

terrestrial mammals is almost certainly more complex than in the barn owl. Instead of acting over the same, relatively restricted frequency range to code for azimuth and elevation, time and intensity differences between the ears of mammals provide cues over different portions of the audible frequency range and both seem to be predominantly used for coding stimulus azimuth. Elevation cues in mammals are thought to result from sound-spectral transformations by the head and by the pinna, the visible part of the outer ear⁹. In fact, information derived from just one ear can, under certain stimulus conditions, lead to sound localization performance in humans that is as accurate as that achieved using two ears⁹.

Nevertheless, several key nuclei in the mammalian auditory pathway bear striking anatomical and physiological similarities to those in the barn owl known to be involved in localization. A topographic representation of IID has been demonstrated in the midbrain of the cat, for example, and two-dimensional neural 'maps' of auditory space have been found in homologous brain regions of several owl and mammalian species¹⁰. It therefore seems likely that at least some of the mechanisms for processing binaural sound localization cues are common in many vertebrate species. □

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Ocean Drilling Program

Breakup of Gondwanaland

*Leg 122 shipboard scientific party**

OLD, sediment-starved, passive continental margins are important for elucidating the thermal and structural processes that lead to rifting and continental breakup. These regions also contain clues about global palaeoenvironmental and climatic changes, as well as the record of sea-level fluctuations. There have been few deep-sea drilling studies of the older parts of continental margins even though their unique record reaches back to the Jurassic and Triassic, when there was only a single continental mass — Pangaea. Pangaea was split subsequently by the Tethys Ocean into Gondwana in the south and Laurasia in the north. We have studied the old Gondwanan passive margin of Exmouth Plateau, off the coast of northwestern Australia, to elucidate the evolution of rifting and drifting, in addition to the environmental changes that accompany and follow such momentous events.

The Exmouth Plateau is a rifted and deeply subsided fragment of continental crust, covered by more than 8 km of sediments, including nearly 1–2 km of post-breakup sediments. The present configuration of this region was initiated in the

Late Triassic to Early Cretaceous (230–130 million years ago, Myr) by East-Gondwanan rifting between northwestern Australia, greater India and other Gondwanan fragments to the north. Leg 122 data suggest that whereas the northern margin of the Exmouth Plateau bordering the Argo Abyssal Plain had rifted before the Late Berriasian (140 Myr), the western margin bordering the Gascoyne Abyssal Plain developed during the late Valanginian (135 Myr) when sea-floor spreading was initiated there.

We drilled at six sites (Fig. 1). Four of these (759–761 and 764) on the Wombat Plateau yielded a composite record of sediments deposited during rifting in the Triassic (248–213 Myr) and during the Cretaceous (144–65 Myr) and Cenozoic

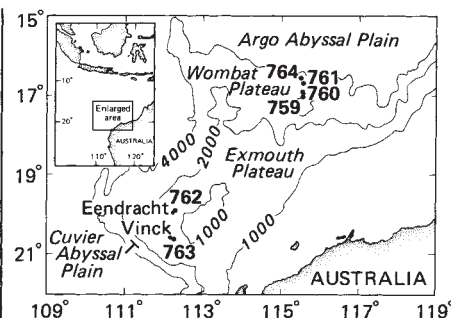


Fig. 1 Leg 122 sites (●) on the Exmouth Plateau. Commercial well sites are also indicated (◐). Bathymetry given in corrected metres. (After von Stackelberg, U. *et al.* *BMR J. Aust. Geol. Geophys.* 5, 113; 1980.)

(65 Myr to the present) following the breakup. The other two sites (762 and 763) reveal the Cretaceous to Cenozoic record of palaeoenvironmental and passive margin evolution of the western part of the central Exmouth Plateau. This record consists of a thick clastic shelf-margin wedge that prograded from a southern source area during the Early Cretaceous late-rift phase, and was there overlain by an Upper Cretaceous to Cenozoic pelagic (marine) sequence.

Deep crustal extension and thinning of the northern Exmouth–Wombat Plateau area occurred during the Permian (286–248 Myr), and was followed by rifting during the Triassic. Carbonate rocks were deposited on the Wombat Plateau during the mid-Carnian (in the Triassic, around 228 Myr), in a southern embayment of a shallow Tethys Sea. The plateau periodically re-emerged until the Rhaetian (ending the Triassic, 213 Myr) when it developed a fully marine carbonate sequence. These carbonates resemble their coeval strata in the western Tethys region of the Alps. ▶

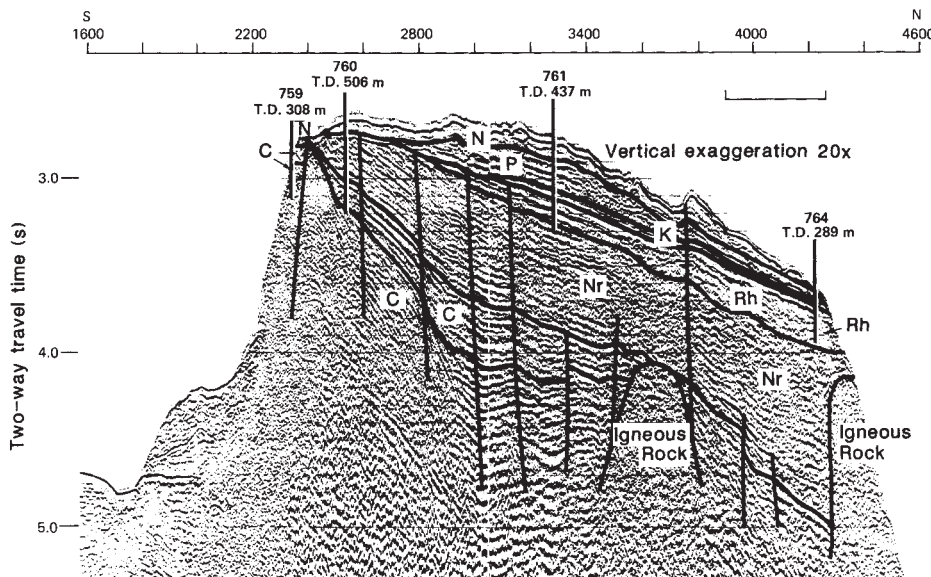


Fig. 2 Interpreted multi-channel seismic section of the Wombat Plateau showing the location of sites 759–761 and 764. Letters within the seismic profile refer to ages as follows: N, Neogene; P, Palaeogene; K, Cretaceous; Rh, Rhaetian; Nr, Norian; and C, Carnian. Scale bar, 10 km.

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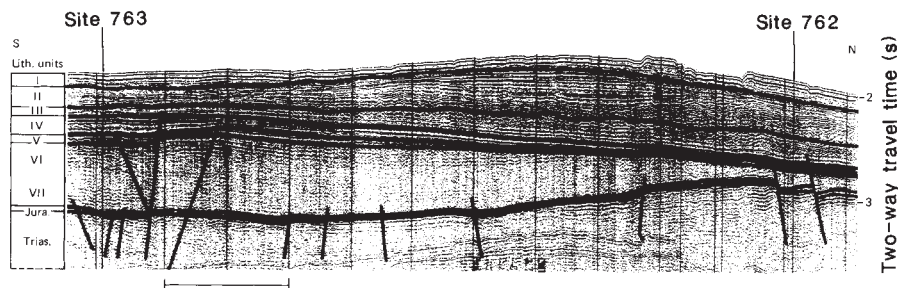


Fig. 3 Interpreted single-channel seismic line through sites 762 and 763 on the central Exmouth Plateau. Note thinning of the clastic wedge (units VI and VII) and thickening of the lower Tertiary sequence (unit II) from south to north. Scale bar, 7 nautical miles.

During the Jurassic (213–144 Myr), northward tilting raised Wombat Plateau above sea level again, and non-deposition or erosion prevented the preservation of Jurassic sequences before the onset of sea-floor spreading in the Argo Abyssal Plain. The plateau subsequently subsided rapidly during the early Cretaceous.

The time of breakup of the western and southern margins of the Exmouth Plateau is constrained by a major erosional unconformity, to around the end of the Neocomian (131–119 Myr), which agrees well with dating from sea-floor magnetic anomalies. Intervals of rising water depth are represented by condensed sections of thin glauconitic limestones and belemnite-rich mudstones. During the mid-Cretaceous (119–91 Myr), when the southern hinterland was drifting north-west with greater India, the southern supply of eroded rocks was cut off. Cyclic deposition of deep-water claystone during the middle to late Aptian (around 115 Myr) marks the onset of hemipelagic deposition (the 'juvenile ocean' stage).

A stagnant period of oxygen depletion

produced a well developed black shale with up to 15 per cent organic carbon at the Cenomanian/Turonian boundary (91 Myr). Post-Cenomanian deposition became dominated by pelagic carbonate deposition, continuous in the northern part of the basin (site 762) and reaching site 763 to the south in the middle Eocene (around 50 Myr).

After isolating unconformities caused by tectonic events, we used a sequence stratigraphic approach to decipher sea-level fluctuations at each site. Our preliminary results indicate that there are important sequence boundaries on the Wombat Plateau between sediments representing the middle and late Carnian, at the Norian/Rhaetian boundary and in sediments of latest Rhaetian age, whose timing conforms well with global changes. Sequence boundaries recognized in the Lower Cretaceous of the central Exmouth Plateau also correlate well with global changes but indicate that the pattern of accumulation of deposits may need to be modified in regions of fast sediment supply. □

Evolutionary biology

Seed of destruction

H. C. J. Godfray and Paul H. Harvey

WHEN Jack Werren and his colleagues attempted¹ to select for the sex ratio in *Nasonia vitripennis*, a parasitoid wasp that attacks houseflies and related species, they found to their surprise that females producing only sons started to appear in the line being selected for male-biased sex ratios. They established by crosses using genetically marked flies that the trait (*psr*, for paternal sex ratio) is extra-chromosomally inherited. This was the first recorded occurrence of cytoplasmic inheritance through the paternal line of an animal. In their most recent work^{2,3}, these authors establish the nature and mode of action of *psr*, and provide an explanation for its evolutionary origin. The serendipitous discovery of what has been termed the most selfish genetic element that has yet been described offers the prospect of new insights into the structure and function of

eukaryotic chromosomes.

Initially, it was uncertain whether *psr* was an infectious venereal disease which causes the death of female progeny, or a cytoplasmic factor transmitted to the egg during fertilization which causes it to become male. *N. vitripennis*, like other hymenopterans, has a haplodiploid genetic system with haploid males developing from unfertilized eggs and diploid females from fertilized eggs. As with many other hymenopterans, the female wasp produces a male-biased sex ratio when her sperm reserves are depleted, and a female-biased sex ratio in circumstances where her progeny tend to mate among themselves^{4,5} or when an appropriate maternally inherited cytoplasmic sex-ratio factor is present⁶. The proportion of progeny carrying the *psr* trait was highest when a female-biased sex ratio was

expected⁵. It therefore appeared that *psr* enters the putative female eggs at fertilization, converting the zygotes to males.

Cytological examination revealed that sperm carrying the *psr* trait enter and fertilize the egg as normal. During the first mitotic division, however, half the chromosomes appear clumped together in a dense mass of chromatin and do not participate in further cell divisions². The embryo, with its now haploid chromosome complement, develops as a normal male wasp. Genetic marker studies reveal that it is the paternal genome which is eliminated.

Extra chromosome

In their new work, Nur, Werren and co-workers reason that *psr* might be discovered by identifying the DNA present in infected but not in uninfected males. They created a λ -phage genomic library from *psr* male DNA, and searched for clones that hybridized with radioactively labelled whole DNA from *psr* males but not with DNA from normal males. They found 36 such clones, and subjected several of them to restriction-enzyme analysis. It turns out that much of the *psr*-specific DNA is in the form of satellite-like, short tandem repeats, the most abundant sequence being 171 base pairs long. This finding is not compatible with the idea that *psr* is a virus or a transposon, but suggests that it could, after all, be a supernumerary chromosome because satellite-like DNA is characteristic of heterochromatized regions of chromosomes. Indeed, detailed cytological study reveals a small chromosome found only in *psr* males.

Supernumerary, or B chromosomes are fairly common in animals and some even show varying degrees of meiotic drive⁷. But the devastating selfishness of *psr* is unique: in a mating between a male bearing *psr* and a female, *psr* first destroys the chromosomes of its original host and then, in the next generation, those of its newly adopted host. Though much of the DNA in the B chromosome is in the form of tandem repeats, specific regions are known to code for a *trans*-acting factor involved in the super-condensation of the parental chromosomes. Analysing the mode of action of *psr* could reveal the mechanism of chromosome condensation, which is poorly understood.

Where does the B chromosome come from and what is its fate? There are now preliminary answers to both questions⁸. There are several cytoplasmically incompatible strains of *N. vitripennis*, and in matings between wasps from two such strains, the paternal chromosomes are broken down. But it is possible to recover fragments of partially destroyed chromosomes that display high transmissibility through the male line but much lower