In a prior investigation involving hypercholesterolemic cynomolgus monkeys, periodic group reorganization also led to increased contact aggression and to greater atherosclerosis (*16*). It is interesting that a high "potential for hostility" represents, among humans, a central component of the type A (coronary-prone) behavior pattern (*17*). Moreover, independent of its association with type A behavior, hostility has been found associated with extent of angiographically documented coronary artery atherosclerosis (*18*). Although these findings reflect only descriptive behavioral similarities, it is noteworthy that aspects of the present data are consistent with studies of psychosocial factors among human beings.

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References and Notes

1. National Heart, Lung, and Blood Institute, *NIH Pub. No. 81-2034* (1981).
2. L. Solberg, S. Enger, I. Hjermann, A. Helgeland, I. Holme, P. Leren, J. Strong, in *Atherosclerosis V*, A. Gotto, L. Smith, B. Allen, Eds. (Springer-Verlag, New York, 1980), p. 57; L. Carlson, in *Metabolic Risk Factors in Ischemic Cardiovascular Disease*, L. Carlson and B. Pernow, Eds. (Raven, New York, 1982), p. 1.
3. H. McGill, M. Frank, J. Geer, *Arch. Pathol.* **71**, 96 (1961).
4. C. Minick, G. Murphy, W. Campbell, Jr., *J. Exp. Med.* **124**, 635 (1966); T. Clarkson and N. Alexander, *J. Clin. Invest.* **65**, 15 (1980).
5. C. Jenkins, *Annu. Rev. Med.* **29**, 543 (1978).
6. J. Kaplan, S. Manuck, T. Clarkson, F. Lusso, D. Taub, *Arteriosclerosis* **2**, 359 (1982).
7. R. M. Nerem, M. J. Levesque, J. F. Cornhill, *Science* **208**, 1475 (1980).
8. H. Ratcliffe, H. Luginbuhl, W. Schnarr, K. Chacko, *J. Comp. Physiol. Psychol.* **68**, 385 (1969).
9. Each 100 g of diet contained 8.0 g of casein, 8.0 g of lactalbumin, 35.0 g of wheat flour, 6.0 g of dextrin, 5.0 g of sucrose, 4.5 g of applesauce, 7.0 g of lard, 1.2 g of safflower oil, 3.0 g of beef tallow, 0.37 g of dried egg yolk, 15.37 g of alphacel, 4.0 g of Hegsted salt mixture, and 2.56 g of vitamin mixture.
10. For reliabilities of measurement and methods for collecting and analyzing behavioral, pathologic, and physiologic data, see (*6*).
11. I. Bernstein, T. Gordon, R. Rose, *Folia Primatol.* **21**, 90 (1974).
12. All tests of significance were two-tailed.
13. S. Moore, *Lab. Invest.* **29**, 478 (1973).
14. D. Gordon, J. Guyton, M. Karnovsky, *ibid.* **45**, 14 (1981).
15. J. Herd, in *Perspectives on Behavioral Medicine*, S. Weiss, J. Herd, B. Fox, Eds. (Academic Press, New York, 1981), p. 55; R. B. Williams, Jr., J. D. Lane, C. M. Kuhn, W. Melosh, A. D. White, S. M. Schanberg, *Science* **218**, 483 (1982).
16. See J. Kaplan *et al.* (*6*). In the previous experiment exacerbated atherosclerosis was observed only in the stressed animals that were socially dominant. Because hierarchical relationships in the stressed group were somewhat less stable in the current investigation, here we were unable to identify similarly well-differentiated dominant and subordinate animals. Nevertheless, 2 of 15 monkeys housed in the stressed condition clearly retained dominant positions throughout the experiment; as in the previous study, these had the most extensive coronary artery atherosclerosis (see Fig. 1).
17. M. Friedman, *Pathogenesis of Coronary Artery Disease* (McGraw-Hill, New York, 1969).
18. R. Williams, T. Haney, K. Lee, Yi-Hong Kong, J. Blumenthal, R. Whalen, *Psychosom. Med.* **42**, 539 (1980).
19. Supported in part by grants from the National Heart, Lung, and Blood Institute (HL 14164 and RO1 HL 26561) and R. J. Reynolds Industries, Inc.

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Parthenogenesis in the Endemic Australian Lizard *Heteronotia binoei* (Gekkonidae)

Abstract. *Chromosome variation in the gekkonid lizard* Heteronotia binoei *reveals that this endemic Australian vertebrate reproduces by parthenogenesis. Triploid parthenogenetic females are distributed throughout central and western Australia and are all heterozygotes for one or more pericentric inversions that also distinguish the extant bisexual diploid cytotypes. These data on karyotype provide strong evidence that the various clones have arisen through multiple hybridization events between bisexual ancestors.*

In vertebrates, all-female populations that reproduce by parthenogenesis have now been reported in several American and European taxa (*1*). A newly discovered parthenogenetic biotype of the endemic lizard *Heteronotia binoei* Gray, which is distributed throughout most of the Australian continent, also exists as diploid bisexual populations for much of its range (Fig. 1A). A cytogenetic analysis of diploid and triploid forms provides evidence for a hybrid origin of the parthenogenetic biotype and multiple hybridization events between the bisexual ancestors appear to have been important in generating the considerable clonal diversity found in *H. binoei*.

Karyological analysis of diploid *H. binoei* (2n = 2x = 42) by both standard Giemsa-stained preparations and G- and C-banding has revealed two major cytotypes, SM6 and A6, distinguished by a pericentric inversion associated with chromosome 6 (Fig. 2A). Within the SM6 cytotype a further pericentric rearrangement (SM6-2) on chromosome 4 was polymorphic in lizards in north-central Australia and absent in those on the western Australian coast (SM6-1). A distal nucleolar organizing satellite on chromosome 6 was found in eastern and southern A6 populations and all SM6 populations. This did not occur in A6 populations from central and western Australia, although the former did maintain an active distal nucleolar organizing region (*2*). The A6 and SM6-2 cytotypes overlap broadly in north-central Australia (Fig. 1A). However, there are no known sympatric localities, and no diploids heterozygous for the inversion on chromosome 6 have been found.

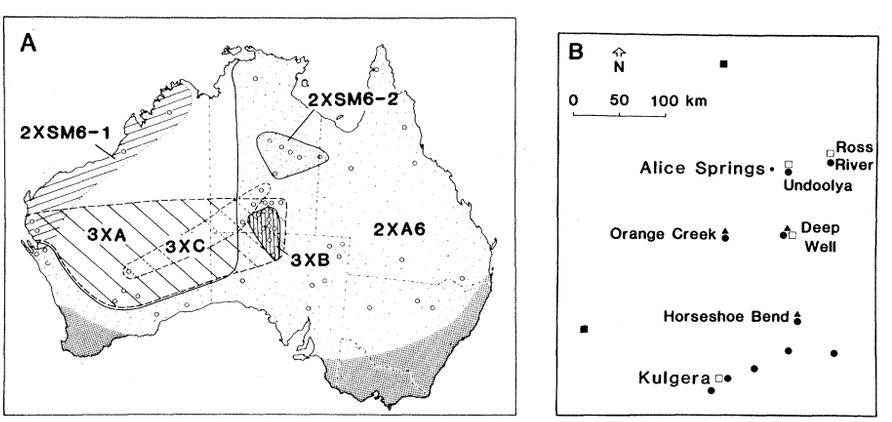

Fig. 1. (A) Distribution of the triploid and diploid cytotypes of *Heteronotia binoei* throughout Australia. Circles represent sampling points and the shaded regions are where *H. binoei* is absent. The boundaries are shown to emphasize the extensive overlap, but more sampling in western Australia is required before the distribution limits of the various cytotypes can be determined. (B) Detailed distribution data for the central Australian region. Symbols: □, diploid A6; ●, triploid clone A; ▲, triploid clone B; and ■, triploid clone C.

Seventy triploid females (2n = 3x = 63), mostly from central Australia, but some from as far as the western Australian coast, have been analyzed. They fall into three major clones (A, B, and C) that can be distinguished by the variants of chromosomes 4 and 6 that they carry (Fig. 2B). Exclusively female triploidy is generally regarded as strong evidence for unisexual reproduction (*3*) and in the case of *H. binoei*, thelytokous parthenogenesis is further supported by the available sex ratio data. In bisexual populations of *H. binoei* the sex ratio is even (*4*). However, extensive collecting in the region between Deep Well and Kulgera (Fig. 1B) resulted in 46 triploid females and no males. The absence of males in this area clearly excludes sperm-dependent modes of unisexual reproduction such as gynogenesis and hybridogenesis (*5*). Hermaphroditism or age-related sex reversal (*5*) are not compatible with triploidy since regular meiosis will result in aneuploid gametes. Also, observations on the reproductive systems of subadult and adult females revealed no testicular material.

Every triploid examined was heterozygous for the chromosome 6 inversion and clone C was also heteromorphic for chromosome 4 (Fig. 2C). Although there is some dissension (*6*), hybridization of genetically distinct bisexual taxa appears to be the most obvious basis for explaining the origin of naturally occurring vertebrate parthenogens (*7*). The origin of the three triploid clones of *H. binoei* can thus best be accounted for by hybridization between the SM6-1 and A6 bisexual cytotypes with subsequent backcrossing of the diploid parthenogen to either of the bisexual cytotypes (Fig. 2B). The alternative hypotheses are the production of triploids by the fusion of haploid sperm and rare diploid egg pronuclei or generation spontaneously of unisexual strains; both predict that triploid clones homozygous for chromosome 6 will predominate, which is clearly inconsistent with the data. The A6 cytotype involved in these hybridization events is invariably the central and western Australian form, which lacks the distal nucleolar organizing satellite on chromosome 6. The postulated diploid parthenogen has not been found in central Australia despite intensive collecting and may be extinct. Chromosomal banding and electrophoretic studies further substantiate the hybrid origin of parthenogenesis in *H. binoei* (*2*).

The triploid biotype of *H. binoei* has the widest distribution yet found for a continental unisexual vertebrate. Within its range the three cytologically distinct clones have widespread and overlapping ranges (Fig. 1A). To date, a detailed analysis of their distribution has been conducted only in central Australia. These populations are of interest for two reasons. First, throughout most of this area the parthenogenetic form is sympatric with the bisexual A6 cytotype of *H. binoei* (Fig. 1B). Extensive sympatry between all-female and bisexual populations, combined with their close morphological similarity, has no doubt obscured the existence of parthenogenesis in this gecko until now (*8*). Two tetraploid females (2n = 4x = 84), each with a single SM6-1 genome and three A6 genomes, have been identified from sympatric localities. These appear to have arisen through insemination of triploid clone A parthenogens by A6 males (*2*). In the one tetraploid female in which the reproductive tract was examined, the ovaries were atrophied. These observations are consistent with reports of hybridization between established parthenogenetic lineages and bisexual forms in which the resultant hybrids are always sterile (*9*).

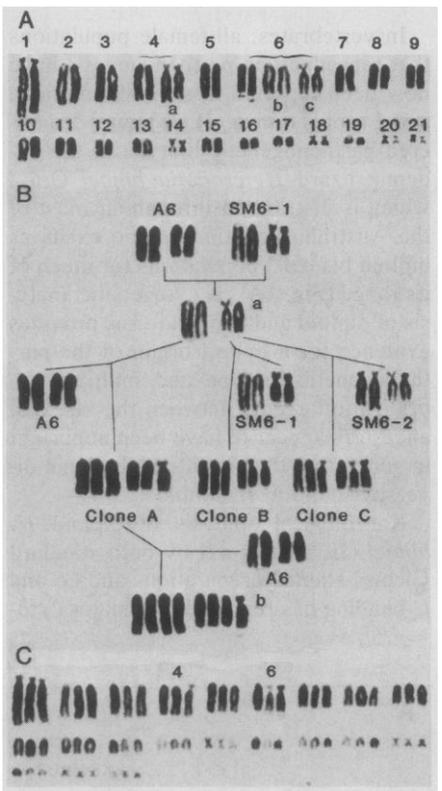

Fig. 2. (A) Diploid karyotype of *Heteronotia binoei* showing variants of chromosomes 4 and 6. (a) Polymorphic pericentric rearrangement of chromosome 4 found in SM6-2 populations; (b) acrocentric chromosome 6 without the terminal satellite; and (c) submetacentric chromosome 6 characteristic of the SM6 cytotypes. (B) Proposed origin of the triploid clones in *H. binoei* showing chromosomes 4 and 6. (a) Diploid parthenogenetic ancestor which subsequently backcrossed to the three extant diploid cytotypes to give rise to triploid clones A to C; (b) clone A when inseminated by A6 males gives rise to the observed sterile tetraploid females. (C) Full karyotype of triploid clone C showing pair 4 and 6 heteromorphisms.

The second interesting feature of the central Australian populations is that all adequately sampled populations have proved to consist of more then one clone. For example, at Horseshoe Bend (N = 9), Deep Well (N = 3), and Orange Creek (N = 5) each sample has clones A and C present (Fig. 2B). Since each collection area covered no more than 200 m^2, it is clear that the two clones are truly sympatric. While other populations with more than five animals examined (Kulgera, Undoolya, Ross River) appear, on the basis of standard Giemsa-stained preparations, to be uniclonal, a more detailed analysis, achieved through C-banding of chromosomes and electrophoresis, has shown clonal diversity within these populations also (*2*).

In contrast to the expectation of greatly reduced genetic variability of parthenogenetic taxa (*10*), detailed studies have repeatedly shown the opposite (*11*). The origin and maintenance of such diversity, in the virtual absence of recombination, now commands the attention of numerous evolutionary biologists (*12*). Two classes of genetic variation, which differ in their evolutionary consequences, must be recognized within unisexual taxa. Extensive intraclonal heterozygosity is generally a consequence of hybrid origin and has been claimed to maximize heterotic gene combinations without genetic load (*13*). Interclonal diversity, essential for adaptive change in parthenogenetic biotypes, may be achieved through mutation within a monophyletic lineage, as has been suggested for curculionid weevils (*14*). Alternatively, limited recombination, combined with multiple hybrid origins, which has been implicated in the teiid lizard *Cnemidophorous tesselatus* (*15*) and the hybridogenetic fish *Poeciliopsis* (*16*), can result in variation between clones. In triploid parthenogenetic biotypes produced by backcrossing, the latter mechanism affords a relatively rapid means of generating clonal diversity. In *H. binoei*, the available evidence suggests that repeated backcrossing of the ancestral diploid parthenogen to genetically distinct bisexual cytotypes has provided the considerable genetic diversity found within this parthenogenetic biotype (*2*).

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References and Notes

1. R. J. Schultz, in *Polyploidy, Biological Relevance*, W. H. Lewis, Ed. (Plenum, New York, 1980), p. 313; J. P. Bogart, in *ibid*, p. 341.
2. C. Moritz, paper presented at the meeting of the Australian Genetics Society, Melbourne, May 1982.
3. T. P. Maslin, *Am. Zool.* **11**, 361 (1971).
4. The ratio of males to females in a museum sample from Norseman, Western Australia, and a study site near Alice Springs is 13:17 and 30:27, respectively. H. R. Bustard [*J. Zool.* **156**, 483 (1968)] reported a ratio of 98:97 in the Pilliga, New South Wales, Australia.
5. L. M. Hardy and C. J. Cole, *J. Morphol.* **170**, 215 (1981).
6. O. Cuellar, *Am. Nat.* **108**, 625 (1974).
7. C. J. Cole, in *Intersexuality in the Animal Kingdom*, R. Reinboth, Ed. (Springer-Verlag, Berlin, 1975), p. 340.
8. The most recent taxonomic treatment of this genus is by A. G. Kluge [*J. R. Soc. West. Aust.* **46**, 63 (1963)]. The available karyological data indicate that diploid *H. binoei* may represent a species complex and that the triploid clones are best regarded as an agamic complex [V. Grant, *Plant Speciation* (Columbia Univ. Press, New York, ed. 2, 1981) p. 434]. More detailed electrophoretic and morphometric studies are needed to clarify the taxonomy of this genus.
9. O. Cuellar and C. O. McKinney, *J. Exp. Zool.* **196**, 341 (1976); C. J. Cole, *J. Hered.* **70**, 95 (1979).
10. C. D. Darlington, *Evolution of Genetic Systems* (Oliver & Boyd, London, 1958), pp. 167–168.
11. E. D. Parker, Jr., *Am. Zool.* **19**, 753 (1979); R. G. Zweifel, *Am. Mus. Novit., No. 2235* (1965).
12. See various papers from a symposium in *Am. Zool.* **19** (1979).
13. M. J. D. White, in *Essays in Evolution and Genetics in Honour of Theodosius Dobzhansky*, M. K. Hecht and W. C. Steere Eds. (North-Holland, Amsterdam, 1970), p. 237.
14. J. Lokki and A. Saura, in *Polyploidy, Biological Relevance*, W. H. Lewis Ed. (Plenum, New York, 1980), p. 277.
15. E. D. Parker, Jr., and R. K. Selander, *Genetics* **84**, 791 (1976).
16. R. C. Vrijenhoek, R. A. Angus, R. J. Schultz, *Evolution* **31**, 767 (1977).

17. I thank S. Donnellan, R. Honeycutt, M. King, M. J. D. White, D. King, G. Mengden, D. Roberts, P. Baverstock, H. Cogger, and T. Schwaner for providing specimens; R. Martin for his able assistance in the field; and R. Honeycutt, B. John, M. J. D. White, D. Shaw, and M. King for discussion and comments on the manuscript. Supported by the ANU and an Australian postgraduate research award.

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Functional Organization of the Second Cortical Visual Area in Primates

Abstract. *The functional organization of the second cortical visual area was examined with three different anatomical markers: 2-[^{14}C]deoxy-D-glucose, cytochrome oxidase, and various myelin stains. All three markers revealed strips running throughout the area, parallel to the cortical surface. The boundaries of these strips provide an anatomical criterion for defining the borders of this extrastriate region. Further, the demonstration of these strips allows a functional and anatomical analysis of modules in the area, just as the recent demonstration of spots in the primary visual cortex has allowed an analysis of modules there. The strips differ structurally and functionally from interstrip regions and these differences are similar to those seen between the spots and the interspot regions in the primary visual cortex. In the macaque the strips and spots differ with regard to binocular organization.*

Primates have at least nine visual areas beyond the primary visual cortex (V1) (*1, 2*). Of these, the second visual cortical area (V2) is certainly one of the most important (*3*). Area V2 is almost as large as V1 (*2, 4*), and, like V1, it contains a well-ordered representation of the visual field within its boundaries (*4, 5*). Area V2 surrounds V1, and considerable information is reciprocally transmitted between these two areas (*1, 2, 4–7*). Most of the information in V1 destined for other cortical visual areas goes first to V2 (*4*). Despite its obvious importance in the chain of cortical visual information processing, V2 has received much less attention than V1. For example, the functional anatomy of the primate V1 has been much studied during the last decade (*8–13*), but little is known about the functional anatomy of the primate V2.

This report describes several basic features of the organization of V2. We have found an array of parallel columnar strips running throughout V2; these strips seem to be the basic modular elements in this cortical area. By using three different markers, we have been able to describe different anatomical and physiological aspects of the strips. The V2 strips resemble the recently discovered spots in V1 (*10–14*) and provide a conspicuous anatomical landmark that should prove useful in defining the borders of V2 in an otherwise vaguely defined cortex. Preliminary results have been presented (*15–17*).

In order to label short-term variations in metabolic activity occurring during visual stimulation, we injected 2-[^{14}C]-deoxy-D-glucose (2DG) while monkeys viewed a particular stimulus. As in V1, different visual stimuli produced different 2DG patterns. During the course of this study, many different visual stimuli were used. In a typical experiment, one stimulus characteristic (for example, orientation, color, spatial frequency, temporal frequency) was held constant while others were varied. More than half of the monkeys viewed binocular patterns, and in these cases the binocular disparity was often varied. The monkeys were then killed, and the brains processed for histology. Early experiments (*15, 16, 18, 19*) indicated a columnar organization of function in V2; in order to see the topography of these columnar systems clearly, we mounted both V2 and V1 flat and cut our sections parallel to the flat-mounted cortical surface (*20*).

In order to label long-term differences in metabolic activity, many of the same tissue sections were treated to reveal cytochrome oxidase, a metabolic enzyme found in all neurons. Concentrations of this enzyme reflect variations in neural activity over periods of weeks or months (*10, 21, 22*).

We also stained some sections for myelin with hematoxylin and Luxol fast blue. In this report, we only include data from macaque and squirrel monkeys, but we have seen many of the same anatomical features in several other primate species.

Since we wish to emphasize the parallels between V1 and V2, we will first briefly describe what is known about the V1 spots and then what we have found about the V2 strips. Area V1 contains spotlike regions of high long-term metabolic activity (as measured by concentrations of cytochrome oxidase), surrounded by regions of lower activity (Fig. 1A) (*10–14*). A less prominent (but otherwise identical) array of spots appears in underlying cortical layers (Fig. 1B). Spotlike differences in cytochrome oxidase activity coincide with certain differences in 2DG activity (*10–12, 17, 18*), in the distribution of putative neurotransmitter (*14, 22*), in single-unit functional properties (*23*), and in afferent terminal distribution (*23, 24*).

Striplike regions of high cytochrome oxidase activity are seen in V2, in the area surrounding V1 (Fig. 1A). The cytochrome oxidase strips are most obvious in layers 4, 5, and the lower part of layer 3 (Fig. 1B), but they often extend through all cortical laminae. Thus, the strips are basically a columnar anatomical organization. The strips run approximately perpendicular to the V1-V2 border in all the primate species we have examined. In the squirrel monkey, the strips are about 0.4 to 0.7 mm wide with an interstrip spacing (center to center) of about 1 to 1.5 mm. In the macaque, the strips are slightly wider, with center-to-center spacings of about 1.5 to 2.5 mm. In the lower layers, the strips are alternately thick and thin (Fig. 1B). In the squirrel monkey, the thin strips merge with the V1-V2 border, but the thick strips fall short of this border by about 0.7 mm.