines is of general interest. There are at present a considerable number of permanent cultures of feloma cells^{1,2} and screening procedures have been used to reveal antibody activity in some of them. This, however, is not a satisfactory source of monoclonal antibodies of predefined specificity. We describe here the derivation of a number of tissue culture cell lines which secrete anti-sheep red blood cell (SRBC) antibodies. The cell lines are made by fusion of a mouse myeloma and mouse spleen cells from an immunised donor. To understand the expression and interactions of the lg chains from the parental lines, fusion experiments between two known mouse myeloma lines were carried out.

Each immunoglobulin chain results from the integrated expression of one of several V and C genes coding respectively for its variable and constant sections. Each cell expresses only one of the two possible alleles (allelic exclusion; reviewed in ref. 3). When two antibody-producing cells are fused, the products of both parental lines are expressed 1.5, and although the light and heavy chains of both parental lines are randomly joined, no evidence of scrambling of V and C sections is observed 1. These results, obtained in an heterologous system involving cells of rat and mouse origin, have now been confirmed by fusing two myeloma cells of the same mouse strain,

The protein secreted (MOPC 21) is an IgG1 (x) which has been fully sequenced7,4. Equal numbers of cells from each parental line were fused using inactivated Sendai virus and samples contining 2×105 cells were grown in selective medium in separate dishes. Four out of ten dishes showed growth in selective medium and these were taken as independent hybrid lines, probably derived from single fusion events. The karyotype of the hybrid cells after 5 months in culture was just under the sum of the two parental lines (Table 1). Figure 1 shows the isoelectric focusing10 (IEF) pattern of the secreted products of different lines. The hybrid cells (samples c-h in Fig. 1) give a much more complex pattern than either parent (a and b) or a mixture of the parental lines (m). The important feature of the new pattern is the presence of extra bands (Fig. 1, arrows). These new bands, however, do not seem to be the result of differences in primary structure; this is indicated by the IEF pattern of the products after reduction to separate the heavy and light chains (Fig. 1B). The IEF pattern of chains of the hybrid clones (Fig. 1B, g) is equivalent to the sum of the IEF pattern (a and b) of chains of the parental clones with no evidence of extra products. We conclude that, as previously shown with interspecies hybrids4,5, new Ig molecules are produced as a result of mixed association between heavy and light chains from the two parents. This process is intracellular as a mixed cell population does not give rise to such hybrid molecules (compare m and g, Fig. 1A). The individual cells must therefore be able to express both isotypes. This result shows that in hybrid cells the expression of one isotype and idiotype does not exclude the expression of another: both heavy chain

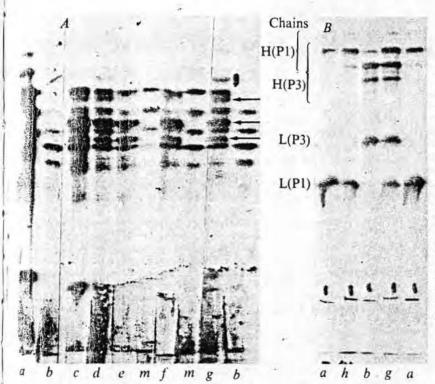


Fig. 1 Autoradiograph of labelled components secreted by the parental and hybrid cell lines analysed by IEF before (A) and after reduction (B). Cells were incubated in the presence of "C-lysine" and the supernatant applied on polyacrylamide slabs. A, pH range 6.0 (bottom) to 8.0 (top) in 4 M urea. B, pH range 5.0 (bottom) to 9.0 (top) in 6 M urea; the supernatant was incubated for 20 min at 37 °C in the presence of 8 M urea, 1.5 M mercaptoethanol and 0.1 M potassium phosphate pH 8.0 before being applied to the right slab. Supernatants from parental cell lines in: a, P1Bu1; b, P3-X67Ag8; and m, mixture of equal number of P1Bul and P3-X67Ag8 cells. Supernatants from two independently derived hybrid lines are shown: e-f, four subclones from Hy-3; g and h, two subclones from Hy-B. Fusion was carried out " using 106 cells of each parental line and 4,000 haemagglutination units inactivated Sendai virus (Searle). Cells were divided into ten equal samples and grown separately in selective medium (HAT medium, ref. 6). Medium was changed every 3 d. Successful hybrid lines were obtained in four of the cultures, and all gave similar IEF patterns. Hy-B and Hy-3 were further cloned in soft agar14. L, Light; H, heavy.

d provide the background for the derivation and underseanding of antibody-secreting hybrid lines in which one of the parental cells is an antibody-producing spleen cell.

Fivo myeloma cell lines of BALB/c origin were used. PIBul resistant to 5-bromo-2'-deoxyuridine¹, does not grow in selective medium (HAT, ref. 6) and secretes a myeloma protein, Adj PC5, which is an IgG2A (k), (ref. 1). Synthesis is not balanced and free light chains are also secreted. The second cell line, P3-X63Ag8, prepared from P3 cells², is resistant to

sotypes (γ l and γ 2a) and both V_H and both V_L regions (idiotypes) are expressed. There are no allotypic markers for the C_K region to provide direct proof for the expression of both parental C_K regions. But this is indicated by the phenotypic link between the V and C regions.

Figure 1A shows that clones derived from different hybridisation experiments and from subclones of one line are indistinguishable. This has also been observed in other experiments (data not shown). Variants were, however, found in a survey of



Fig. 2 Isolation of an anti-SRBC antibody, secreting cell clone. Activity was revealed by a halo of haemolysed SRBC. Direct plaques given by: a, 6,000 hybrid cells Sp-1; b, clones grown in soft agar from an inoculum of 2,000 Sp-1 cells; e, recloning of one of the positive clones Sp-1/7; d, higher magnification of a positive clone. Myeloma cells (107 P3-X67A g8) were fused to 108 spleen cells from an immunised BALB/c mouse. Mice were immunised by intraperitoneal injection of 0.2 ml packed SRBC diluted 1:10, boosted after I month and the spleens collected 4 d later. After fusion, cells (Sp-1) were grown for 8 d in HAT medium, changed at 1-3 d intervals. Cells were then grown in Dulbecco modified Eagle's medium, supplemented for 2 weeks with hypoxanthine and thymidine. Forty days after fusion the presence of anti-SRBC act. ivity was revealed as shown in a. The ratio of plaque forming cells/total number of hybrid cells was 1/30. This hybrid cell population was cloned in soft agar (50% cloning ef-ficiency). A modified plaque assay was used to reveal positive clones shown in b-d as follows. When cell clones had reached a suitable size, they were overlaid in sterile conditions with 2 ml 0.6% agarose in phosphate-buffered saline containing 25 µl packed SRBC and 0.2 ml fresh guinea pig serum (absorbed with SRBC) as source of complement. b, Taken after overnight incubation at 37 °C. The ratio of positive/total number of clones was 1/33. A suitable positive clone was picked out and grown in suspension. This clone was called Sp-1/7, and was recloned as shown in c; over 90% of the clones gave positive lysis. A second experiment in which 10° P3-X67Ag8 cells were fused with 10° spleen cells was the source of a clone giving rise to indirect plaques (clone Sp-2/3-3). Indirect plaques were produced by the addition of 1:20 sheep anti-MOPC 21 antibody to the agarose overlay,

in the ratios of the different chains and occasionally with the total disappearance of one or other of the chains. Such events are best visualised on IEF analysis of the separated chains (for/example, Fig. 1h, in which the heavy chain of P3 is no longer observed). The important point that no new chains are detected by IEF complements a previous study4 of a rat-mouse hybrid line in which scrambling of V and C regions from the light chains of rat and mouse was not observed. In this study, both light chains have identical Cx regions and therefore scrambled V_L - C_L molecules would be undetected. On the other hand, the heavy chains are of different subclasses and we expect scrambled V_H-C_H to be detectable by IEF. They were not observed in the clones studied and if they occur must do so at a lower frequency. We conclude that in syngeneic cell hybrids (as well as in interspecies cell hybrids) V-C integration is not the result cytoplasmic events. Integration as a result of DNA translocation or rearrangement during transcription is also suggested by the presence of integrated mRNA molecules11 and by the existence of defective heavy chains in which a deletion of V and C sections seems to take place in already committed cells12

The cell line P3-X63Ag8 described above dies when exposed to HAT medium. Spleen cells from an immunised mouse also die in growth medium. When both cells are fused by Sendai virus and the resulting mixture is grown in HAT medium, surviving clones can be observed to grow and become established after a few weeks. We have used SRBC as immunogen, which enabled us, after culturing the fused lines, to determine the presence of specific antibody-producing cells by a plaque assay technique¹³ (Fig. 2a). The hybrid cells were cloned in soft agar¹⁴ and clones producing antibody were easily detected by an overlay of SRBC and complement (Fig. 2b). Individual clones were isolated and shown to retain their phenotype as mirnost all the clones of the derived purified line are capable of lysing SRBC (Fig. 2c). The clones were visible to the naked

assays18 have been used to detect specific clones and representative clones of both types have been characterised and studied.

The derived lines (Sp hybrids) are hybrid cell lines for the following reasons. They grow in selective medium. Their karyotype after 4 months in culture (Table 1) is a little naller than the sum of the two parental lines but more than twice the chromosome number of normal BALB/c cells, indicating that the lines are not the result of fusion between spleen cells. In addition the lines contain a metacentric chromosome also present in the parental P3-X67Ag8. Finally, the secreted immunoglobulins contain MOPC 21 protein in addition to new, unknown components. The latter presumably represent the chains derived from the specific anti-SRBC antibody. Figure 3A shows the IEF pattern of the material secreted by two such Sp hybrid clones. The IEF bands derived from the parental P3 line are visible in the pattern of the hybrid cells, although obscured by the presence of a number of new bands. The pattern is very complex, but the complexity of hybrids of this type is likely to result from the random recombination of chains (see above, Fig. 1). Indeed, IEF patterns of the reduced material secreted by the spleen-P3 hybrid clones gave a simpler pattern of Ig chains. The heavy and light chains of the P3 parental line became prominent, and new bands were apparent.

The hybrid Sp-1 gave direct plaques and this suggested that it produces an IgM antibody. This is confirmed in Fig. 4 which shows the inhibition of SRBC lysis by a specific anti-IgM

Table 1 Number of chromosomes in parental and hybrid cell lines

Cell line	Number of chromosomes per cell	Mean
P3-X67Ag8	66,65,65,65,65	65
PIBul	Ref. 4	55
Mouse spleen cells	_	40
Hy-B (P1-P3)	112,110,104,104,102	106
Sp-1/7-2	93,90,89,89,87	90
Sp-2/3-3	97,98,95,96,94,88	95



atthody. IEF techniques usually do not reveal 19S IgM plecules. IgM is therefore unlikely to be present in the areduced sample a (Fig. 3B) but μ chains should contribute the pattern obtained after reduction (sample a, Fig. 3A).

The above results show that cell fusion techniques are a sowerful tool to produce specific antibody directed against a redetermined antigen. It further shows that it is possible to plate hybrid lines producing different antibodies directed ainst the same antigen and carrying different effector funcas (direct and indirect plaque).

The uncloned population of P3-spleen hybrid cells seems guite heterogeneous. Using suitable detection procedures it hould be possible to isolate tissue culture cell lines making different classes of antibody. To facilitate our studies we have It used a myeloma parental line which itself produced an lg. variants in which one of the parental chains is no longer expressed seem fairly common in the case of P1-P3 hybrids Fig. 1h). Therefore selection of lines in which only the specific atibody chains are expressed seems reasonably simple. g. Alternatively, non-producing variants of myeloma lines could i. the used for fusion.

We used SRBC as antigen. Three different fusion experiments us were successful in producing a large number of antibody-Winteducing cells. Three weeks after the initial fusion, 33/1,086

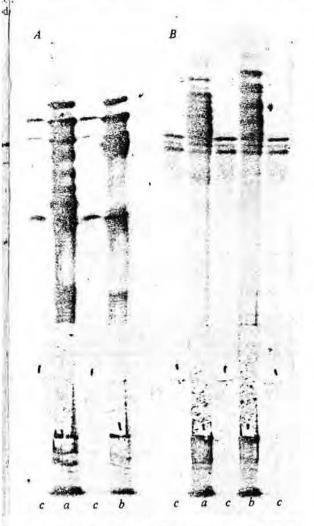


Fig. 3 Autoradiograph of labelled components secreted by anti-SRBC specific hybrid lines. Fractionation before (B) and after (A) reduction was by IEF. pH gradient was 5.0 (bottom) to 9.0 (top) in the presence of 6 M urea. Other conditions as in Fig. 1. Supernatants from: a, hybrid clone Sp-1/7-2; b, hybrid clone Sp-2/3-3;

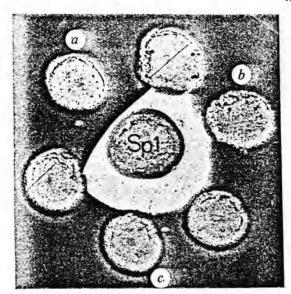


Fig. 4 Inhibition of haemolysis by antibody secreted by hybrid fig. 4 Inhibition of naemotysis by antibody secreted by hybrid clone Sp-1/7-2. The reaction was in a 9-cm Petri dish with a layer of 5 ml 0.6% agarose in phosphate-buffered saline containing 1/80 (v/v) SRBC. Centre well contains 2.5 µl 20 times concentrated culture medium of clone Sp-1/7-2 and 2.5 µl mouse serum. a, Sheep specific anti-mouse macroglobulin (MOPC 104E, Dr Feinstein); b, sheep anti-Adi PC-5 (1967a) absorbed with MOPC 21 (P3) IgG1 absorbed with MOPC 21. PC-5; c, sheep anti-Adj PC-5 (IgG2a) absorbed with MOPC 21. After overnight incubation at room temperature the plate was developed with guinea pig serum diluted 1:10 in Dulbecco's medium without serum.

clones (3%) were positive by the direct plaque assay. The cloning efficiency in the experiment was 50%. In another experiment, however, the proportion of positive clones was considerably lower (about 0.2%). In a third experiment the hybrid population was studied by limiting dilution analysis. From 157 independent hybrids, as many as 15 had anti-SRBC activity. The proportion of positive over negative clones is remarkably high. It is possible that spleen cells which have been triggered during immunisation are particularly successful in giving rise to viable hybrids. It remains to be seen whether similar results can be obtained using other antigenes.

The cells used in this study are all of BALB/c origin and the hybrid clones can be injected into BALB/c mice to produce solid tumours and serum having anti-SRBC activity. It is possible to hybridise antibody-producing cells from different origins^{1,5}. Such cells can be grown in vitro in massive cultures to provide specific antibody. Such cultures could be valuable for medical and industrial use.

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Received May 14; accepted June 26, 1975.

Received May 14; accepted June 26, 1975.

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