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The interrelationships of the Osteolepiformes *

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Many recent phylogenies of the Sarcopterygii have placed three fish groups, the Rhizodontida, Osteolepiformes and Elpistostegalia (= Panderichthyida) as successively more crownward members of the tetrapod stem group. However, while the Rhizodontida are an unambiguous clade and the Elpistostegalia are a small and uniform group, the Osteolepiformes are a large and heterogeneous assemblage. Several authors have suspected that the Osteolepiformes are paraphyletic, but only a few serious analyses of the group have been undertaken. The most recent is that by Chang and Yu, which makes the Osteolepiformes paraphyletic to both Dipnoi and Tetrapoda, with *Eusthenopteron* on the tetrapod branch but all osteolepidids in the dipnoan stem group. However, this analysis utilized published data from Baltic *"Thursius"* specimens which were in part incorrectly described.

Our analysis draws on that of Chang and Yu but uses a larger and partly different data set. It places all the traditionally recognized Osteolepiformes as a paraphyletic array in the tetrapod stem group, below Elpistostegalia + Tetrapoda. The most crownward osteolepiform group is the Tristichopteridae (= Eusthenopteridae). The Rhizodontida fall within the Osteolepiformes, immediately below the Tristichopteridae, while the bottom part of the tetrapod stem group consists of paraphyletically arranged "osteolepidids". *Kenichthys,* described as an osteolepiform, falls on the dipnoan stem group.

The common ancestor of dipnoans and tetrapods would probably closely resemble an osteolepidid. Within the tetrapod stem group, trends towards large size, elaborate anterior dentition and reduced median fins occur in parallel in rhizodonts, tristichopterids and elpistostegids + tetrapods. This may reflect common ecological factors in the evolution of these groups.

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Late Pleistocene to Holocene faunal sequences from the Bird's Head, Irian Jaya and the Aru Islands, Indonesia *

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Faunal sequences spanning the late Pleistocene to Holocene are reported from two regions of western New Guinea, the Ayamaru Lakes area of the Bird's Head of Irian Jaya, and the Aru Islands in the Arafura Sea. The Bird's Head sequences come from two caves, one (Kria) with a continuous sequence from early Holocene to present, the other (Toé) with a basal unit of presumed late Pleistocene age and an upper unit of late Holocene age. The extremely rich Aru sequence (Lemdubu Cave), is currently undated but appears to extend back into the late Pleistocene.

The Bird's Head fauna records a transition from Lower Montane to Lowland Rainforest communities at the close of the last glaciation, and contains several previously unknown mammal species.

The Aru fauna documents the former occurrence of extensive savanna habitats, and the presence of a more diverse fauna including several taxa with Australian affinities. Several bones of a large macropodid of uncertain affinity were recovered from the lower part of the sequence. The uppermost levels document the recent expansion of rainforests.

Both faunas are dominated by the remains of macropodids, suggesting a human economy with an unusual degree of specialization.

* Part pertaining to the Bird's Head, Irian Jaya published in full in this volume: 351–387.

The use of fossils to clarify long-term survival trends

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Long-term fossil records can provide information of value in determining conservation status. As an example, based on Oligocene to Miocene records at Riversleigh, the Oligocene record in central Australia and general Pliocene to Holocene records, it is possible to characterize 'lineage health' for modern mammal groups in the Wet

Tropics rainforests as follows.

1. Those that have become extinct in Australia's rainforests: thylacinids, notoryctids, most potoroids, phascolarctids, vombatids, *Distoechurus*-like acrobatids, *Burramys, Strigocuscus,* mystacinids.
2. Those in long-term decline: ornithorhynchids, *Pseudochirops,* acrobatids, petaurids, most hipposiderid lineages.
3. Those that appear to be stable: hypsiprymnodontids, *Trichosurus, Cercartetus, Dactylopsila,* some *Hipposideros* lineages, megadermatids.
4. Those on a long-term rise: dasyurids (particularly dasyurines), peramelids, peroryctids, macropodids, *Hemibelideus, Pseudochirulus, Pseudocheirus, Phalanger,* rhinolophids, vespertilionids, pteropodids, uromyines.

For some there are contradictory long-term indications. E.g., despite a long-term decline in phascolarctid species diversity (>6 Oligocene, 3 early Miocene, 2 middle Miocene and 1 each in the late Miocene, Pliocene and Pleistocene/Holocene), a record sufficiently similar to that of thylacines to cause concern, the modern Koala is more common and probably more widespread than any predecessor. Information from the fossil record should be added to that from other sources for a better overall view of the conservation status of modern groups.

An early-mid Miocene cave deposit at Riversleigh

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AL90 is significant among Riversleigh's Oligo-Miocene fossil deposits for the potential of its rich taxonomic, taphonomic and geological resources to provide detailed insights into some of Riversleigh's Oligo-Miocene communities and environments. The deposit is primarily travertine which, in addition to the prevalence of well-preserved bat material, indicates the presence of cave conditions. This cave may have acted as a natural pitfall trap that accumulated a relatively high number of skeletal parts preserved in close association and in some cases articulation. The rich and diverse terrestrial vertebrate assemblage includes balbarine and balungamayine kangaroos, bandicoots, a ringtail possum, snakes, bats, a large diprotodontid (possibly *Neohelos*), a thylacinid and the sheep-sized diprotodontid *Nimbadon lavarackorum*. The geology of the deposit records the history of an early to mid-Miocene primary cave system followed by later secondary cave formation and infill which is characterized not only by contrasts in geology, but also in the associated fossil faunas.

TIMS U/Th dating of secondary carbonates, theory and application to a mid-Pleistocene fossil deposit

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The lack of accurate ages for faunal deposits of early to mid Pleistocene age, a time characterized by large scale fluctuations in global climates, colonization of Australia by humans and megafaunal extinction, has been a limiting factor in many palaeontological and palaeoecological studies. The U-Th dating method offers a way to extend the chronologies of certain terrestrial deposits beyond the radiocarbon limit. With recent improvements in the precision of uranium and thorium isotope measurements using TIMS (Thermal Ionization Mass Spectrometry) it is now possible to obtain reliable chronologies back to half a million years. This dating method exploits the differential transport of parent U from daughter Th decay products in surficial waters. Secondary minerals forming from these surficial waters contain U but no daughter Th isotopes. Th growing back into "equilibrium" with its parent U isotopes gives a measure of time since formation of this secondary mineral phase.

Calcium carbonate deposits found in limestone caves (speleothems) are usually very suitable for U-Th dating. Besides the direct dating of associated faunal deposits U-Th dating of cave formation can also be used to reconstruct past precipitation regimes. As speleothems are formed by chemical interactions between rain water, biogenic soil CO_2 and the limestone bedrock, the extent of their formation is controlled by the regional hydrological balance. The frequency of speleothem formation over time therefore, can be used as a proxy for effective precipitation.

We have applied the U-Th dating method to speleothems from Naracoorte Caves in South Australia to determine the ages of associated megafauna-rich cave sediments, and to generate a record of speleothem growth over the last 500 kyr. Results indicate that there have been four distinct periods of greater than present effective precipitation during the last ~400 kyr (420-340, 300-270, 220-155 and 115-20 kyr) separated by extended arid periods. Dates on flowstones bracketing five megafauna-rich sediments within this cave system suggest that sediment emplacement took place during the arid phases. The youngest date for megafaunal deposits at Naracoorte is 78 kyr but this is likely to be a minimum age, all of the other sites investigated dated to greater than 160 kyr ago.

Through such an integrated dating approach as that adopted at Naracoorte it is hoped to gain insights into the causes of faunal change, at this, and other sites in Australia over the last half a million years.

A new Frasnian tooth-plated dipnoan and its significance for the evolution of toothplates *

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The commonest dipnoan species from the Frasnian Gogo Formation are *Chirodipterus australis* Miles and *Griphognathus whitei* Miles. Less abundant are *Holodipterus* species, *Pillararhynchus longi* Barwick and Campbell, and *Gogodipterus paddyensis* (Miles). Many more representatives of tooth-plated forms of the *Dipterus*-type would have been expected in faunas of this age, but these had not been found. More recently a small number of individuals belonging to the tooth-plated group have been discovered; including a juvenile as well as adults. These have been prepared to show how tooth plates of this kind grew, and the outstanding features they produce in adults. Amongst the features of particular importance shown in the new genus are: 1, the skull roof with the lateral line passing through bone I; 2, the addition of new tissue in the lingual furrow in the juvenile tooth-plates; 3, the adult tooth plates with teeth added to margins affixed to bone; no enamel-covered dentine around the lateral margins, though some enamel between the tooth rows; 4, dentine in the tooth ridge spaces is pallial dentine integrated with hardened tissue; 5, support of the plate by the pterygoids is shown in both SEM's and outline. The significance of these features in the evolution of tooth-plated lungfish will be briefly examined.

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Emsian thelodonts from the Buchan and Taemas areas of southeastern Australia

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The absolutely last remake of *Beau Geste*: yet another review of the Australian megafaunal radiocarbon dates

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A review of the literature has revealed 91 radiocarbon age determinations for Australia, 77 finite and 14 infinite, either from sediments containing megafauna or directly from their remains. Ages as young as 6000 yr BP have been accepted by some authors, whereas some dates as old as 35,000 yr BP have been rejected as not truly associated with the megafaunal material. In general there has been a trend over the last three decades for the ages of acceptable dates to become older and older. When the Meltzer and Mead criteria are applied to the Australian dates, the vast majority prove to be unreliable, including all dates younger than 28,000 yr BP. It is likely that many of the Australian finite radiocarbon dates, paticularly those based upon charcoal (a reliable material by the Meltzer and Mead criteria), represent the "radiocarbon barrier", the limit of the method, rather than the true ages of the samples. It has been argued that because of possible taphonomic bias in assemblages, sites that lack megafauna cannot contribute information on the chronology of their extinctions. However, although negative evidence is theoretically less desirable, and more difficult to assess, the weight of negative evidence from sites dated to as much as 35,000 yr BP that has been generated in the last two decades can no longer be ignored.

The origins of coral reef fishes

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The origins of extant coral reef fish lineages and the role of coral reefs in the evolution of reef fishes are examined. This study is based on evidence from the fossil record, phylogenetic analyses and biogeographic analyses of living reef fish faunas on the Great Barrier Reef and in other reef regions. The results suggest that extant reef fish lineages first appeared in the late Cretaceous to early Tertiary, with perciform-dominated assemblages being established by the Eocene. At this time almost all extant reef fish families were present and the faunas probably represented reef fish assemblages, i.e. coral reef associations were likely. However, this reef dwelling habit is a derived condition. Living reef fish assemblages are a composite of lineages whose origins encompass a range of non-reef habitats. Coral reefs probably represent a habitat within which these lineages survived and diversified rather than a habitat within which they first evolved.

Upper Permian fish from the South African Karoo Basin

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The fluviatile Beaufort Group (Upper Permian to Middle Triassic) situated in the Karoo Basin, has hitherto been well known for its wealth of mammal-like reptiles, although a number of sites yielding well preserved fossil fish, in particular palaeoniscoid actinopterygians, has been recorded. Generally the fish remains have not been comprehensively documented, apart from the rich and enigmatic site on the Bekkerskraal farm, in the *Cynognathus* Assemblage Zone, Upper Beaufort Group, which, in spite of a number of attempts, has never been relocated. Eighteen palaeoniscoid species, a shark (*Hybodus africanus*), three species of lungfish (*Ceratodus* sp.) and one coelacanth (*Coelacanthus africanus*) have been described (Brough 1931). Several of the palaeoniscoid families are common to the Middle Triassic Brookvale site in the Sydney Basin, New South Wales (Hutchinson 1973).

Two other palaeoniscoid-rich sites have been recorded in the Karoo Basin, both in the Lower Beaufort Group and studied for the first time by the author. They are roadside localities in the central Karoo region and appear to be situated in different biostratigraphic zones (although this is presently unconfirmed).

The Wilgerbosch site, situated in the *Dicynodon* Assemblage Zone, has yielded an abundance (250+ total specimens) of relatively well preserved palaeoniscoid fossils, all quarried from within a typically lacustrine mudstone/siltstone/sandstone sequence: effectively a "palaeo-pond" approximately 10 m x 9 m in lateral extent. Four species have been identified including: *Atherstonia scutata* Woodward, 1889 with its well-developed fins (in particular an elongated, robust caudal), large complete row of ridge scales and a moderately oblique suspensorium; the genus is apparently also known from Madagascar, Australia and Russia; a deep-bodied form; a form with 3 to 4 supraorbital bones, and a form possibly related to the "*Mesopoma* Group" of Gardiner and Schaeffer (1989).

A possibly older second study site on the farm Blourug (unconfirmed biostratigraphic position), near Victoria West has yielded a number of well-preserved specimens in a laterally extensive sandstone unit. At least four species are present including a form similar to *A. scutata*, a deep-bodied form similar to the Wilgerbosch form and a form similar to the "*Mesopoma* Group" specimens from Wilgerbosch.

Up to now, on the basis of preliminary mammal-like reptile biostratigraphic work, the Blourug palaeoniscoid horizon and its surrounding area was believed to be about 10 million years older than the Wilgerbosch site. The presence of the laterally extensive sandstone with abundent fish fossils could be invaluable in clarifying the biostratigraphy in this part of the Karoo Basin. Furthermore, the relatively abundant palaeoniscoid fossils from the Upper Permian section of the Beaufort Group can be used to supplement the biostratigraphy of the Karoo Basin, and ultimately contribute to Gondwanan biostratigraphy and biogeography.

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Charadriiformes from the Early Eocene Tingamarra Local Fauna, Murgon, Queensland, Australia

Walter E. Boles

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The operational details of marsupial megafaunal overkill in Australia

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The extraordinarily long period of occupation of Australia by humans severely limits research into the initial ecological impact of their colonization. Indeed, currently there is no agreement amongst archaeologists as to the timing of human colonization, with estimates ranging between 120 000 and 40 000 years (e.g. Chippendale 1996). This inability to date the arrival of the Pleistocene Australians, coupled with rudimentary and disputed chronologies for the demise of the marsupial megafauna has rendered the ongoing arguments about the cause of extinctions impotent. Obviously, for these debates to advance beyond speculation much firmer chronologies are required. But even if robust chronologies demonstrate that human colonization was synchronized with the demise of the giant marsupials, these historical facts do not of themselves demonstrate a causal relationship between human colonization and megafaunal extinction. This point is well illustrated by the ongoing dispute concerning the cause of the loss of the north American megafauna despite superb chronologies that demonstrate a coincidence between megafaunal extinction and the colonization of north America by humans (e.g. Beck 1996).

Currently in Australia there is widespread support for the hypothesis that over-hunting by humans caused the extinction of the megafauna. However, proof of this requires other lines of evidence in addition to robust chronologies. Particularly important is the clear articulation of the operational details of the alleged over-hunting by Pleistocene colonists. Workers in the Northern Hemisphere have sought to describe the process of over-hunting using mathematical models (e.g. Budyko 1967; Mithen 1993). Because such a modelling approach had not been previously used in Australia, we (Choquenot and Bowman in press) applied this technique to consider levels of Aboriginal hunting effort necessary to exterminate the marsupial megafauna. The purpose of this short note is to briefly summarize our paper. Readers are referred to Choquenot and Bowman (in press) for mathematical details and critical discussion of various assumptions made in the model.

Our model considered a hypothetical tract of tropical *Eucalyptus* savanna. We selected this environment for the following three reasons. First, the most accurate estimates of Aboriginal population densities prior to European colonization are from Arnhem Land, a large area of tropical savanna in the northeast of the Northern Territory (Altman 1987; White *et al.* 1990). Second, the most detailed information of the consumption of meat derived from hunted wild or feral herbivores (e.g. kangaroos and swamp buffalo), by Aborigines living a semi-subsistence lifestyle, is also from Arnhem Land (Altman 1987). Third, there is some evidence to suggest that the tropical savanna environment existed during the Pleistocene, albeit displaced north some 4° of latitude due to drier glacial climates and the associated exposure of the continental shelf (Nix and Kalma 1972).

Our model was based on a two species predator-prey system where megafauna of a particular body mass (for reasons discussed below) were the prey of the Pleistocene hunters (Caughley and Sinclair 1994). We used the model to explore the combined effect of the variation in Pleistocene Australian population densities and variation in the search efficiency of hunters on the equilibrium density of the prey population. The equilibrium density of the prey population is the balance between the capacity of the prey population to increase and the off-take of prey by the Pleistocene hunters. Extinction occurs where prey off-take is greater than the prey population's ability to replace itself.

Clearly such a model requires data on the carrying capacity of the prey population and the rate of increase of the prey population once it is reduced below this carrying capacity. These parameters were estimated using published body mass relationships. Caughley and Krebs (1983) demonstrated a predictable relationship between the body mass of a wide range of herbivorous mammalian species and these species' intrinsic rate of population increase. Freeland (1990) refined the relationship developed by Damuth (1981) which showed a predictable relationship between the body mass of a wide range of herbivorous mammalian species and the carrying capacity of these herbivores. We assumed that these mathematical relationships could realistically describe the rate of increase and carrying capacity of the marsupial megafaunal species with different body masses. The predator-prey model was run to explore the response of megafauna prey 'species' with 250, 500 and 1000 kg body masses to different levels of hunting off-take.

Each simulation was based on the unrealistic assumption that all meat is derived from a single 'species' (as defined by body mass) of megafauna. It becomes mathematically intractable to model the population dynamics of numerous prey 'species' with different body masses including smaller marsupial herbivores that are still extant. The unrealistic assumption that the Pleistocene Australians hunted only a single 'species' of marsupial megafauna makes our model extremely conservative. The model also unrealistically assumed that the hunters were able to find substitute food resources once megafauna had become extinct, implying that there was no linkage between the population density of the Pleistocene Australians and that of their megafaunal prey. This assumption also makes the model highly conservative in terms of the capacity of marsupial megafaunal populations to withstand harvesting by humans.

Harvesting off-take was estimated as the product of human population density and meat consumption of each individual. Based on anthropological research undertaken in Arnhem Land it was assumed that, on average, 2.25 kg of meat per person would satiate the daily meat intake demand of men, women and children living a subsistence lifestyle. Further, it was assumed that 25% of the fresh body mass of every butchered megafauna would be wasted, as this is the proportion of swamp buffalo discarded by contemporary Aboriginal people in Arnhem Land (Altman 1982).

The model was based on the assumption that prey would be uniformly distributed through the savanna and that hunters systematically searched areas of savanna to

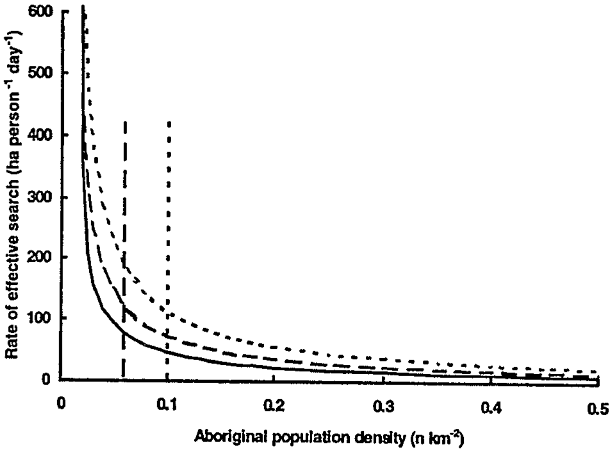

Figure 1 Thresholds for the extinction of three 'species' of marsupial megafauna in relation to human population density and the search efficiency of hunters. The three curves are extinction isoclines for the three different megafaunal 'species' defined by body mass where dotted lines = 1000 kg body mass species, dashed lines = 500 kg body mass species and solid lines = 250 kg body mass species. For each of these curves the area above the line defines various combinations of human population density and hunting efficiency that would drive the particular megafauna species (as defined by body mass) to extinction. The area below the curve defines the various combinations of hunting effort and human population density where the particular megafauna (as defined by body mass) can persist. Estimates of contemporary Aboriginal population densities in Arnhem Land, an area least effected by European colonization, are indicated as lines crossing the lower axis. The estimate indicated by the dotted line (0.1 persons km^{-2}) comes from Altman (1987) and that indicated by the dashed line (0.06 persons km^{-2}) from White *et al.* (1990).

locate prey. Once a megafaunal prey was located it was assumed unable to evade hunters and therefore would be killed and consumed. This aspect of the model explicitly incorporated the notion advanced by Flannery (1990) that the marsupial megafauna were 'naive prey' being unable to actively avoid hunters.

The results of the model can be summarized in a single diagram (Figure 1). Three curves refer to marsupial megafaunal 'species' that were defined by the three body mass classes (1000, 500 and 250 kg). The area above each curve defines the various combinations of human population density and the hunter search efficiency that results in the extinction of the three different megafaunal 'species'. Overlaid on this graph are the two available estimates of Aboriginal population density in the savannas of Arnhem Land. It is of interest that the Arnhem Land Aboriginal population density estimates overlie sections of the three curves where there is a marked inverse relationship between population density and hunting efficiency (Figure 1). At human population densities lower than those reported for Arnhem Land, hunter efficiency must substantially increase to exterminate megafauna.

An apparently counter-intuitive finding of the model was that the smallest megafauna 'species' considered (250 kg) were most vulnerable to over-hunting while the largest megafauna (1000 kg) were least vulnerable (Figure 1). This result is explained by the greater off-take of smaller animals to satisfy the meat demand for a given human population.

Our model provided a context to consider the plausibility of over-hunting by Pleistocene Australians as being the exclusive cause of the extinction of the marsupial megafauna. It suggested that under observed Aboriginal population densities extinction could only occur if the Pleistocene Australians were extremely efficient hunters being able to search about 100 ha per person per day. Remarkably little is known about Aboriginal hunting efficiencies so it is difficult to place this result into a meaningful context. The recent attempts to exterminate feral swamp buffalo in the Northern Territory suggests that a helicopter-borne shooter has a hunting efficiency of about 600 ha per day. By analogy the daily search effciency of each Pleistocene Australian, in a population equivalent to those reported for Aborigines in Arnhem Land in the recent past, would be one sixth of that of a helicopter-borne shooter. Alternatively, six Pleistocene Australians would have had to be as efficient as a helicopter-borne shooter in order to exterminate the megafauna. Such high efficiencies seem unreasonable given the bounds of normal human ability, especially given that it is unrealistic to assume that every individual in the population, regardless of age and gender, would hunt. Further, it is unlikely that human population densities in the Pleistocene would have been higher than recorded today and quite possibly they were lower. For these reasons we concluded that hunting alone did not lead to the megafaunal extermination. Our model led us to reject the overkill hypothesis without being able to identify the specific factor that caused the extinction. This finding is analogous to a mathematician who is able to show that a proposed proof of an unsolved mathematical problem is flawed while being unable to provide the correct mathematical proof.

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An articulated acanthodian tail from the Late Silurian of Victoria, Australia

Carole J. Burrow and Gavin C. Young

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Cretaceous ichthyosaurs of the Giralia Anticline, Carnarvon Basin, Western Australia

Brian Choo

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Big eyes, small brains and large snouts: actinopt origins – revised

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The primitive actinopterygian *'Rhadinichthys' planti* is redescribed and re-assigned to the genus *Mesopoma* on the basis of remarkable specimens from the Westphalian A of the Burnley coalfield, Lancashire, U.K. This material includes three-dimensional natural casts of the dermal skull and endocranial cavities. These endocranial casts provide detailed information about gross brain morphology (including large optic lobes and well-developed cerebellar auriculae), and the anterior oculomotor muscle insertion (the anterodorsal myodome saddled the forebrain). Morphological characters derived from these data and other recently described genera (particularly those from the Namurian Bearsden fauna, Glasgow, U.K.) are combined with results from recent analyses of enamel structure, posterior myodome pattern, and paired fin morphology to contribute to a reanalysis of primitive actinopterygian interrelationships. This tests Gardiner and Schaeffer's (1989) widely accepted hypothesis of primitive actinopterygian phylogeny, and results indicate that (a) chondrostean and neopterygian lineages diverged at a more primitive node than they propose, and (b) that most 'palaeoniscid' genera, such as *Mesopoma*, branch from the base of the neopterygian stem-lineage. Emergent patterns of primitive brain morphology highlight likely derived conditions in extant non-teleostean actinopterygians.

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Tails from the riverbank: Devonian tetrapods, the rear end

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Phylogenetic analysis places *Acanthostega* (Famennian: East Greenland) as the sister-group of *Ichthyostega* plus all more advanced tetrapods. *Tulerpeton* appears to be a primitive member of the amniote lineage, pegging the divergence of amphibian and amniote total-groups to the uppermost Devonian. Postcranial morphological trends spanning the fish-tetrapod divide include: tail elongation; supraneural radial development; endoskeletal girdle enlargement followed by digited limbs; plus complex tarsal and carpal articulations following the origin of digits. Changes to the axial skeleton such as rib-repatterning, the spread of vertebral interarticulation, and reorientation of the neural arches and spines, occur in a consistently anterior to posterior direction. Other emergent patterns include the proximalization of appendicular muscle insertions, and the independent stabilization of pentadactylous limbs in amphibian and amniote clades (including the first evidence of a 5-digit colosteid forelimb). Use of postcranial characters in current analyses also identifies the likely anthracosauroid affinities of *Caerorhachis*, formerly identified as a temnospondyl. Diversity among Devonian tetrapods is illustrated by striking morphological differences. The spinous ribs, paddle-like fore- and hind-limbs, and weak girdles of *Acanthostega* contrast strongly with the massive forelimbs, girdles and broad-bladed ribs of *Ichthyostega*. Curiously, *Ichthyostega* is also now known to have had large-bladed postsacral ribs in the caudal region.

Fossil kangaroos and kangaroo phylogeny *

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Flannery, Archer and Plane (1983) erected two new subfamilies of macropodoids, Balbarinae and Bulungamayinae, to accommodate new species of fossil lophodont kangaroos. They placed Balbarinae within Macropodidae, which includes the lophodont macropodines and sthenurines. Bulungamayinae was placed in the Potoroidae, which also included bunodont/bunolophodont potoroines, propleopines and hypsiprymnodontines. Case (1984) argued that because of their lophodonty, bulungamayines should be included within Macropodidae.

Recent studies of the fossil kangaroos of Riversleigh have identified 15 new species and a new genus of balbarines, and six new species and three new genera of bulungamayines. When added to species already known from Riversleigh and from the Namba, Etadunna and Wipajiri Formations, the new species demonstrate that these kangaroos had achieved a high species diversity as early as late Oligocene to early Miocene times.

Molar morphology of the new Riversleigh species demonstrates that lophodonty evolved independently and by different means in balbarines and bulungamayines, and most recently among bulungamayines. Flannery (1989) suggested that balbarines are ancestral to macropodines and sthenurines. However, evidence for separate evolution of lophodonty among bulungamayines forces their consideration as potentially ancestral to these macropodids.

Bulungamayines can be shown to share more derived cranial and dental characters with macropodids than do balbarines. Bulungamayines are therefore here proposed as being more closely ancestral to macropodids than are balbarines. This hypothesis is supported by the fossil record at Riversleigh and elsewhere in Australia. Balbarine species diversity is greatest in the Late Oligocene Namba, Etadunna and Wipajiri Formations and the late Oligocene/early Miocene deposits of Riversleigh Systems A and B. Only a single species is known from the mid- to later Miocene deposits of Riversleigh System C and only one species from the mid- to late Miocene Camfield Beds at Bullock Creek.

Kangaroo faunas of the Riversleigh System C deposits are dominated by bulungamayines.

A cladistic analysis incorporating representatives of the new taxa, previously known fossil taxa and modern taxa, indicates Balbarinae as the most basal macropodoid clade. A hypsiprymnodontine/propleopine clade is the next most basal, supporting the monophyly of Hypsiprymnodontidae Ride, 1993 which includes those taxa. Potoroinae is indicated as polyphyletic and Bulungamayinae as paraphyletic. Bulungamayine species are shown as members of a large, pectinately branched clade which also includes some fossil potoroines as more basal members and macropodines and sthenurines as its most derived members.

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A new subfamily, genus and species of Miralinidae (Marsupialia: Phalangeroidea) from the early Miocene of Riversleigh, northwestern Queensland

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A new genus and species of Miralinidae has been found in the early Miocene freshwater limestones of Riversleigh, northwestern Queensland. The sample comprises two dentaries and a partial maxilla from Wayne's Wok Site. Phylogenetic analysis suggests that the new genus is the sister taxon of *Miralina*. Shared features include: an elongate I_1; a sectorial P^3_3 with many cuspules; metaconid of M_{2-4} higher than the adjoining lophid; loss of the M_1 metaconid; hypolophid of M_{2-4} meets the postentocristid, not the entoconid; M_1 protoconid lingually displaced; a steep rise in the anterior cingulum of upper molars to meet the parastyle; and presence of a well-defined neometaconule on the upper molars. Large morphological differences suggest that these genera should be distinguished at the subfamilial level. A study of molar morphology and occlusion shows that the buccal cusps of the upper molars of the new genus lie outside the occlusal surface of the lower molars, perhaps suggesting that these cusps are stylar cusps. Thus the 'neometaconule' and 'paraconule' would be re-identified as the metacone and paracone, respectively. This supports hypotheses that the metacone and paracone have been incorporated into the transverse lophs, with the buccal cusps being stylar cusps.

Plesiosaurs in a Gondwanan context: recent research on Cretaceous faunas in South Africa, Australia and New Zealand *

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Plesiosaurs were predaceous Mesozoic marine reptiles. They can be divided into macrophagous pliosauroids and microphagous plesiosauroids. A small (<2 m) pliosauroid from the Early Cretaceous (Valanginian) of South Africa has been redescribed, and confirmed as being congeneric with the English Barremian *Leptocleidus*. They are placed in two species, with little difference between them. Newly collected pliosauroid material from the Birdrong Sandstone (Barremian-Hauterivian) of Western Australia is assigned to a new species, which is somewhat larger. An Aptian-Albian specimen, (ERIC), (under study) from South Australia, also belongs to *Leptocleidus*. It is about the same size as the English and South African material. Leptocleidids are descendants of the large (>5 m) early Jurassic rhomaleosaurids. The (?Albian) Queensland 'Richmond Pliosaur' (also under study) differs from the leptocleidids in having a much longer snout, but is also not very large. All of these seem to have lived in relatively shallow water, with distinct freshwater associations. In the latest Cretaceous of South Island, New Zealand, a rich fauna of plesiosauroids has been known for over 100 years (Hiller, Mannering and Jones abstract this volume). A recent addition to this fauna is a large (6 m), aberrant, plesiosauroid which may have affinities with specimens described from Chile, Argentina and Antarctica.

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* See also pp. 201–205 in this volume.

Gyracanthides murrayi from Mansfield, Victoria, comes out of the cupboard!

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The Lower Carboniferous acanthodian fish *Gyracanthides murrayi* (Acanthodii: Gyracanthidae) was described by Woodward (1906), from articulated specimens of probable Tournasian age from Mansfield, Victoria. Isolated gyracanth fin spines from the Lower Carboniferous of the Bowen Basin, central Queensland, have historically also been assigned to *G. murrayi*. Recently discovered additional fin spines cf *G. murrayi* from the mid-Visean Ducabrook Formation, Queensland, are currently being described by Turner *et al.* Different parts of Woodward's original description have now been challenged, with Woodward's reconstruction of the elements of the pectoral girdle being the most contentious. In 1973 Miles questioned Woodward's description of an anterior and posterior pair of free pectoral spines, proposing that only the posterior pair were present and that these were homologous with those of other acanthodians. A re-examination of the Mansfield specimens has re-affirmed the validity of Woodward's original description, adding weight to the discovery by Randall in 1996 of elements of the pectoral girdle of the closely related genus *Gyracanthus* sp., which are identical to the anterior free pectoral spine of *G. murrayi*. The morphology of the ornament of the fin spines of *G. murrayi* may be a useful character in the determination of the relationships of *Gyracanthides* spp.

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Evolution and biogeography of capitosauroid amphibians

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Capitosauroid amphibians, so far known to comprise three families, 12 genera and 44 species, were the most abundant, widespread and taxonomically diverse temnospondyl amphibians of the Triassic. Capitosauroids probably arose in the Late Permian from rhinesuchoid-grade temnospondyls (endemic to South Africa), with which they share numerous derived characters. At the base of the Triassic, however, capitosauroids were present in abundance (though restricted to three genera) in both Gondwana and Laurasia, where rhinesuchoids are unknown. A Gondwanan origin for the group would appear likely, but is not in accord with the apparent absence of capitosauroids in the *Lystrosaurus* Zone of South Africa. Two equally possible scenarios can be considered. First, that capitosauroids spread rapidly throughout Pangaea in the latest Permian or earliest Triassic, or the group is diphyletic. The marked morphological uniformity between the earliest capitosauroids in Laurasia and Gondwana suggests the former possibility, and a cladistic analysis of the Capitosauroidea supports the monophyly of the group. Capitosauroids radiated rapidly toward the close of the Scythian and achieved maximum diversity during the Middle Triassic, when capitosaurids occupied every continent, while benthosuchids and mastodonsaurids remained endemic to Laurasia. Capitosauroid diversity declined toward the close of the Middle Triassic so that only two genera, *Cyclotosaurus* and *Mastodonsaurus*, are known with certainty from Late Triassic deposits.

Evolution of the genus *Macropus*: ecophysiological aspects of speciation and extinction

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A complex pattern of speciation and extinction is demonstrated for large marsupial herbivores in southeastern Australia throughout the last 5 million years. *Macropus* is the only genus containing large species to survive throughout the period and go on to become a dominant modern taxon. Although some members of the modern fauna can be traced back to the Pliocene or early Pleistocene, most of these species first appear in the last 700 kyr (the majority before about 200 kyr BP, but with another burst of speciation occurring during the last 100 kyr). It is suggested that ecophysiological adaptations (rather than morphological change or body size) have permitted the success of this predominantly grazing genus. It is further speculated that similar ecophysiological factors contributed to the lack of ability of the browsing diprotodontids, browsing macropodines (i.e. *Protemnodon* spp.) and sthenurines to adapt to deteriorating environmental conditions, including oscillating unpredictable climate, vegetation change (with associated increasing incidence of fire over the last 200,000 years), the arrival of humans and the final extreme aridity of the last glacial maximum — in that order.

The surviving *Macropus* (*Macropus*) *giganteus/titan* lineage, the *M.* (*Osphranter*) *altus/robustus* lineage and the *M.* (*Notamacropus*) *agilis/siva* lineage co-existed with the diprotodontids and sthenurines (often occurring as fossils in the same sites) throughout the last third of the Pleistocene, despite the above-mentioned environmental stresses. The surviving macropodid taxa were similar in size, or larger than most of those that became extinct. We consider that body size was less important in extinctions than the relationship between available forage and digestive strategies as well as reproductive flexibility; hence suggest that the term 'megafauna' is a 'white elephant'.

The environmental context of the Late Quaternary extinction of *Petrogale* in south-western Western Australia

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Petrogale lateralis (the Black-footed Rock-wallaby) is well represented in vertebrate faunal assemblages from Late Pleistocene human occupation deposits at Devil's Lair and Tunnel Cave in the Leeuwin-Naturaliste Region, southwestern Australia, but is absent from the early Holocene faunal assemblages at both sites. The disappearance of this species, which is thought to have been an important human food resource, from the Devil's Lair faunal sequence was attributed by Merrilees (1979) to a change in regional climate encouraging an expansion of *Eucalyptus diversicolor* (Karri) tall forest. Species identifications of charcoal fragments from Tunnel Cave support Merrilees' proposition of floristic change at the end of the Pleistocene. However, the Tunnel Cave and Devil's Lair records of Aboriginal occupation raise the question — were changes in firing or hunting practices additional factors in *Petrogale*'s decline?

Merrilees, D. (1979). Prehistoric rock wallabies (Marsupialia, Macropodidae, Petrogale) in the far south-west of Western Australia. *Journal of the Royal Society of Western Australia* **61**: 73-96.

Early Carboniferous fish from the Waaipoort Formation (upper Witteberg Group) of South Africa

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The Waaipoort Formation forms the upper-most part of the Lake Mentz Subgroup (Witteberg Group) and represents the most significant fossiliferous unit of Visean age in southern Africa. Ichthyofaunas in this formation include palaeoniscoids, which predominate, acanthodians (*Gyracanthides* and *Acanthodes*) and rarer ctenacanth and protacrodontid sharks. These three groups are represented by existing and new specimens, with some of the last two groups being recognized, described and figured for the first time. The eight genera of palaeoniscoids, including fusiform and deep-bodied forms, most of which are fully articulated and laterally preserved impressions, represent some of the earliest fish of their kind in southern Africa — earlier specimens comprise a few disarticulated scales from the Late Devonian Witpoort Formation (Witteberg Group). Some original descriptions of the palaeoniscoids have been emended, while large recent and existing collections may reveal new species.

The Waaipoort was deposited within a fresh to brackish water, extensive, thermally stratified lake, at a sub-polar palaeolatitude. The lake was open and experienced episodes of bottom anoxia and varying rates of sedimentation. The formation represents a near-shore environment, and the associated lake sub-environments possibly account for the significant lateral and vertical intra-formational variation. Previous environmental interpretations include a mud-flat, lake, non-deltaic shelf and lagoon.

Whitehill Formation (Ecca Group) palaeoniscoids from the Permian of South Africa

Fiona J. Evans and Patrick Bender

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Investigating human/megafauna interactions in Australia: evidence from the Cuddie Springs site

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At the present time, Cuddie Springs provides the only known secure evidence for an overlap and interaction of humans and megafauna on the Australian continent. The evidence, in the form of bone and flaked and ground stone, charcoal and ochre, was recovered from a claypan on an ancient lake floor in the semi arid zone. Cuddie Springs has been known as a fossil megafauna site for over a century, though the archaeology was not reported until excavation during 1991 (Furby 1991). The evidence of overlap and association is found in a series of lacustrine clays and within a sealed unit, ~70 cm deep, from 1.7 m to 1 m depth. Archaeological and palaeoenvironmental evidence has been compiled in order to evaluate the lake history and the depositional environment of the fossil finds (Dodson *et al.* 1993; Furby 1995). Today, the site is in the semi-arid zone, but during the last glacial period it was part of the expanded arid zone. People first arrived at Cuddie Springs before 30,000 BP, during a lake full period similar to a waterhole scenario (level 1). Around 30,000 BP a return to ephemeral lake conditions meant irregular inundation with occasional occupation of the lake floor by people. Megafauna disappeared from Cuddie Springs by about 28,000 BP. Direct evidence of human interaction with some species of kangaroo is found in these upper levels (level 2), i.e. *Macropus rufus* and possibly *Sthenurus* sp. Stone artefact assemblages from the lowest levels at Cuddie Springs are consistent with butchering assemblages from elsewhere, with usewear and residue studies indicating that they were used for butchering activities. In subsequent occupation levels more generalized activities have been identified such as plant processing (Fullagar and Field in press) and higher relative numbers of extant species compared to extinct species. The occupation phases identified at Cuddie Springs correlate to the hydrology of the lake with changes in stone artefact assemblages and possibly faunal assemblages related to local environmental conditions.

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(1993). Humans and megafauna in a late Pleistocene environment from Cuddie Springs, north western New South Wales. *Archaeology in Oceania* **28**: 94-99.

Fullagar, R. and Field, J. (in press). Pleistocene grinding stones from the Australian arid zone. *Antiquity* **71**: in press.

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Determining the relative roles of climate vs regional tectonics in the formation of the vertebrate fossil record: an example from the Late Cretaceous of western North America

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Speleothem chronology and its implications for biochronology, Wellington Caves, New South Wales

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The Cainozoic deposits at Wellington Caves consist of three major units (from oldest to youngest): the Phosphate Mine Beds, the Big Sink beds, and the Mitchell Cave Beds (Osborne 1997). In an earlier examination, the Big Sink beds were considered to be part of the Phosphate Mine Beds (Osborne 1983), but major disconformities have now been recognized between all three units. The faunal remains from the Big Sink beds (including *Protemnondon* sp. cf. *P. devisi, Thylacoleo crassidentatus, Petauroides stirtoni* and *Macroderma koppa*) suggest an early-mid Pliocene age (Hand *et al.* 1988) [also Dawson *et al.* this volume, ed.]. In the Mitchell Cave Beds, a breccia unit (the Bone Cave Breccia), contains many Pleistocene forms including *Diprotodon optatum, Sthenurus atlas,* and species of *Macropus* and *Procoptodon* which are not found in the underlying beds (Hand *et al.* 1988). Recent investigations of the faunal material in the Bone Cave Breccia suggests a terminal Pliocene age (Dawson and Augee 1995).

A flowstone lying between the Big Sink beds and the Mitchell Cave Beds has been investigated as part of this study. $^{234}U/^{238}U$ analysis has constrained the age of the flowstone to less than 1.5 Myr, whilst the normal magnetic polarity of the deposit is strongly suggestive of deposition since 0.78 Myr, during the Brunhes polarity chron. $^{230}Th/^{234}U$ analysis by alpha-spectrometry has further limited the age of the flowstone to <350 kyr, whilst mass spectrometric analysis has yielded an age of deposition of ~272 ± 4 kyr. This result has significant implications for the biostratigraphy and biochronology of the deposits at Wellington Caves.

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The Pleistocene mammal fauna of Kelangurr Cave, montane Irian Jaya, Indonesia

Timothy F. Flannery

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Quaternary extinctions in Melanesia

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With only six extinct Pleistocene taxa known, the New Guinean megafaunal assemblage is much smaller than that of Australia. Proportionately, it represents only 2.7% of the total indigenous, pre-human mammal fauna of the island. It is argued that the presently known New Guinean megafauna is a gross underestimate of its true diversity. Articulated or associated skeletons of megafaunal species have been found at only three sites in New Guinea, all of which are associated with minimum ages of at least 38,000 yr BP. Non-articulated remains at another site have been associated with ESR dates of 41,000-80,000 yr BP.

Association of megafaunal fossils with the more recent dates (24,000-14,000 yr BP) from Nombe rockshelter is so poorly substantiated that it can probably be discounted. Holocene extinction of *Thylacinus* and *Thylogale* (two species) has occurred in New Guinea. Insular Holocene extinctions are widespread. Two large, extinct murids have been described from Buka Island, Solomon Islands, which were probably terrestrial in habit. An extinct murid has been described from New Ireland, and marsupials from Halmahera. Locally extinct bats have been recorded from the Cook Islands, 'Eua and Tonga.

These extinctions seem to have occurred predominantly, if not entirely, within the last three or four millennia. They coincide roughly with the introduction of the New Guinea wild dog (*Canis familiaris*), and the introduction of a variety of placental mammals (from dogs to pigs and rats) to the Melanesian islands. All of these extinctions coincide broadly with the arrival of Lapita people in the region.

Extinctions of murids (many terrestrial) have continued in the Solomon Islands into historic times, with at least four taxa disappearing from the central Solomons over the past century. These seem to represent a continuation of Holocene extinction trends. Other apparent extinctions are less explicable.

On Jinmium dates

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Sediments from excavations at Jinmium, Northern Territory, have been dated by thermoluminescence (TL), suggesting a long chronology for human occupation, perhaps more than 116,000 years. Debate has focused on the TL ages themselves, which can only be properly assessed by further field evidence and by further dating programmes which have been under way for about two years. While it is unlikely that new OSL and other results will be available for a few months, a recently completed study of the region's rock art strongly supports the contention that weathered engraved cupules found at many archaeological sites are the earliest in the Keep River sequence, as for elsewhere in northern Australia. Although there is evidence for recent engraved cupules, no Aboriginal people in the Keep River area have any knowledge of their production (apart from reference to mythological spirit beings). A reasonable hypothesis is that most vertical wall panels of cupules in this area were produced prior to about 40,000 years as suggested by dated sediments from Jinmium.

Phylogenetic relationships of the lampreys

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An extensive search of the literature, and an examination of preserved lampreys, was conducted in order to assemble a set of characters for use in a phylogenetic analysis of the lampreys. The search yielded over 30 characters from species representing all of the 10 extant genera and the four fossil genera, *Jamoytius, Mayomyzon, Hardistiella* and *Pipiscius*. Characters include dentition, velar tentacles, oral papillae, position of the eyes and otic capsule, shape and arrangement of the dorsal and caudal fins, and karyology. Analysis of the character matrix supports the monophyly of the northern hemisphere lampreys, i.e. the Petromyzontidae. The intergeneric relationships of the Petromyzontidae and their relationships with the southern hemisphere lampreys will be discussed.

New observations on *Romundina* (Placodermi, Acanthothoraci) and their impact on placoderm interrelationships

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Among placoderm fishes, the acanthothoracids have long been considered as oddities due to the scarcity of their remains. The best known of them is *Romundina stellina* Ørvig, 1975, of which remarkable fossils were collected in 1970 in marine Lower Devonian limestones-dolostones of the Drake Bay Formation of western Prince of Wales Island (Northwest Territories, Canada). The material, preserved as three dimensional objects, has been acid prepared. Most of the head elements were described, but some of the body armour and cheek plates were still to be found.

During an expedition to the type locality in 1995, several new specimens were collected, amongst which are the plates missing from the original sample. The discovery of several specimens demonstrating a well-developed ventral cover of body armour corroborates hypotheses that extensive belly cover is the "primitive" condition in placoderm fishes.

Acid preparation has revealed the perichondrally ossified visceral elements fused to the dermal cheek plates (suborbital and submarginal) which throw light on the homologous elements in rhenanids as indicators of relationships. A phylogenetic analysis of the whole class Placodermi, taking into account these new data, groups acanthothoracids and rhenanids at the base of the cladogram and suggests that the short armour present in various taxa represents convergent reductions from an original extensive complex of bony plates.

ESR dating of Australian megafauna

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Electron spin resonance (ESR) dating became systematically applied in the geological sciences from the mid-1970s. It has, since then, been successfully applied to a wide variety of geological and palaeontological materials. These include speleothems, spring deposited travertines, mollusc shells, corals, tooth enamel and quartz.

ESR dating is based upon the identification of a number of paramagnetic centres in a mineral. These centres are the product of the exposure of minerals to alpha-, beta-, and gamma-radiation from various abundant radioactive elements. The ESR intensity of these centres is directly proportional to the time of exposure, thus allowing estimation of exposure time or burial/archaeological age. To allow age assessment two parameters must be determined: the accumulated dose (AD) and the dose rate (D) to which a sample was exposed. AD is determined by the additive dose method and D is determined by various infield measurements and analytical analysis of isotopic contents of dating materials.

A new ESR method was recently developed by our laboratory which allows for the semi non-destructive dating of very small fragments of enamel. Pieces as small as 5 mg can be successfully dated and refitted to teeth, with little evidence of removal. ESR has been applied to several Australian megafauna sites, and the results of dating studies at Tambar Springs and Lancefield are presented.

Cladistics and amniote phylogeny: consensus or chaos

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Despite claims that cladistic analyses produce consensus with respect to the general pattern of early amniote phylogeny, the affinities of 'problematic' groups, such as turtles and procolophonids, are as controversial today as they were around the turn of the century. A critical appraisal of recent studies of amniote phylogeny reveals a high degree of character and topological incongruence within and between the various analyses. In addition the characters used in these analyses are frequently poorly defined and within-group polymorphism is often ignored — especially in the case of the synapsids which are usually assumed to form a monophyletic group and are coded for character state on the basis of a reconstructed (hypothetical) 'primitive morphotype'. To investigate the effects of these factors, a recent cladistic analysis by Laurin and Reisz in 1995, was repeated in a revised form: poorly substantiated or ill-defined characters were discarded and the remaining characters were recoded to include corrections and known polymorphisms for all groups; the caseids were treated as a separate group from the rest of the synapsids. The new analysis produced two equally parsimonious trees, both noticeably different from that of the previous analysis and in both of which the caseids were the basal group of a clade comprising caseids, procolophonids, pareiasaurs and turtles. Both trees contained a clearly-defined diapsid clade comprised of the captorhinids, *Palaeothyris*, areoscelids and younginiforms, and in both instances the millerettids and mesosaurids were more closely aligned with synapsids and caseids than with the diapsid group. In both trees the synapsids (minus the caseids) were a poorly defined group identified by only one autapomorphy. The new analysis calls into question the consensus that aligns the parareptiles more closely with the diapsids than the 'synapsids' and cautions against *ad hoc* assumptions of monophyly, especially for groups with high levels of polymorphism.

On the histology of some recently discovered shark teeth from the Middle to Late Devonian of the Antarctic continent

Oliver Hampe

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Origin of New Zealand's endemic mammals solved *

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Three bat species comprise New Zealand's only endemic mammals. The vespertilionid *Chalinolobus tuberculatus* has been demonstrated to be closely related to Australian congeners, but the origins and relationships of NZ's two mystacinids, *Mystacina tuberculata* and the recently extinct *M. robusta*, have remained obscure. Taxonomists have variously placed them in three microchiropteran superfamilies. The issue appeared resolved when molecular data showed them to be basal members of the South American superfamily Noctilionoidea (= Phyllostomoidea), their dispersal to NZ from South America evidently occurring more than 35 million years (Myr) ago (Pierson *et al.* 1986). Recently it was suggested by Simmons (in press) on the basis of a variety of data that mystacinids are probably basal to a large group including the cosmopolitan Vespertilionidae, Molossidae and Nataloidea. This implies that ancestral mystacinids diverged from other bat lineages at least 55 Myr. Now the first pre-Pleistocene record for mystacinids has been found in Australia. Three species of *Icarops* n. gen. are known from lower teeth and dentary fragments from the middle Miocene Bullock Creek deposit, Northern Territory and early Miocene Wayne's Wok and Neville's Garden Sites at Riversleigh, Queensland (Hand, Murray, Megirian, Archer and Godthelp 1998), and more dental and very distinctive postcranial material has been recovered from at least two other Australian Tertiary localities. Australian fossil mystacinids are characterized by a suite of apomorphies that are shared only by Recent mystacinids and which exclude them from being ancestral to other living bats. The fossil mystacinids are generally plesiomorphic with respect to Recent taxa and suggest an Australian origin for NZ's mystacinids. Recent mystacinids are noted for their peculiar terrestrial habits, behaviours reflected in their skeletal morphology. However, wing bones of fossil and Recent mystacinids also exhibit derived features typically associated with highly efficient flight and long distance dispersal. New Zealand separated from the rest of Gondwana 80-90 Myr ago. For some 30-35 Myr, much of NZ was submerged and any Gondwanan mammals it might have carried may have vanished during that time. A late Oligocene dispersal by mystacinids to New Zealand from Australia is possibly indicated. Further, a new bat family recently found in Australian Miocene sediments, allied to the Mystacinidae, suggests that NZ's *M. tuberculata* is the sole surviving member of an extensive Tertiary radiation of "TOZNZIAN" bats.

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* Published in full: Hand, S.J., Murray, P.F., Megirian, D., Archer, M. and Godthelp. H. (1998). Mystacinid bats (Microchiroptera) from the Australian Tertiary. *Journal of Paleontology* **72**: 538–545.

Mauisaurus haasti – a new look at an old species of plesiosaur

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A newly-prepared specimen of an elasmosaurid plesiosaur, from the Haumurian (Late Cretaceous) Conway Formation of North Canterbury, is more complete than any found previously in New Zealand. The specimen, a young adult, comprises posterior fragments of the skull, almost the entire vertebral column, fragments of the major bones of both pectoral and pelvic girdles, and portions of all four limbs. Direct comparison with the lectotype of *Mauisaurus haasti* Hector, 1874, suggests that it can be assigned to that species.

The new material provides much additional information on *M. haasti* and, along with specimens previously assigned to the species, permits more meaningful comparisons with other Late Cretaceous elasmosaurs. Features of the vertebral column, pectoral and pelvic girdles, and limbs serve to verify the status of the species and genus as separate from previously described forms. The species is characterized by having 85 presacral vertebrae, 65 of which are cervicals. The coracoids possess a pronounced ventral process and a broad rounded transverse ridge on their dorsal surfaces. In large adults the medial profile becomes markedly sigmoidal. The femur is about two-thirds as wide as long with a large hemispherical capitulum; the humerus is relatively broad with an elliptical capitulum. In life, the animal would have been in excess of 6 m long.

Pleistocene agamid and scincid lizards from southeast Queensland

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Recent collections made from Pleistocene sites in southeast Queensland have yielded many small vertebrates, including the remains of reasonable numbers of dragons and skinks. Squamates from southeast Queensland have been reviewed most recently by Molnar (1991). Extant dragon and skink species have been identified from the following sites: Russendon Cave (RC), Texas, Cement Mills (CM), Gore, and the eastern Darling Downs (DD). In particular *Tympanocryptis lineata* (DD), *Hypsilurus* sp. cf. *H. spinipes* (RC), *Cyclodomorphus gerrardii* (RC), *Tiliqua rugosa* (CM and DD), *Physignathus lesueurii* (DD) and *Tympanocryptis* sp. cf. *T. intima* (DD) have been recorded. A new genus of agamid has been described from Pearson's Locality, eastern Darling Downs. Posteriorly reclined dentary acrodont teeth with unusual wear diagnose the taxon and pose questions about this dragon's diet. New studies of agamid osteology, centring on cranial morphology, have identified taxonomic features that distinguish *Tympanocryptis diemensis* from *Tympanocryptis* (*s.s.*), therefore promoting its position within *Rankinia*. Osteological relationships seen amongst agamid genera illustrate that *Physignathus, Chelosania, Hypsilurus* and *Lophognathus* are closely related and this relationship ties them to the 'amphiboluroid' dragons. This study provides a start in agamid palaeontology in Australia; something that has been almost entirely lacking up until now.

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Times to extinction and the New Zealand extinction chronology

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The presence or absence of vertebrates vulnerable to predation by the Pacific rat *Rattus exulans* on islands, provides information on the time since the rat was introduced to each island. Variation in body mass, behaviour, and life history strategy can be used to predict times to extinction for selected species undergoing different levels of predation on different life history stages. The predictions can be tested by reference to the 'natural experiments' on the offshore islands and the mainland of New Zealand, and to terminal dates for the taxa from radiometric and other dating systems. A detailed chronology of the extinction event is being developed.

OSL and radiocarbon dating of late Holocene faunal sites in New Zealand

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The chronology of New Zealand's extinct and extant late Quaternary fauna is presently based almost exclusively on radiocarbon determinations. The absence of suitable organic remains at some sites, allied with issues of potential sample contamination and the practical upper limit of 40 kyr for radiocarbon dating, has prompted the application of optically stimulated luminescence (OSL) methods of dating fauna-bearing sediments. In this presentation, we shall outline the principles behind OSL dating and describe some recent results from late Quaternary palaeontological sites in the North and South Islands. At the most recent end of the time scale, sites containing the remains of *Rattus exulans* have been investigated, to determine the timing of arrival of this commensal species and to help resolve the current dispute over the reliability of AMS radiocarbon dating of bone gelatin.

Megafaunal extinctions: the Pleistocene lakes of western N.S.W.

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The Pleistocene lunettes on the lakes of western N.S.W. contain some of the oldest Aboriginal sites in Australia as well as the fossils of both extant and extinct animals. The Menindee and Willandra Lakes lie along palaeochannels of the Darling and Lachlan Rivers respectively, but Lake Victoria has always been connected with the Murray River. The lunettes formed on the eastern shores of the lakes as sands and clays blew off the lake beds under different climatic regimes; soil horizons mark stable lake conditions. The lunette stratigraphy is distinctive and accessible, and organic materials preserve well. Even so the relationship between the megafaunal remains and the archaeological sites is as ambiguous here as it is elsewhere in Australia.

The best record is at Tandou lunette where a marker soil horizon separates fossil-bearing older sediments from archaeological younger sediments. The few extinct taxa in the younger units are attributed to reworking, and some archaeological material seems to be older. The soil is bracketed by dates of 27 kyr and 34 kyr (Hope *et al.* 1983). In contrast the Willandra lunettes are characterized by the rarity of extinct species even in the 30-40 kyr units, where archaeological sites are common. Finally, in the massive Lake Victoria lunette the oldest dated archaeological sites, only 17 kyr, are restricted to the higher levels. It was suggested that the megafauna here were also this young, but new TL dates, from a study on lake shore erosion, have pushed the lunette sediments back to at least 40 kyr (Chen 1992, 1995). One TL sample dated at 31.9 kyr originated from near a 'giant kangaroo bone'.

There has been no other new research on these sites, but the results so far suggest that there were both megafauna and Aboriginal people living in western N.S.W. in the range 30-40 kyr, and the question of their association merits further attention. The current Lake Victoria Project commenced in 1994 to conserve major Aboriginal burial grounds. Related archaeological research shows that the lake was an important centre of Aboriginal occupation in the late Holocene, but no new work has yet been done on the lunette.

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Life history parameters and their effects on the survival of mammals during periods of environmental change *

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The complex, pulsatory environmental changes of the Pleistocene Epoch produced high levels of stress in the biotic communities of the nontropics. During this time, the distributions of most large-bodied, mammalian taxa changed markedly and many taxa became extinct. Examination of the patterns of distribution for five catarrhine genera (*Gigantopithecus, Pongo, Hylobates, Macaca,* and *Rhinopithecus*) during the Pleistocene and Holocene in China indicated that the geographical ranges of individual genera shifted independently of one another in response to conditions of increasing seasonality. The differences in patterns of response to environmental change demonstrated by the various catarrhine genera are of great interest because of their ultimate origins in the biology of those genera. It is now widely recognized that changes in patterns of climatic seasonality have profound effects on animals and especially on those mammals like primates with long generation times and energy- and time-intensive modes of raising offspring.

All genera examined saw their distributions shift southward, with the shifting subtropical and tropical zones, during the Pleistocene. This occurred earlier in the Pleistocene for the larger apes, and later for smaller forms. This apparent paradox is readily explained by the inability of large-bodied apes to satisfy the high metabolic demands of a relatively large brain as well as those of an absolutely larger body. The extinction of *Gigantopithecus* during this time epitomizes this problem. Monkeys were somewhat less affected and their greater relative success is attributed to their abilities to survive in more highly seasonal environments by exploiting a wider variety of plant foods and to produce offspring more quickly, thanks to shorter gestation times and shorter interbirth intervals. The pattern of re-radiation of catarrhine primates from tropical refugia into subtropical and temperate environments of East Asia during the Holocene was also strongly influenced by the life history parameters and the intrinsic rate of population increase of the species involved.

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Environmental change during the Quaternary in East Asia and its consequences for mammals *

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Environmental change has been viewed as one of the most potent influences on organismal evolution, but the establishment of clear cause-and-effect relationships between environmental change and organismal response has been difficult, particularly with larger, long-lived vertebrates. The nature and magnitude of environmental change necessary to cause a noticeable reaction in a population will depend on a large number of factors related to the reproductive success of the organisms in that population. The reaction, when it occurs, may be spatial — causing the population to move from a less favourable to a more favourable environment — physiological, or both. The absence of a reaction, for whatever reason, could lead to extinction of the population.

The most dramatic and best documented environmental changes experienced by terrestrial mammals in recent geological history occurred during the Pleistocene. In eastern Asia, Quaternary climate change was influenced not only by the same Earth orbital parameters which affected all global environments, but by the potent local influence of the then newly elevated Qinghai-Xizang (Tibetan) Plateau. The most important consequences of these changes for mammalian populations were marked increases in environmental seasonality at all latitudes, increasing environmental heterogeneity and fragmentation, and an increasing potential for physical isolation of populations as a result of habitat fragmentation and changes in the configuration of biogeographic corridors.

In the present study, the changes in distribution of selected groups of medium- to large-sized mammals for the Pleistocene of East Asia were examined and the reasons for these changes were explored. Visualization and analysis of these changes were conducted using a geographical information system (GIS). Using GIS, it was possible to test hypotheses of species co-occurrence as well as examine relationships between species' distributions and environmental characteristics. The study involved, firstly, the construction of time-specific palaeoenvironmental maps on which changes in the position of environmental zones, loess cover, glacial cover and sea level were plotted. These maps were then integrated with data on fossil mammal occurrences from a specially created Eurasian Fossil Mammal Database in order to produce time-specific plots of mammalian distributions relative to the environments of the time. Emphasis was placed on the examination of trends in the distributions of catarrhine primate taxa, including hominids, and on examination of changes in the spatial relationships of hominids to other mammalian taxa. The study revealed that significant shifts in distribution occurred for most mammalian taxa, and that these shifts could be explained in terms of the life history parameters of the species concerned.

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New Rhizodontida (Sarcopterygii) from Canowindra, N.S.W. *

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The sarcopterygian portion of the Upper Devonian fish fauna from near Canowindra, NSW, is dominated by "Osteolepiformes", with one canowindrid and two tristichopterid taxa. The identity of a fourth sarcopterygian, known until recently from only a single skull, has been more problematic. Within the last year, several new specimens have been discovered, including a second skull, pectoral fins in which the lepidotrichia have long unjointed proximal segments, and a cleithrum with a proportionately short dorsal lamina. This latter specimen has proved to belong to the same individual as the first skull. The materials indicate that the "fourth sarcopterygian" is a member of the Rhizodontida. It probably occupies a basal position within the Rhizodontida clade, as the unbranched basal parts of the pectoral fin lepidotrichia are proportionately shorter than in other rhizodonts, and the dorsal lamina of the cleithrum lacks a posterior flange and is of equal width throughout its length. Most Rhizodontida are Carboniferous in age; older taxa are known from the Late Devonian of North America and Turkey, the Grenfell region of N.S.W., and now from Canowindra, while the oldest rhizodontiform is *Notorhizodon*, from the Givetian of the Antarctic. The phylogenetic position of the Australian and Antarctic forms relative to more derived Northern Hemisphere taxa assigned to the Rhizodontidae (*Screbodinus, Rhizodus, Strepsodus*) provides additional evidence supporting earlier suggestions that the Rhizodontida arose on the eastern Gondwanan landmass.

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Cretaceous sharks and palaeoenvironments of the Eromanga Basin in Queensland

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Further studies on the sharks teeth collected from the Rolling Downs Group have allowed for a considerable refinement of earlier identifications e.g. from about eight lamniform taxa to more than a dozen lamniform genera. More than two dozen taxa in all have been identified representing Hexanchiformes, Squaliformes, Heterodontiformes, Orectolobiformes, Lamniformes, Carcharhiniformes and Rajiformes.

Hundreds of teeth of pelagic taxa from the earliest Late Albian Toolebuc Formation reflect a normal nekton. New, rare finds of a few bottom-dwelling taxa (two or three genera of orectolobiforms) do not change the overall picture, shown also by the invertebrates, of a normal, well-oxygenated water column with hypersaline bottom conditions and an oxic-anoxic interface at, or very near, the water-sediment boundary. The Bramble Shark, *Echinorhinus*, represented by thousands of teeth, is the most common elasmobranch in the Toolebuc. Extant species are considered sluggish bottom dwellers. The late Albian *Echinorhinus* was perhaps more tolerant of the low oxygen-higher salinity bottom waters or was a predator on the numerous belemnites and other invertebrates, as well as teleosts, some of which could have become easier prey when they strayed into the bottom water and became partially asphyxiated.

New seaways opened in the Late Albian, producing diferent circulatory patterns resulting in normal conditions with an *Echinorhinus*-poor fauna but with a good representation of benthic as well as pelagic elasmobranchs.

Dinosaurs of Italy

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Dinosaur tracks and bones have only recently been discovered in Italy. Italian Mesozoic geology was previously seen as mainly marine. A small Upper Carnian dinosaur footprint from the Quarziti Viola Zonate Formation (Monte Pisano, Pisa) was described by Huene (1941) as *Coelurosaurichnus*, but it is probably *Grallator* sp. (Leonardi and Lockley 1995). A number of small dinosaurian tracks (Ceratosauria, Prosauropoda, Ornithischia) was recently discovered at Lerici (La Spezia; Norian) and is under study. A lowermost Norian tracksite consisting of about 100 dinosaur footprints was found on a layer of stromatolitic dolomite (Dolomia Principale Formation) at Mt Pelmetto (Dolomites, Belluno). Four of the trackways are attributed to small Ceratosauria; one to an ornithopod; another one to a prosauropod (Mietto 1988). Other Norian dinosaur tracks, mainly ceratosaurian, have been found in the same Dolomites region at Monte Tre Cime di Lavaredo and Monte Averau (Belluno), at Monte Puez (Bolzano) and in the Cellina Valley (Pordenone). The richest Italian track site is that at Lavini di Marco, about 40 km S. of Trento. In the Calcari Grigi Formation (carbonate platform) the tracks of more than 200 dinosaurs occur in a Sinemurian level. About 100 are ceratosaurian; 15 are sauropodian; 12 are ornithopodian; 10 large iguanodontid-like tracks are rather puzzling (Leonardi and Lanzinger 1992). Tracks of bipedal dinosaurs, mainly Ceratosauria, were also discovered in other sites in the same formation at Chizzola (Trento; Sinemurian) and at Bella Lasta (Revolto, Verona; Pliensbachian). Some probable carnosaur tracks have been found in the Cellina Limestone Formation of the Cansiglio Plateau

(Pordenone; Hauterivian); other poorly-preserved bipedal tracks are known from Monte Bernadia (Nimis, Udine; Aptian).

Dinosaurs bones are quite rare in Italy. A tiny skeleton (tailless, 25 cm long) of a juvenile maniraptoran coelurosaur was found at Pietraroia (Benevento) in the Lower Albian "Calcari ad Ittioliti" Formation (Leonardi and Teruzzi 1993). Unpublished bone material of Hadrosauria was recently found at Duino (Trieste).

The discovery of so many tracks and bones of dinosaurs and other reptiles since 1984, mainly from tidal flat environments, started a major debate, changed the ideas on Italian palaeoenvironment and palaeogeography, and created a difficult dilemma. On the one hand, the occurrence of so many dinosaurs, sometimes gigantic for their time, and other reptiles, in so many formations and sites, ranging all the way from Upper Triassic to Upper Cretaceous, demonstrates that in Mesozoic times Italy was more frequently and extensively above sea-level than geologists had previously believed; and the presence of an abundant animal biomass suggests an even more abundant biomass of vegetation. On the other hand, tidal flats are not the ideal environment for such vegetation. In fact, there is little indication of plants associated with the tracks found to date.

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Eurasian mammoth evolution, specialization and extinction

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The earliest fossils assigned to the mammoth lineage are *Mammuthus subplanifrons* of south and east Africa, at about 4.5 Myr. In the range 3 - 2.5 Myr, the first mammoths appeared in Europe, as *M. meridionalis.* A lineage can then be traced in Europe from the Early Pleistocene *M. meridionalis* to the Middle Pleistocene *M. trogontherii* to the Late Pleistocene *M. primigenius.* These species show a trend of increasing specialization to the cold, open steppic habitats which came to predominate over much of northern Eurasia as the ice ages intensified. Some of the clearest trends are seen in the dentition, where there is a sequential increase in the number of enamel lophs, and heightening of the tooth crown: both tripled from *M. subplanifrons* (8 lophs) to *M. primigenius* (24 lophs). These dental changes can be correlated to a transition from a temperate, wooded habitat, where the main food was browse, to an increasingly open habitat where abrasive grasses formed the staple, with concomitant stress on the dentition.

M. trogontherii, the 'steppe mammoth', is the European species intermediate in many ways between *M. meridionalis* and *M. primigenius.* It has generally been recognized only from the pre-Anglian/Elsterian deposits of the Cromerian Complex (c. 700-500 kyr), and was a very large animal with 17-22 lophs in its M3. Conversely, mammoth fossils from late Middle Pleistocene interglacials postdating the Anglian glaciation (400-200 kyr), have been regarded as early *M. primigenius.* This has been based, in part, on their higher lamellar frequency (LF, the number of lophs in 10 cm of tooth length) than typical *M. trogontherii.* However, these animals were also smaller in size than Cromerian *M. trogontherii,* so their molar lophs were compressed together, raising LF artificially, while total loph number, the true index of evolutionary level, was virtually unaltered. They were probably small, late survivors of the *trogontherii* lineage.

In other Late Middle Pleistocene deposits, including those from colder intervals, genuinely more advanced mammoths, with distinctly higher loph numbers, are found, and may be referred to true *M. primigenius* (woolly mammoth). By the Last Cold Stage, and possibly earlier, the more primitive *trogontherii*-like mammoth had disappeared, and only the *M. primigenius* remained. There is evidence from some localities that the two types of mammoths may have co-existed for a period, implying that they were distinct species, and work in progress suggests that the *M. primigenius* type may have immigrated from Siberia, replacing the resident *M. trogontherii* populations in Europe (Sher and Lister, in prep.).

One of the common objections to the climatic theory of Late Pleistocene megafaunal extinction is encapsulated in the question 'Why did the large mammals become extinct only at the Pleistocene-Holocene boundary, and not during earlier climatic cycles?', often answered with 'Because Man's hunting influence was insignificant until the latest Pleistocene'. For European mammoths at least, the above data suggest an alternative contributing factor. The mammoths of earlier interglacials retained 'primitive', *trogontherii* features, and were not fully adapted to the ice-age habitat and so did not become extinct at the onset of interglacial conditions, and indeed are found in temperate contexts. They died out, however, either as a result of severe cold phases or by introgressive hybridization with the more specialized woolly mammoths. The latter, conversely, became so tied to the cold, steppic environment that they were unable to survive the transition to the Holocene, and the interglacial mammoth was no longer available to take its place.

Adaptive specialization is therefore suggested as a contributing factor to mammoth extinction, but does not explain the extinction of the many other large mammals around the world at about the same time. This indicates that although it is quite valid to search for general causes of global impact, the total extinction phenomenon may be very complex, with individual factors being important for particular species and/or areas.

Large mammals endemic on offshore islands: evolution, dwarfing, and extinction

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Reduction in body size of large mammals on offshore islands is a common phenomenon in the Pleistocene. Until recently, very little was understood about the rates and modes of this process, chiefly because the island faunas were very poorly dated. However, refinements in dating and stratigraphy now allow us to plot the origin and fate of some island endemics. In this paper, two contrasting examples of dwarfing among deer in Europe will be explored.

Red deer (*Cervus elaphus*) became dwarfed on the island of Jersey in the English Channel, in the Last Interglacial, *c.* 120 kyr. A consideration of sea-level changes shows that the deer had only a few thousand years to become dwarfed during the island's isolation from the mainland. In deposits preceding and following this episode, normal, large-sized deer are found on the 'island'. The deer show an estimated sixfold weight reduction, but few if any other adaptive changes; for example, distal limb-bones are not shortened. But some automatic developmental effects of size reduction, such as an increased tooth to body size ratio, are seen. Antlers are stunted but not fundamentally altered from the red deer pattern. There is no reason to regard the Jersey dwarfs as other than a subspecies of red deer (*C. e. jerseyensis*).

This contrasts with the situation on Crete, where a series of endemic deer of the genus *Candiacervus* was studied by de Vos. Here the island was isolated throughout the Pleistocene, and the endemic deer evolved over several hundred thousand years. Some, such as *C. ropalophorus*, were dwarfed. This species shows not only size reduction, but also fusions of tarsal bones and shortening of metapodials — regarded as adaptive to the island habitat. Tooth to body size ratio has returned to the 'normal' condition for deer. Most interestingly, the deer evolved unique antler structures, suggesting a novel specific mate recognition system and therefore that the endemic form was a new species.

These examples suggest a two-stage process for the origin of island dwarfs. In the first stage, taking a few hundred or thousand years, there was a strong selective pressure for size reduction, probably because of resource limitation. This was accompanied by directly linked allometric and other developmental effects, such as distorted tooth to body size ratio, and stunted display organs. The endemic did not become truly speciated from its mainland ancestor. In the case of the Jersey deer, the island was soon re-joined to the mainland, and full-sized deer took over the island. The endemic form was lost, a form of 'extinction' due presumably either to competition from, or introgressive hybridization with, the mainland animals. It is appropriate to speak of the 'extinction' of a subspecies, but the phenotype may be lost by gene flow rather than by termination of the lineage.

If the dwarf survived long enough, the second stage of its evolution proceeded, exemplified by the Cretan deer. Natural selection produced adaptive changes, both adjusting the development and structure of the animal to retain 'internal' integrity (e.g. producing normal tooth to body size ratio), and readapting it in terms of function to the outside world (e.g. locomotory adapations to the island habitat). During this stage also, speciation often occurred, exemplified by novel antler structures. The mainland progenitor of *Candiacervus* is uncertain.

The Cretan deer were more robust to extinction than those of Jersey for several reasons. Their island remained isolated through climatic cycles, inhibiting the immigration of congeners or other competitors; the species had become adaptively suited to their island habitat; and even if there were further immigrations from the mainland, gene flow was limited or absent. The diversity of Cretan deer decreased though the Late Pleistocene, but the last species did not become extinct until into the Holocene, perhaps as a result of human arrivals.

Splendid isolation: geographic, taxonomic and temporal patterns of range collapse in animals

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The study of patterns of range collapse is an especially interesting and important topic for those attempting to understand recent extinctions and minimize extinctions in the near future. Given that species and their component populations vary non-randomly across geographic, taxonomic and temporal dimensions, we expect them to exhibit non-random patterns of range dynamics as they become increasingly more rare and eventually extinct. For example, because population densities of most animals tend to be highest and more stable near the centres of the species' geographic ranges, biogeographers and other ecologists predicted that geographic ranges should collapse inward, with the last remnant populations persisting near the centre of the range. Based on this and related assumptions, some conservation biologists have recommended that re-introductions and surveys for remnant populations of endangered species be restricted to the core of the species' geographic range, while the range periphery was often viewed as the domain of 'zombies', the 'living dead', with little value for conserving the species. Contrary to these assumptions, we have found that for a variety of animal taxa, range collapse tended to be towards the periphery, with remnant populations persisting along the edge of the species' geographic ranges. Variation in patterns of range collapse among geographic regions and taxa, and sequential trends from initial contraction to final collapse and extinction, are consistent with a 'contagion' hypothesis. That is, an overwhelming majority of recent extinctions resulted from anthropogenic forces which tended to spread across the landscape like a contagion. The last populations to suffer extinctions were the most isolated ones: i.e., those on true islands, isolated montane regions, or along the edge of the species' geographic range.

A primitive new coelacanth (Osteichthyes; Actinistia) from the late Middle Devonian of Mt Howitt, Victoria

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The Devonian fishes of West Gondwana: new discoveries from South Africa *

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Devonian fish remains, spanning the Emsian to Famennian, have been reported from South Africa (West Gondwana), yet scant reference to the material has been cited in the literature. Recent explorations have focused on Middle (Givetian) freshwater and Late (Famennian) estuarine sites in the south and west of the country. The Emsian material is scarce, consisting of fragments of an antiarch, an elasmobranch and an acanthodian. The Givetian ichthyofauna is characterized by a high proportion of sharks to placoderms and no agnathans, actinopterygians or dipnoans, and only a single crossopterygian (*Onychodus* sp.). The better-explored brackish Famennian has a high diversity of endemic forms, and at higher taxonomic levels is comparable with that of the slightly earlier Mount Howitt site, reflecting the cosmopolitanism of freshwater fish distributions in the Late Devonian. The Givetian, however, in its diversity of sharks, comparable to that of the Aztec Siltstone of Antarctica, and its absence of thelodonts, antiarchs and major sarcopterygian groups, is interpreted as an uncharacteristic assemblage unaffected by cosmopolitan distributional trends occurring at the time, which is probably a high-latitude effect.

* See also pp. 157–168 in this volume.

Climate models for Pleistocene extinction of megafauna

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Cause(s) of Pleistocene megafauna extinction has been a contentious issue for decades. Principal explanations are human predation and climate change (Martin and Klein 1984). A diverse array of models is grouped under the broad umbrella of climate change, and range from effects of greater seasonality on reproductive success (Kiltie 1984) to various implications of vegetational reorganization, habitat destruction (Graham and Lundelius 1984) and reduced nutritional value of plant resources (Guthrie 1984).

Temporal coincidence must be demonstrated before any mechanism can be considered as a cause, but temporal correlation cannot be used as proof unless it is the only mechanism restricted to the time of extinction. In North America the megafaunal extinction between 11,200 and 10,800 radiocarbon years before present overlaps with both human predation and climate change (Haynes 1991). In Australia, climate change and human colonization are diachronic, but the timing of the extinction event is currently uncertain (Flannery 1990).

One major problem for climate models has been the lack of extinctions associated with previous glacial/interglacial fluctuations. However, Webb (1984) has shown a high correspondence between climate change and lesser extinctions in the early-middle Pleistocene and more massive ones in the late Tertiary of North America. Also, Wood and Barnosky (1994) have documented that earlier glacial/interglacial cycles did not result in significant changes in the species composition of faunas, although relative abundances of environmentally sensitive species were altered. In other words, these faunal and environmental fluctuations are not the same as those at the Pleistocene/Holocene boundary.

A new model invoking natural habitat destruction and reduction in geographic distributions (Graham *et al.* in press) satisfies many of the criticisms of older models. Uniqueness of the Pleistocene/Holocene climate change is not a factor in this model because once geographic ranges are reduced to a critical size, then any major climate change can serve as a trigger. The rapid climate changes of the Bølling/Allerød and Younger Dryas are temporally concurrent with the extinction. Also, since home range is a function of body size, reduction in geographic range would select for the extinction of larger species. Reduction in distribution also makes populations more vulnerable to stochastic processes such as disease, drought, and fire which would suggest that extinctions were caused by a multiplicity of factors, but climate change would have been the primary driving force. Finally, this model can be refuted since it predicts shrinking geographic ranges throughout the Pleistocene.

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The role of heterochrony in vertebrate evolution

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Heterochrony can be defined as changes to the rate and/or timing of development between ancestor and descendant. By increasing the rate of growth (acceleration), or extending the period of growth by terminal extension (hypermorphosis), or by earlier onset of growth (predisplacement), peramorphic descendants are produced. By decreasing the rate of growth (neoteny), or contracting the period of growth by premature offset (progenesis), or by a delay in onset of growth (postdisplacement), paedomorphic descendants are produced.

Heterochrony can be regarded as the 'missing link' in evolutionary theory between natural selection and genetics, for without it the 'neodarwinian synthesis' is incomplete. The renaissance in studies of heterochrony in both extant and extinct vertebrates over the last two decades has revealed that heterochrony is a very important, but much neglected, aspect of evolution.

Heterochrony provides the raw material for natural selection to work on. It plays a critical role in the generation of intraspecific variation. Breeds of domestic dog are an excellent example. Recent research has highlighted that many organisms are the product of dissociated heterochrony, some traits being paedomorphic, others peramorphic. Many examples of sexual dimorphism, in particular those where there are size differences, are the product of differences in either growth rate or maturation times between sexes. Examples will be discussed in fishes and mammals.

A number of recent studies has shown that there is often a close relationship between heterochrony and life history strategies. Thus, for example, in cases where species are predominantly paedomorphic, did selection target the juvenile ancestral morphology *per se*, that was retained into the descendant adult; or did it target the smaller size, perhaps as an antipredation strategy; or was some other aspect of life history being selected for, such as rapid reproduction, again perhaps, as a means of minimizing predation pressure?

In the 1900s recapitulation was the flavour of the century, articulated by Haeckel in his 'Biogenetic Law', as "ontogeny recapitulates phylogeny". However, during this century recapitulation became a dirty word. Now that we call it peramorphosis it is once again respectable. Peramorphosis has played a very important role in the evolution of major groups of vertebrates, in particular dinosaurs and humans.

Many organisms, however, are an evolutionary cocktail of both paedomorphic and peramorphic features, such as flightless birds. Long touted as examples of the all-pervasive force of paedomorphosis (well they have such pathetic wings, don't they?), I re-examine them in the light of recent advances in heterochronic studies, to show that they are a classic evolutionary cocktail of paedo- and peramorphic features, which arise from tightly constrained developmental trade-offs — wings reduce in size and complexity, but body size and legs increase.

Heterochrony can also play a critical role in the evolution of major morphological novelties. One of the most significant to vertebrates is the evolution of digits in tetrapods. Heterochrony was likewise significant in the evolution of birds, pterosaurs and bats, as well as in the evolution of vertebrates themselves.

Amongst some of the more fascinating studies of heterochrony in the last few years are those linking heterochrony and the evolution of behavioural changes. Recent work on bird song, bird nesting behaviour and domestic dogs, is highlighting the fact that behaviour is the target of selection, just as much, or in some cases more so, than shape, size or life history strategy.

The effect of heterochrony can be seen not only in descendant adults. A much-neglected aspect of heterochronic studies is its operation throughout development. This can be seen in extensions or contractions to ontogenetic growth stages, inducing changes to preadult life history strategies and behaviour, as well as in the evolution of major morphological novelties. Known as 'sequential heterochrony', examples of this are illustrated in lampreys, that classic example of "neoteny" — the axolotl, and in hominid evolution.

Heterochrony has been an all-pervasive, though largely neglected, influence in vertebrate evolution. Its renaissance as an integral part of evolutionary theory is long overdue.

The chronological and palaeoenvironmental context of megafaunal extinction at Lake Eyre

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H.Y.L. Brown first found vertebrate fossils in the Lake Eyre Basin in 1894, followed soon after by the famous Gregory expedition. In the century that followed, great strides were made, particularly since the 1950s, in elucidating the late Cainozoic stratigraphy, palaeoenvironmental history and vertebrate fossil record of the basin (Tedford and Wells 1990). What has been lacking is an absolute chronology, particularly for the Katipiri Formation which includes the last major lake-full phase and the youngest megafaunal remains.

The application of luminescence (TL and OSL), thermal ionization mass spectrometry (TIMS) uranium series, amino acid racemization (AAR) and accelerator mass spectrometry (AMS) radiocarbon dating techniques has allowed a detailed reconstruction of the past 130 kyr (kyr = 1000 years) of Lake Eyre stratigraphy (Magee *et al.* 1995; Croke *et al.* 1996; Magee and Miller in press). Several lake-full phases, indicating a more effective monsoon rainfall regime, are separated by dry episodes which are marked by saline groundwater-controlled deflation. The wettest phase was apparently between 130 and 110 kyr followed by two successively less effective lake-full events (100 to 80 kyr and 70 to 60 kyr). During these wet phases, enhanced fluvial activity in the Cooper and Diamantina systems deposited the Katipiri Formation and its contained megafaunal assemblage (Tedford and Wells 1990). A major deflation event excavated the present playa-lake basin between 60 and 50 kyr and dunes deposited during this deflation episode contain abundant *Genyornis* eggshell (Miller *et al.* this conference). Between 50 and 35 kyr the evidence is equivocal as to lacustrine conditions but a perennial lake existed at close to playa levels at about 45 kyr. There is strong evidence that the lake was dry from about 35 to 12 kyr. A minor lacustrine event early in the Holocene was followed by establishment of the modern ephemeral regime at about 4 to 3 kyr. No megafaunal remains younger than about 45 kyr are known from the Lake Eyre region.

The application of multiple dating techniques to the Lake Eyre stratigraphy has allowed the possibility, perhaps for the first time in Australia, of relating the fossil record of a region to a well dated palaeoenvironmental record. This is a fundamental step towards elucidating the biostratigraphy of the region, understanding the evolution of the continent's fauna and unravelling the timing and causes of megafauna extinction.

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The late Pleistocene palaeoavifauna from Minatogawa, Okinawa Island: implications for avifaunal change in the Ryukyu Archipelago

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The Ryukyu Archipelago is an island arc stretching south-west from the main Japanese islands to just east of Taiwan. Numerous vertebrate fossils, including human remains, have been recovered from fissure fill deposits, radiocarbon dated at 18,250 ± 650 and 16,600 ± 300 yr BP, from the village of Minatogawa, in the southern part of Okinawa Island (Suzuki and Hanihara 1982). So far, 15 species of birds (representing 9 families in 7 orders) have been identified by the author in the fossil assemblage. Some species identified among the fossils do not inhabit the southern part of Okinawa today. For example, *Garrulus lidthi*, the Purple Jay, presently occurs only on Amami-Oshima Island, 150 km to the north of Okinawa, but in the late Pleistocene its range extended as far south as Minatogawa. *Rallus okinawae*, an almost flightless rail, is recognized in the fossil assemblage, but it is restricted at present to the mountainous area in the northern part of Okinawa. The present distribution of these species might have been a result of palaeoendemism (i.e. they are relict species left by the extinction of their close relatives).

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Dry-preserved dung and the Pleistocene extinction record of the arid southwest U.S.A.

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Certain dry caves in arid America have yielded unusual perishable remains of extinct Pleistocene (Rancholabrean) mammals. Beyond their significance as palaeontological curiosities, the perishable remains provide high quality organic specimens for radiocarbon dating and microbotanical analyses. Although dry and semi-dry caves containing dry-preserved remains are known from many states, the Colorado Plateau provides a unique habitat for such deposits, found there in greater abundance than anywhere else in North America. Over 20 localities from the Colorado Plateau contain dung of megaherbivores. Besides the dung record of rodents and lagomorphs (including *Ochotona*), seven species of megaherbivores are recorded: *Bison* (bison), cf. *Equus* (horse), cf. *Euceratherium* (shrubox), cf. *Camelops* (camel), *Mammuthus* (mammoth), *Nothrotheriops* (ground sloth), *Oreamnos* (mountain goat), and *Ovis* (bighorn sheep). A recent analysis of 79 radiocarbon dates on dry-preserved remains provides a review of the extinction process. Although *Bison* and *Ovis* avoided extinction and local extirpation, dung remains of *Mammuthus*, *Oreamnos harringtoni*, *Nothrotheriops*, and *Euceratherium* became absent from the caves (and the animals assumed extinct) sometime between 11,800 and 11,000 radiocarbon years ago (using weighted averages of youngest ^{14}C dates). Additional detailed radiocarbon dating of new dung finds should help determine if all megaherbivores became extinct during this same interval (an event) or if there was a temporally different die-off of taxa during the late glacial (a process). A rapid climatic change and the arrival of humans have been proposed as the culprits; both are a possibility. Such dry-preserved organic remains, and therefore a detailed record of biology and chronology, should be recoverable in arid and semi-arid regions of Australia, central Asia, and South America.

Application of amino acid racemization in avian eggshell to the timing and cause of Late Pleistocene megafaunal extinctions *

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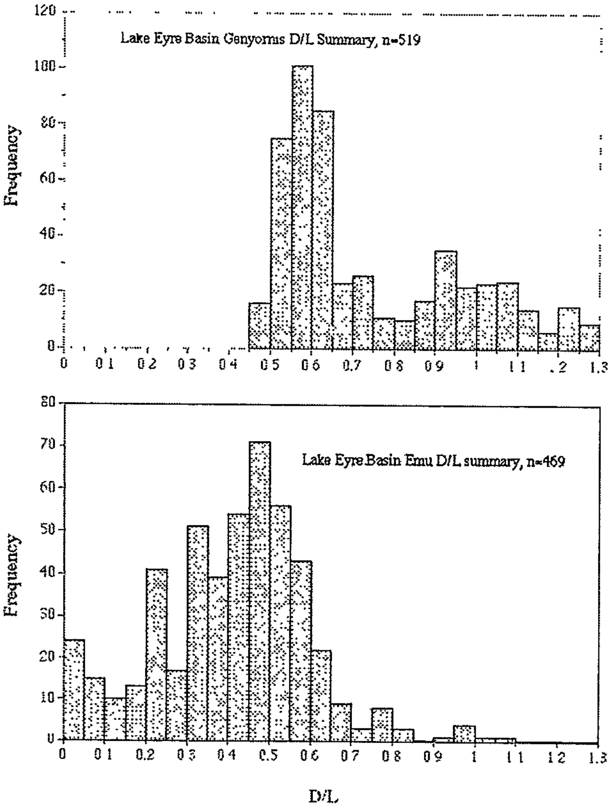
The conversion of indigenous protein amino acids preserved in carbonate fossils to an equilibrium mixture of D- and L- forms has been applied to Quaternary geochronology and palaeothermometry for more than 40 years. Protein contained within carbonate biominerals consists exclusively of L amino acids, which undergo a systematic inversion to their D configurations at a rate that is primarily dependent on the diagenetic temperature. Although most early applications utilized molluscan fossils, the intracrystalline incorporation of amino acids in avian eggshells results in a much closer approximation to a true closed system. Following initial studies on eggshells of the African Ostrich (*Struthio camelus*), we have evaluated the epimerization of isoleucine in eggshells of the Australian Emu (*Dromaius novaehollandiae*), various waterbirds (mostly Pelican) and the extinct giant Mihirung, *Genyornis newtoni*. Mathematical descriptions of reaction kinetics allow us to calculate sample age or effective diagenetic temperature from the D/L ratio if either is known. Calibration of the reaction using paired AMS ^{14}C dating and D/L measurements has provided quantitative estimates of palaeotemperatures for the past 50 kyr in the Lake Eyre and Lake Victoria regions, suggesting Pleistocene temperature reductions of 8 to 10°C.

Figure 1



Extinction events can be evaluated for the Lake Eyre and Lake Victoria regions by plotting the frequency histograms of D/L ratios in *Genyornis* and *Dromaius* eggshell (Figure 1). The frequency distributions are controlled by 1) the number of birds nesting, 2) the potential for preservation of the eggshell (requires rapid burial), and 3) the potential for exposure of the eggshell-bearing sedimentary unit. Of these factors, 2) is the most significant. Both birds appear to have nested in similar environments; their eggshells commonly co-exist in fossil localities. From the Lake Eyre region, more than 500 different fragments of *Genyornis* eggshell have been analyzed. They indicate common nesting of the birds in the region through the Late Pleistocene until a sudden and complete disappearance event that occurred at about the limit of ^{14}C dating. No radiocarbon dates on *Genyornis* eggshell younger than 36 kyr have been obtained, but the eggshells are common in dunes luminescence dated to 50 kyr. In contrast, *Dromaius* eggshell (nearly 500 fragments) is common both before and after the *Genyornis* extinction event. A similar pattern occurs for the Lake Victoria region, although the dataset is smaller. The *Genyornis* extinction also occurred at least 35 kyr ago, whereas *Dromaius* continues to the present day. Furthermore, preliminary work strongly suggests that in the Willandra Lakes, *Genyornis* occurs in sediments of Lower Mungo age (older than 36 kyr), but is absent from younger units, whereas *Dromaius* occurs throughout.

Roughly coincident with the extinction event, the proportion of C3 and C4 plants in the diet of both

Dromaius and *Genyornis* around Lake Eyre shifted from dominantly C4 to dominantly C3 vegetation, a shift we interpret to indicate weakening of the summer monsoon and consequent reduction in grass, whereas Lake Victoria eggshell reflects continuous domination by C3 dietary intake and that the region was never within the influence of the monsoon. The simultaneous disappearance of *Genyornis* in two distinct climate regions suggests an aclimatic cause.

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Pleistocene fauna and taphonomy at Ned's Gully, eastern Darling Downs, Queensland

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In winter 1990 a major Pleistocene vertebrate site was discovered on the eastern Darling Downs. The site is near the head of Ned's Gully, which joins King Creek east of Clifton. The recovery of diprotodont skulls and articulate remains, and a semi-articulate macropod skeleton is extremely unusual for the eastern Downs. Associated wombat and rodent remains were also found, but further excavation produced nothing else so presumably all specimens present were collected. This allows a superb opportunity for taphonomic study. The remains were concentrated in an area of 11 square metres of muddy sediments overlying a cemented cobble bed. The presence of large (diprotodont) and small (rodent) elements suggests that there was no size bias in accumulation or preservation of the bones, and together with the occurrence of articulate remains, no transportation. The specimens indicate no scavenging. The absence of significant numbers of freshwater shells or aquatic vertebrates indicates the gully was not a permanent water course, but probably an overbank flood channel. Carbonate nodule beds higher in the section were interrupted just where the remains occurred. Slumping of an unstable gully wall could account for the preservation of the Ned's Gully specimens.

Three decades of dating of Victoria Cave Fossil Chamber, Naracoorte: pitfalls in dating a pitfall

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The Naracoorte Caves formed in the Pliocene and Early Pleistocene and have been isolated from erosion and stream flow since uplift of the limestone more than 500 kyr BP. The remarkable bone deposits have therefore been subjected to minimal reworking, largely caused by runoff water flowing through the pitfall entrances and redistributing sediments from the cones onto distal fans as in the Fossil Chamber of Victoria Fossil Cave. Within the Fossil Chamber several stratigraphic units can be correlated between the various pits with confidence. Since discovery of the Fossil Chamber in 1969 there has been a continuous increase in the dates obtained from the bone deposits. For the first decade (1970s) radiocarbon dating of charcoal, bone apatite and collagen suggested an age of less than 35 kyr, i.e. in the latest Pleistocene, and this is still quoted in references. Some preliminary (and doubtful) amino-acid racemization dating of bone in the late 1970s suggested the upper layers of the deposit contained bone older than 50 kyr, but this could be explained by reworking of older bone. In the 1980s new U/Th dating techniques on bones suggested a minimum age of around 100 kyr. New developments in the U/Th dating of speleothems also allowed the determination of reliable ages for flowstone bracketed bone deposits in the adjoining Grant Hall. This demonstrated that bone dates were greatly understating the real age and that this small deposit, which is similar in lithology and fauna to the Fossil Chamber, accumulated sometime between 220 and 73 kyr. In the mid 1990s, preliminary luminescence dating of the associated quartz in the bone deposits indicated surprisingly older dates for the Fossil Chamber: 297 ± 122 kyr near the surface and 172 ± 75 kyr in the lower sequence. The most reliable and accurate dating method is on speleothem material but the Fossil Chamber lacks significant formation. Bracketing flowstone was not discovered until 1995 when a thin flowstone layer was excavated from within a small sediment cone under a solution tube in the roof of the chamber. Further excavation to expose the stratigraphy indicates that the cone is superimposed on, and therefore postdates, all other layers in the deposit. U/Th TIMS dating of the flowstone and stalactites on the roof above resulted in dates of ~213 ± 8 kyr and ~212 ± 5 kyr. Therefore all material in the cave fills had to have accumulated at least 205,000 years ago. ESR dates on large *Zygomaturus* teeth from upper and lower sequences — equivalent to the OSL dated samples — indicate dates of 321 and 326 ± 17 kyr for the lower part of the deposit and from 161 ± 13 kyr to 337 ± 30 kyr (four teeth) for the upper deposit. Apart from confirming a Middle Pleistocene age for the Fossil Chamber, the results suggest mixing of bones into the upper part of the deposit, probably by reworking of older sediments. This can be tested by more dating from all levels. We are attempting to re-measure the radiocarbon dates on new samples. While some of the early dates may have analytical error, some of them are probably correct and we therefore conclude that the bone and charcoal are subject to contamination by various processes. Ages of older bone deposits which are based on one dating method must therefore be corroborated by other methods.

Modern extinction processes: problems and prognoses

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Extinction is a fascinating biological phenomenon, but it is not that alone. For conservation biologists it is a matter of anxiety and pain, as they watch the world sliding deeper into an extinction spasm of record proportions. Conservation biologists agree about the "evil quartet" — overkill, habitat destruction, introduced species, and chains of extinction — but they also manage to disagree about a substantial number of topics. I mention some of these disagreements, such as the role of genetic factors in extinction, and the arguments about whether we should focus our attention on the causes of declining populations rather than on problems inherent in maintaining small populations. I will also note emerging debates such as the possibility that different agents of decline may interact to produce far worse effects than predicted by simple summation of the impact of those agents. Finally, what might these debates mean for conservation of biodiversity in Australia: can we use our knowledge to link biology better to management of the continent? The answer is "Yes"; but in arriving at that answer I will suggest that we are consistently shying away from some uncomfortable realities.

Monotreme evolution with a focus on the platypus family *

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This review synthesizes the knowledge to date about the evolution of monotremes, the egg-laying mammals which today are represented by the platypus and echidnas, but which have a history that predates the Cretaceous and a distribution that once included at the least South America and Antarctica as well as Australia and New Guinea. While the palaeontological history of both living monotreme families is presented, it is the Ornithorhynchidae (the platypus family) that is the focus for most of monotreme palaeontology because of the lengthy record (primarily of dentition) for platypus-like animals, and because in most respects platypuses appear to be less derived than the edentate, ant-eating echidnas. *Kollikodon ritchiei*, a very specialized Cretaceous monotreme represented by a partial jaw with bunodont molars, was recently excavated from the same deposits that also produced the earliest platypus-like monotreme, *Steropodon galmani*. This brings the number of monotreme families to four (*Steropodon* at present is placed in its own family), and indicates a greater past diversity for this enigmatic group than had been assumed.

Ornithorhynchid morphology is examined here primarily for resolution of intrafamilial relationships, with the caveat that, although the past decade has seen an exponential increase in the collection of fossil ornithorhynchid material, remains are still quite fragmentary and scarce. The distinctive ornithorhynchid double-bladed molar morphology is followed chronologically from the Cretaceous to the present (juvenile Platypuses retaining degenerate molar teeth). The meaning of such apparent monotreme synapomorphies as multiple molar roots is discussed. Through fortuitous preservational bias, dentaries have been recovered for most taxa; these show a progressive flattening of the jaw beneath the tooth row in concert with the trend towards loss of functional teeth in ornithorhynchids, illustrated in part by gradual reduction of molar root length. Explorations in skull evolution have been limited to comparisons between the Miocene *Obdurodon dicksoni* and the living *Ornithorhynchus anatinus* because of the absence of other cranial material. However, the excellent state of preservation of the *Obdurodon* skull has allowed for detailed comparisons between the two taxa that led to some interesting questions, notably whether or not this possibly derived platypus might have been a specialized offshoot of the ornithorhynchid line rather than directly ancestral to *Ornithorhynchus*. The review concludes with a discussion on the biogeographical and palaeoecological factors that have figured heavily in the evolutionary history of the group.

* Published in full: Musser, A.M. (1998). Evolution, biogeography and palaeoecology of the Ornithorhynchidae. *Australian Mammalogy* 20: 147-162.

Kuterintja ngama, new material from the late Oligocene of Riversleigh: illuminating an elusive ilariid

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Discovery of ilariid material at Riversleigh has so far been confined to the late Oligocene (System A) White Hunter Site. We assign the Riversleigh ilariid to *Kuterintja ngama*, significantly expanding the known material for this species, previously comprising a single upper molar. The holotype, described as a left M^4, is here re-identified as a left M^3. Molar cusp morphologies are compared with those of other ilariids and vombatiforms.

Previous to this study classification of *Ku. ngama* as an ilariid was tentative (Pledge 1987) and controversy surrounded the placement of *Koobor*. Intrafamilial phylogenetic analysis suggests that: 1) *Ku. ngama* is an ilariid; 2) *Koobor* is not an ilariid, perhaps representing a distinct family of vombatiform marsupials; and 3) ilariids form a monophyletic clade with wynyardiids, although the relationships of these taxa to other vombatomorphians are not resolved.

A tentative correlation is made of the White Hunter Local Fauna with the Ngama Local Fauna of the Etadunna Formation at 24.7 - 25.0 Myr.

Pledge, N.S. (1987). *Kuterintja ngama*, a new genus and species of primitive vombatoid marsupial from the medial Miocene Ngama Local Fauna of South Australia. *In* Archer, M. (ed.) *Possums and opossums: studies in evolution*: 419-422, Surrey Beatty & Sons Chipping Norton, N.S.W.

Palaeoecology of two sites from the Early Triassic Arcadia Formation, Queensland

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The taphonomic history of fossilized material collected as surface assemblages is generally overprinted by recent processes. Nevertheless the meagre taphonomic information I was able to extract from collections made from the two largest Early Triassic Arcadia Formation sites have enabled me to make a tentative reconstruction of their palaeoecology. Several lines of evidence were studied, including the skeletal element representation of each taxon, the extent of weathering damage, the degree of abrasion, the age structure of the fauna, the presence of toothmarks, and the likelihood that the assemblage was time averaged. It was apparent that the most common temnospondyl family occupied a range of environments while other families were more restricted in habitat. Terrestrial members of the fauna were rare at both sites but particularly at the smaller of the two. Procolophonids were an exception, being well represented at both sites and thought to have occupied proximal floodplains and channel banks.

I included an investigation of the coprolites from the two Arcadia Formation sites in the palaeoecological analysis. These provided evidence of an abundant fish fauna which was not otherwise apparent at the sites. Numerous other unexpected inclusions attested to the value of incorporating a study of coprolites as part of palaeoecological analyses.

Imaging acanthodian scale microstructure with confocal scanning laser microscopy

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A 35 mm thick horizontal crown section of an acanthodian scale from the Siluro-Devonian Roberts Mountains Formation (*crispa - woschmidti* zones), Nevada, was examined using confocal scanning laser microscopy (CSLM). CSLM permits convenient, high-resolution, non-destructive optical sectioning and three-dimensional (3-D) image acquisition. Its potential utility in micropalaeontology for morphometric analysis, and as an alternative to scanning electron microscopy, has previously been discussed by Birkmann and Lundin (1996). CSLM was used in this study to acquire sets of consecutive optical slices of internal microstructure at cellular level that are displayed as serial sequences, or rotated 3-D reconstructions. Crown expansion by superimposition of dentine layers is evident during playback of serial sequences. Rotated 3-D reconstructions show, with outstanding clarity, the shape of individual dentine tubules, and the spatial relationships between them. CSLM represents an important methodological improvement for study of the palaeohistology of vertebrate microremains.

Birkmann, H. and Lundin, R.F. (1996). Confocal microscopy: potential applications in micropaleontology. *Journal of Paleontology* **70**: 1084-1087.

A giant bettong (Diprotodontia, Macropodoidea) from the Pleistocene of Western Australia

Gavin J. Prideaux

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Palaeontology and stratigraphy of Tight Entrance Cave, southwestern Western Australia

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Tight Entrance Cave, located near Margaret River in southwestern Western Australia, is the richest and most diverse assemblage of Pleistocene vertebrates known from the western half of Australia. Currently, 39 species have been identified from the deposit, giving a fauna that contains a larger proportion of megafaunal species than nearby Mammoth Cave. Numerically, macropodids dominate; with the weight of evidence suggesting animals entered the cave by falling through now blocked solution tubes connected to the surface. Although much of the main chamber contains fossiliferous sediment scattered amongst rockfall, >2 m of sandy sediments occur in one area between a very large fallen block and the end wall; this is where the excavations have been sited. Sedimentological and faunal comparisons are made between the stratigraphic units, and implications for palaeoenvironmental and climatic changes discussed. Tight Entrance Cave provides the first opportunity to examine Pleistocene faunal succession in Western Australia, beyond the temporal limits of Devil's Lair. Along with the recently discovered Lindsay Hall Cave deposit on the Nullarbor Plain, Tight Entrance Cave will play an important role in progressing toward a more detailed reconstruction of Pleistocene species and community distribution patterns across Australia.

A taphonomic study of the disarticulation of macropodid skeletons in a semi-arid environment

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This study presents a post-mortem disarticulation sequence for the Western Grey Kangaroo, *Macropus fuliginosus*, from surface bone assemblages in a semi-arid environment. The process of disarticulation reduces a skeleton to individual parts and sub-assemblies, exposing these units to surface processes and transport which may eventually lead to accumulation and fossilization. Comparison with published disarticulation sequences for African ungulates (Hill 1979; Hill and Behrensmeyer 1984), reveals significant differences in the kangaroo sequence e.g. early disarticulation of the cervical and forelimb elements, late separation of the cranium from the atlas and the forelimbs from the scapulae, later disarticulation of the hindlimb long bones, and significantly later disarticulation of the caudal vertebrae. These variations reflect differences in the joints, ligaments and general structure of the kangaroo skeleton e.g. proportionately shorter neck supporting a lighter skull, forelimbs with limited weight bearing function, massive hindlimbs and tail, and also differences in locomotion and stance e.g. bipedal vs quadrupedal. Other factors influencing disarticulation such as climate and the type and activity of scavengers also differ. Ongoing work involves determining how these factors influence disarticulation, to provide a basis for predicting the sequences in extinct species.

Hill, A. (1979). Disarticulation and scattering of mammal skeletons. *Paleobiology* **5**: 261-274.

Hill, A. and Behrensmeyer, A.K. (1984). Disarticulation patterns of some modern East African mammals. *Paleobiology* **10**: 366-376.

Dating of late Quaternary megafaunal sites in Australia: a chronological investigation of faunal extinctions and human colonization

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The impact of prehistoric humans on the Australian fauna is among the most contentious but poorly documented topics in archaeology, palaeontology and ecology. Most giant mammals, reptiles and birds (the "megafauna") perished sometime in the late Quaternary, but the lack of a reliable dating framework at megafaunal and archaeological sites has thwarted any clear understanding of megafaunal extinctions and the role of humans. The two authors, plus a group of collaborative investigators, this year received funding from the Australian Research Council to undertake a comprehensive dating programme of megafaunal sites around Australia. A group of sites with articulated anatomical remains of megafauna has been selected from different regions of the continent, including Papua New Guinea and Irian Jaya. A range of species is represented at these mid to late Quaternary sites, a major aspect of our investigation being to determine the importance of faunal attenuation over the last few glacial/interglacial cycles for individual species in diverse environmental regions of the continent. Luminescence dating (primarily OSL) will be deployed at each site to determine the elapsed time since the fauna-bearing sediments were last exposed to sunlight. Other dating methods (radiocarbon, uranium-series, electron spin resonance and amino-acid racemization) will be used to date specimens directly where suitable materials are preserved. This project complements work already being done (by the first author) at archaeological sites around Australia and will enable the timing of initial human colonization and megafaunal extinctions to be compared. The site selection procedure and chronological techniques chosen will be presented at the Extinction Symposium, the aim being to encourage audience feedback at this early stage in the project.

The earliest therapsids from South Africa and their biostratigraphic significance

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The rocks of the Karoo in South Africa are internationally renowned for their wealth of therapsid mammal-like-reptiles which have been used in biostratigraphic subdivision of the Beaufort Group. This subdivision has long been used as the standard for global biozonation of Late Permian and Early Triassic continental deposits.

By far the thickest biozone is the *Tapinocephalus* Assemblage Zone (the lowermost biozone of the Beaufort Group). The tetrapod fauna of this biozone has been extensively researched by Boonstra and considered to be roughly equivalent to that of the Russian Zone II. More recently an even older biozone containing a diverse and very primitve therapsid fauna has been discovered in rocks of the lowermost Beaufort Group (immediately above the Ecca-Beaufort boundary). This fauna correlates with the oldest and most primitive therapsids known, suggesting that the earliest therapsid fossil fauna now occurs in southern Africa as well.

Systematic collecting along the Ecca-Beaufort boundary reveals that this primitive fauna is restricted to the southern-western part of the basin, and that the fauna changes as one proceeds eastwards in the basin. It also appears that it is now possible to biostratigraphically subdivide the *Tapinocephalus* Assemblage Zone, a fact which has important consequences in our understanding of the development of the Karoo basin.

A guide to utilizing ancient DNA

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Since the development of the Polymerase Chain Reaction (PCR) in the 1980s, it has been theoretically possible to amplify a single copy of DNA to a level where it may be studied. This has enabled the study of tiny amounts of highly degraded DNA from forensic material and ancient remains. The information gained from genetic analysis of these sources has the potential to: clarify phylogenetic affinities of extinct species; identify and sex remains; facilitate studies of population dynamics; track dispersal events; and determine the kinship of ancient remains. Ancient DNA has been successfully extracted and used to address these questions. Some samples, from which genetic analysis has been successful, include: tissue from a 10,000 year old woolly mammoth; 8,000 year old human brain tissues; a 120 million year old weevil entombed in amber; and 14,000 year old bones of a sabre-toothed cat.

Studying the DNA from ancient remains presents a number of difficulties, including:

- contamination of the ancient sample by other sources of DNA. Contamination sources commonly include DNA from the collector and preparator, other samples in the deposit, and other DNA samples handled in the laboratory.
- the extreme degradation of DNA which occurs in ancient samples. The post mortem environment determines the extent to which DNA is degraded. DNA shearing is most common in acid environments and when the remains were not dried rapidly post mortem.
- that DNA which has been retained by ancient bone samples is usually very tightly bound to the bone matrix, this presents difficulties with extracting the DNA.
- inhibition of the PCR reaction by chemicals derived from soil, which are embedded in ancient remains.

This talk will use case studies to illustrate:

- the types of preservations which are most likely to have retained useful amounts of DNA.
- precautions which will prevent contamination of samples collected for ancient DNA analysis.
- the basic procedures involved in recovering genetic information from ancient remains.
- that information provided by ancient DNA analysis is an additional source of useful data.

A terminal Pleistocene amphibian, reptile, and mammalian fauna, Little Beaver Cave, Missouri, U.S.A.

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Previous investigations of late Pleistocene vertebrate faunas from the Ozark Highland (an uplifted carbonaceous dome today covered in thick deciduous forests) are numerous but either lack systematic excavations, temporal control, and/or sufficient microvertebrate components which are essential for interpreting palaeoecology. At Little Beaver Cave, three high resolution radiocarbon dates on bone specific amino acids, systematic sampling, fine mesh (0.7 mm) wet sieving, and diverse micromammal components provide an ecological basis for interpreting the terminal Pleistocene (approximately 12,000-10,000 yr BP). The amphibians and reptiles are currently under analysis and thus far no extralimital or extinct taxa have been identified. In contrast, the mammals have been thoroughly analyzed and numerous extinct and extralimital taxa are reported herein.

Extinct mammals represented are *Megalonyx jeffersonii* (Jefferson's ground sloth), *Mylohyus nasutus* (long-nosed peccary), *Platygonus compressus* (flat-headed peccary), and *Dasypus bellus* (beautiful armadillo). Of these, only *D. bellus* and *P. compressus* were recovered from controlled samples. A radiocarbon date of 11,000 ± 60 on a *D. bellus* dermal ossicle represents the youngest reliable date on this taxon. Seven extralimital small mammals (1 shrew, 2 squirrels, and 4 voles) were recovered from systematic excavations. *Blarina* sp. cf. *B. brevicauda*, *Spermophilus* sp. cf. *S. tridecemlineatus*, and *Microtus pennsylvanicus* are locally extralimital and suggest open and moist habitats with some forest cover. *Tamiasciurus* sp. cf. *T. hudsonicus*, *Clethrionomys* sp. cf. *C. gapperi*, *Phenacomys* sp. cf. *P. intermedius*, and *M. xanthognathus* are extralimital taxa that require cool summers and boreal environments.

The association of extralimital taxa with current residents species in the Little Beaver Cave deposits may reflect a mosaic of coniferous, deciduous, and open habitats during the waning years of the Wisconsinan for the Ozark Highland. A cool and moist equable climate provides a possible hypothesis for this nonanalogous faunal assemblage. Further, having a retention of strong boreal affinities up to the Pleistocene/Holocene boundary in the Ozarks, supports a rapid transition into the climatic severity characteristic of the Holocene, and therefore, may have important environmental implications in terms of terminal Pleistocene extinctions.

Environmental turnover and extinction in Beringida during the Pleistocene termination

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Although Northeast Siberia was the most likely route for human immigration to North America, the human overkill paradigm receives little support from this region. Only one Late Palaeolithic site, Berelyokh on the lower Indigirka River (ca 12 kyr, non-calibrated ^{14}C age), is known in the area. It is associated with an enormous bone accumulation, but hardly anyone interprets it as a kill-site. On the contrary, arguments for environmental explanations of the Late Pleistocene extinctions are strongly supported. Various lines of palaeoecological evidence suggest a highly continental Arctic climate during most of the Pleistocene. Despite very low annual temperatures, lack of moisture prevented formation of ice sheets during the glacials. Instead, unparalleled development of "underground glaciation" occurred. Syncryogenic ice-bonded deposits are widespread all over Beringida, i.e., Northeast Siberia, Alaska, Yukon and the unglaciated Northwest Territories.

Until the very end of the Pleistocene, this climate supported dry Arctic grassland, a non-analogue environment, called "tundra-steppe" by Russian scientists. It was quite favourable for cold-adapted grazers, such as woolly rhino, woolly mammoth, horse, bison and saiga antelope. We infer that the tundra-steppe fauna originated in the continental areas of Beringida as early as about one million years ago, spreading south during the cold (glacial) stages. The continental areas of Beringida could shelter tundra-steppe communities and mammals that could not survive changing conditions in the south during the interglacials.

The Pleistocene termination in Western (Siberian) Beringida started around 12.5 kyr. Sedimentation of syncryogenic deposits stopped, and the first indications of thermokarst (thaw) appeared on their surface. The amount of grass and herb pollen, dominating the Pleistocene spectra, sharply decreased, while shrub and dwarf shrub pollen increased. The range of the woolly mammoth, shortly before embracing most of Europe and Siberia, rapidly shrank to the high Arctic (north of 70°N.). The second, critical stage of the environmental turnover (11-8 kyr), was marked by very active regional thaw, and resulted in the appearance of myriads of thermokarst lakes and bogs. The irreversible character of this turnover was probably related to the very fast inundation of the shallow continental shelf by cold Arctic waters, which not only wiped out huge area of pastures, but also radically changed the regional climate. It was the time of the final demise of the grassland communities and the extinction of mammoth everywhere, except a relic population on Wrangel Island, that was separated from the mainland during the post-glacial sea level rise.

The mammoth population on Wrangel Island was evidently able to survive the critical period of the environmental turnover owing to the preservation of relic patches of dry grassland, supported by local climate, but also due to decreasing body size of 25-30%. The size of the population was minimal between 12 and 8 kyr (no fossil record found yet), when the dwarfing occurred, and the other populations became extinct. After those critical times the island population became large enough to survive for almost 4,000 years more. Survival of mammoth into historical times (3,700 BP) on Wrangel Island is an exception to the rule, confirming the environmental theory of extinction.

The role of predation in the extinction of mammals in Australia over the past 200 years

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Eighteen species of mammals have become extinct in Australia since European settlement 200 years ago. An additional 26 species are either extinct on mainland Australia or have declined to occupy less than 10% of their former range. Possible causes include loss of habitat due to land clearing, deterioration of habitat quality from grazing by introduced herbivores such as stock or rabbits, changed fire regimes as Aboriginal hunting has declined, disease, drought, climate change, fragmentation of habitat, predation by introduced predators, or some combination of these.

Predation by introduced predators, principally foxes and feral cats, has typically been regarded as a secondary agent of decline acting on remnant populations reduced by loss or deterioration of habitat. The reluctance to accept predation as a major cause of declines and extinctions derives largely from the apparent loss of mammal species from some regions prior to the arrival of foxes. However, there is evidence to suggest that species persisted for several decades longer than is currently accepted.

Information from recent attempts to re-establish new populations of threatened mammals has suggested a more pivotal role for predation in the decline and extinction of species. Evidence comes from collation of results from past reintroduction of macropods; the loss of reintroduced mammals to predators at desert sites where habitat structure had been reconstructed by simulating former fire regimes; observations of the behaviour of threatened mammals in the presence of exotic predators; and observations of surplus killing of threatened mammals by predators.

It appears that evolutionary isolation of Australian mammals has led to a mismatch in their behaviour and population dynamics compared to that of exotic predators. This mismatch frequently leads to the decline and eventual extinction of prey species if no refuges are available to them. The invasion of native mammal communities by rabbits and house mice and the consequent elevation of prey densities may be necessary to drive this process for cats, but is unlikely to be necessary for foxes due to their broader dietary niche and ability to take a wide spectrum of prey sizes. Fox predation is not controlled by the abundance of any one prey species and kill rates do not appear to be tied necessarily to food satiation. This "evolutionary isolation" model predicts that the introduction of an exotic generalist predator to a community of native mammals will lead to the loss of all species other than those with a refuge in habitat, lifestyle, body size or range. The dynamics of the predator at any site will ultimately be controlled by the prey species with the highest rate of increase and year-round availability.

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Smith, A.P. and Quin, D.G. (1996). Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* 77: 243-267.

A giant lamniform shark from the mid Cretaceous Gearle Siltstone in the southern Carnarvon Basin of Western Australia

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A natural association of 68 teeth and 10 vertebrae from a giant lamniform shark was uncovered in April 1996 from the uppermost metre of the Gearle Siltstone (Cenomanian) in the Giralia Anticline, Western Australia. On the basis of its unique heterodont pattern and dental formula the Western Australian shark represents a new family within the order Lamniformes. Its specific and generic status are uncertain pending the revision of the poorly known *Pseudoisurus tomosus* from the Cenomanian of the Saratov region in Russia. The size of the recovered vertebral centra indicates that the shark measured at least 5 metres in total length, which makes it the largest known shark in the world of Cenomanian age. Its teeth are comparatively small relative to the estimated body size with the largest tooth, the second lower anterior, measuring 36 mm in height. Other characteristic features include a strong dignathic heterodonty and the presence of three anterior tooth-files in the upper jaw. Current data suggest that the species-group to which the Giralia shark belongs, inhabited mainly temperate off-shore waters.

AMS ^{14}C chronologies for late Pleistocene mammal extinctions and human migrations in North America

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Animal extinctions and human migrations were worldwide occurrences during the late Pleistocene. What differs geographically are the timing of these events and their causes. Accurate geologic time measurements are fundamental to describing and understanding whether climate changes, human behaviour, a combination of these two, or other causes were responsible for worldwide reorganizations of human and animal populations during the past 30,000 years.

Developing theories to explain these population changes depends on 1) Well-controlled stratigraphy, 2) Understanding depositional and post-deposition geochemical processes, 3) Dating multiple sample materials with emphasis on fossil bones, 4) Using rigorous chemistry techniques, and 5) Repetitive testing of results at additional localities.

Examples from North America typify problems and their solutions worldwide. Most difficulties are overcome by excavating sites in 5 cm stratigraphic intervals, and using complex chemical pretreatments on charcoal, sediments and fossil bone. Dating sediments, charcoal and bone simultaneously uncovers chronological problems not evident from one sample type. AMS radiocarbon dating of bone has proven the most definitive chronological tool because these fossils are most directly related to the biological question, samples are abundant, and pretreatment chemistry is well established.

The greatest impediment to establishing chronologies for ecosystem reconstructions, extinctions and immigrations is overcoming paradigms and psychologies that prevent error detection. Radiocarbon dates are labelled "accurate" or "inaccurate" because they support or negate hypotheses, not because the dates have inherent accuracy. For example, North American extinct mammal dates >11,000 yr BP are rarely questioned, whereas specimens dating <10,000 yr BP are. In reality, both dates may be in error by several thousand years.

The results from our research are that chronologies promulgated for extinction events in North America are in error by several thousand years. Similar errors apply to human fossils and palaeoecological reconstructions. Consequently, it has been impossible until the last 10 years to adequately develop hypotheses explaining human, animal and ecosystem changes during the late Pleistocene.

Our conclusions regarding North American palaeobiology are 1) The late Pleistocene megafauna extinction occurred within a 150 radiocarbon years long interval centered on 10,900 yr BP, 2) Extinctions were not in waves of species, 3) Elephants were the last animals to go extinct; therefore, mammoths and mastodonts were not pivotal species ecologically, and 4) Most North American megafauna species may have already been extinct before Clovis peoples entered the New World ca 11,200 yr BP.

Other conclusions regarding human populations and ecosystems are: 1) The earliest direct dates on humans in North America range from 10,900 to 11,500 yr BP, 2) These early human populations overlapped with mammoth and mastodonts by at least 500 radiocarbon years, and 3) Disharmonious or non-analog mammal communities, and therefore non-analog ecosystems, have been conclusively demonstrated as existing in North America from ca 16,000 to 12,000 yr BP.

Avian extinctions and fossil bones on Pitt Island, Chatham Islands

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About 3,500 fossil bird bones representing about 50 species were collected on Pitt Island (6,190 ha) in the Chatham group (east of New Zealand) between 1947 and 1993, from deposits up to 4,500 years old. More than half of these species no longer occur on Pitt Island and 11 are totally extinct. Apparently the most common birds used to be small burrowing seabirds — the fairy prion (*Pachyptila turtur*) and diving petrel (*Pelecanoides urinatrix*) — which are now extinct on the island. Other species commonly found in the deposits include the extinct Dieffenbach's rail (*Gallirallus dieffenbachii*) and a crested penguin (*Eudyptes* ?n. sp.) and the threatened Chatham Island pigeon (*Hemiphaga chathamensis*) and Chatham Island petrel (*Pterodroma axillaris*). Albatrosses (*Diomedea* sp.) once used to nest on the island. The causes of the demise of the avifauna are the introduction of pigs, cats and wekas (*Gallirallus australis*), land clearance for farming and probably human hunting during the last 500 years.

New dinosaur tracks from the Walloon Coal Measures (Middle Jurassic) of Queensland

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The *Queensland Government Mining Journal* for December 1933 reported the first discovery of dinosaur footprints in Australia. The footprints had originated from underground workings in the Walloon Coal Measures (Middle Jurassic; ?Bajocian), near the town of Rosewood in southeast Queensland, about 55 km west of Brisbane. Subsequently there were several more finds of dinosaur footprints in collieries around Rosewood, and also (somewhat later) at Balgowan colliery, near the town of Oakey, nearly 100 km further west. Reports of dinosaur tracks declined dramatically after 1960, mainly because of colliery closures, increasing mechanization and the shift from underground to opencut workings. With rare exceptions the Walloon footprints were attributed to large theropod dinosaurs. New evidence, including footprints discovered at Oakleigh No. 3 (underground) colliery, near Rosewood, and the New Hope opencut colliery at Jeebropilly, near Amberley, confirms the existence of a more diverse dinosaurian ichnofauna. Dinosaur tracks identified to date include those of large theropods (some tracks, at least, comparable to the ichnogenus *Eubrontes*), small bipedal ornithopods (cf. *Anomoepus*) and large bipedal ornithopods (iguanodontians). In addition some unusual tracks are attributed to a small ornithopod in quadrupedal walking gait (cf. *Wintonopus*).

The biostratigraphic implications of isolated scales from Late Devonian palaeoniscoids

Katherine M. Trinajstic

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Palaeozoic sharks of Western Australia

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Chondrichthyan microvertebrate faunas from the Devonian sediments of Western Australia are known from the Bonaparte Gulf, Carnarvon and Canning Basins, occasionally associated with macrovertebrate assemblages. The Carnarvon Basin assemblage of fishes from the upper Givetian-Lower Frasnian Gneudna Fm, has yielded a new shark of uncertain affinity (Trinajstic pers. comm.). The Late Devonian Canning Basin faunas, known mostly from borehole samples from the Famennian, comprise *Thrinacodus ferox*, and a bicuspid form *Xenacanthus* sp., also occur in the Lower Carboniferous Laurel Formation. Isolated shark's teeth were first found in the Carboniferous Laurel Formation (Thomas 1957, 1959). *Stethacanthus thomasi* (Turner, 1982) is now known to be widespread in the Fairfield Group of the Canning Basin in association with *Protacrodus* sp. phoebodontids, eugeneodontids, and helodonts; in the Oscar Range; Mt Percy, Fairfield Group. A new stethacanthid with articulated jaws showing numerous teeth and scales comes from the Utting Calcarenite of the Bonaparte Gulf Basin. Gilbert-Tomlinson (in Veevers and Roberts 1968) noted *Ctenacanthus* spine in the Enga Formation and Utting Calcarenite. *Psephodus* sp. has been recorded from the Lower Carboniferous Moogooree Limestone of the Kennedy Range. Permian remains are as yet sparse. Despite searching, no recent specimens of *Helicoprion davisii* (Woodward, 1886), found in the Gascoyne River region, have come to light. Teichert (1940, 1943) and Turner (1993) reviewed the Permian vertebrate faunas of W.A., recording *Crassidonta subcrenulata*, and further specimens of *Helicoprion davisii*. Recently, stethacanthid teeth were described from the Irwin River region (Holmwood Shale) by Daymond (1993). The biostratigraphic value of Palaeozoic chondrichthyan remains is emphasized.

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Getting a grip on the dating game; Lancefield Swamp, how old is it really?

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Badgers, cassowaries and oddities: the extant and extinct fauna of King Island, Bass Strait

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The extinct and extant faunas of King Island represent a geographically isolated biota subjected to repeated periods of connection and disconnection with the Australian mainland during the late Quaternary/ Holocene (Jennings 1959). It was during this time that King Island evolved its unique fauna, which includes several endemic species. The Island has also undergone a series of localized extinctions, the cause of which are, as yet, conjectural. There is some evidence to suggest that the prehistoric extinctions are related to climatic changes over the past 100,000 years, and may be contemporaneous with those on the mainland (Hope 1984; Flannery 1990). Historically recent extinctions, (those occurring over the last 200 years) were probably caused by the arrival of European settlers (Sullivan nd).

The late Quaternary oscillations from a glacial to interglacial climate have been linked to changes in precipitation and temperature in southern Australia (Bowler 1982; Galloway and Kemp 1984). Evidence for these changes can be seen in both the sediments and the fossils deposited at a number of sites on King Island (D'Costa *et al.* 1993; Murray-Wallace and Goede 1995; Van Huet unpublished observations). They are characterized by raised beaches, mass flow deposits and the development and migration of dunes.

Of the areas investigated, one site is of special interest. At Pass River on the central west coast, *in situ* sub-fossil material has been recovered from each of five horizons preserved in superpositional order. It is anticipated that the biostratigraphic information from Pass River will record faunal change over time. Many late Pleistocene and Holocene sites in Australia have returned only single facies data. Pass River may provide a rare example of an area where superposition of late Quaternary biologic events can be demonstrated.

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Early tetrapods from Australia: filling the Carboniferous gap

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The first Carboniferous tetrapod fauna in the southern hemisphere comes from the mid-Viséan Ducabrook Formation, Drummond Basin, Queensland (Thulborn *et al.* 1996). The fauna is fragmentary but comprises at least two types of tetrapods (an anthracosaur or more primitive stem tetrapod and a second taxon which is closer to the temnospondyls) together with non-marine fishes *Gyracanthides*, a rhizodont, xenacanthoid and other sharks and lungfish. The tetrapods rank among the oldest representatives of their clades. Hitherto the entire record of Devonian and Early Carboniferous tetrapods in Gondwana was a single jaw and footprints, all from the Devonian of Australia so that our understanding of early tetrapods has been derived from the more substantial record of western Europe and North America. Despite its remote palaeogeographic location, the Queensland fauna bears striking resemblance to those of the Euramerican Mississippian Tetrapod Province. For example, the Late Viséan fauna of Delta, Iowa was located virtually at the opposite pole of the Early Carboniferous globe yet shares a similar faunal association. Evidently, Carboniferous tetrapods may have extended through a tropical belt across the whole of Pangaea.

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Why big fierce animals are especially rare in Australia and the implications of their scarcity for the vexed question of why the megamarsupials became extinct *

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One of the more contentious issues in prehistory is whether people were the main cause of the extinction of the large mammals that seem, particularly in the Americas and Australia, to have disappeared within millennia of human arrival; or whether other factors, such as climatic change, were also involved. Flannery (1994) recently explained the rapid extinction of the Australian megafauna by arguing that prior to human arrival the endemic herbivores developed a pattern of mosaic grazing, permitting them to flourish, despite the unpredictable climate and poor food resources available. Then humans arrived and upset the pre-existing delicate ecological balance by hunting the herbivores and burning the country to maintain patchiness, thereby depleting the ecosystem and exterminating the megafauna so quickly that no 'kill sites' have yet been found.

This scenario is queried because (i) as Baynes (this conference) shows, the time of extinction of the megafauna is unknown, but appears to lie beyond the range of ^{14}C dating (>35,000 BP), (ii) the time of human arrival is also unknown, but appears to be about 60,000 BP, (iii) finding palynological evidence for Aboriginal burning is not easy and (iv) there is little or no archaeological evidence that people killed and/or butchered the species that became extinct.

Therefore, I will be argue that, irrespective of human arrival, the fragility of the Australian ecosystem explains megafaunal extinction, because the continent has an unusually low carrying capacity for large mammals. Its herbivores are few, small (<90 kg) and non-gregarious and 75% of its living carnivores weigh <50 g. The Pleistocene large carnivore suite was also depauperate. It comprised three species, each much smaller than its felid, canid and mustelid analogue, indeed too small to prey on the megaherbivores that became extinct: *Thylacoleo carnifex* (20 kg), which disappeared soon after human arrival, *Thylacinus cynocephalus* (15 kg), which was replaced by *Canis familiaris*, and *Sarcophilus harrisii* (8 kg), which survives, just. This paucity contrasts markedly with the fossil record of, say, South America.

Although 10-30% larger than the surviving species, the marsupial megaherbivores were also markedly smaller than their placental analogues. Diprotodons (2000 kg) compare with elephants and rhinoceroses (<6000 kg), Protemnodons and Sthenurines (200 kg) with large artiodactyls (1500 kg), which were also highly gregarious. These data suggest that Australia had an inherently low carrying capacity that was unable to support many large carnivores simultaneously. In which case, human arrival may have been sufficient *de esse* to upset the pre-existing ecological balance and facilitate megafaunal extinction.

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'Giant mice and tiny mammoths': insular endemism and the peopling of the Americas. Why did the dwarf mammoth on the Northern Channel Islands of California become extinct?

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The Northern Channel Islands lie 20-50 km off the south Californian coast opposite Santa Barbara at 34°N. latitude and comprise from west to east, San Miguel, Santa Rosa, Santa Cruz and Anacapa. They rise <750 m amsl and receive 150-300 mm/yr of rain, which supports grassland with stands of pine, cypress and Douglas Fir. Their aggregate area is presently about 500 km^2, but the islands are not conjoined. However, glacio-eustatic reduction in sealevel to -50 m created the palaeoisland of *Santarosae*, which enlarged to >2000 km^2 during glacial maxima, although it was still separated from the mainland by a water barrier >6.5 km wide. Hence, the island/s was/are 'oceanic' in biogeographic terms. The non-volant terrestrial species found there arrived by swimming and/or rafted waif dispersal.

Therefore, the living insular fauna is considerably impoverished compared to that known on the Californian mainland, while the Pleistocene mammal fauna was even more depauperate. It comprised two species of giant mice (*Peromyscus* spp.) and a dwarfed form of mammoth (*Mammuthus exilis*). Finds on Santa Rosa of mammoth bones associated with flaked stones, which have been interpreted as human artefacts, and extensive 'burnt' areas have been cited as evidence that people entered the New World earlier than is often supposed: ^{14}C dating suggests that some of the burnt areas may be >40,000 years old. The disappearance of the mammoths about 11,000 BP has also been attributed to human predation on a singularly vulnerable species. However, recent archaeological research suggests that people did not occupy the Channel Islands until after the mammoth became extinct.

This fauna is interesting because the composition of its living representatives illustrates the 'sweepstake' effects of over-water dispersal on the ability of species to colonize islands successfully, while the body size changes recorded in the Pleistocene species are a classic example of insular endemism. Whether or not the living faunas have reached equilibrium will be reviewed in the light of biogeographic theories on insular carrying capacity quantified by the species/area relationship. The cause of the extinction of the Pleistocene fauna will also be addressed. Not only were Chumash Indians apparently unable to survive on the Northern Channel

Islands on a year-round basis in the recent past, but there is also no conclusive evidence that Palaeoindians lived on *Santarosae*, either. Therefore, I suggest that, as sealevel rose with the onset of deglaciation after 15,000 BP, the dwarf mammoth succumbed to habitat loss as *Santarosae* was inundated and the islands took their present configuration, rather than to human hunting.

The landbridge filter effect and the pattern of colonization of the British Isles by thermophilous terrestrial mammals during the later Pleistocene

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During past glacial cycles Britain was joined to continental Europe by a landbridge that moved steadily northwards over time. Non-volant mammals, including humans, would have been able to colonize the country unaided at such times. However, the environment would then have been inhospitable for many thermophilous species, because most of Britain was covered by ice. Conversely, during interglacials the British Isles would have been isolated from continental Europe by the sea, which inhibited colonization by non-volant animals. There was, therefore, probably only a brief period during each cycle, as the glaciers retreated, but before sea level rose, when unaided immigration to the British Isles was possible for thermophilous terrestrial mammals. Whether or not a particular species managed to establish itself then would have depended on the distance from its refuge to the archipelago, its rate of migration, the barriers it encountered en route and the competition it faced on arrival. For example, humans appear not to have reached Britain during the last interglacial.

A number of distinctive thermophilous faunas has been identified in Britain from deposits attributed, mainly on stratigraphic grounds because few sites yet have radiometric dates, to successive interglacials. While it is clear that these faunas span the Middle and Upper Pleistocene, the precise number of interglacials they represent and how, or even whether, they can be correlated to the deep sea oxygen isotope record, is more controversial. The most extensive glaciation to cover Britain, the Anglian, deflected the Thames into its present valley, destroying most traces of earlier cycles in the process, although faunas attributed to the preceding Cromerian interglacial, or complex of interglacials, are well known.

Beginning with the Cromerian, the known interglacial faunas will be considered sequentially to see whether the same or descendant species of non-volant thermophilous mammals established themselves in Britain during successive warm periods. Changes in the composition and diversity of the known faunas illuminate the effect that the migration of the landbridge northwards had on determining which species were successful. The depauperate nature of Ireland's Recent fauna, compared with that of Britain, well-illustrates the landbridge filter effect.

The number of species identified from each interglacial will also be examined via the species/area relationship to determine whether successive faunas had reached equilibrium with their environment, or whether they were 'super-saturated', suggesting that equilibrium had not been reached between thermophilous immigrants and cold-tolerant residents or that the species involved actually represent more than one interglacial, or were depauperate, suggesting that the fauna is inadequately known or does not represent fully interglacial conditions.

The functional morphology of the marsupial hind limb in the Diprotodontidae and some extant species

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The following investigation is a comparative morphometric study of certain elements of the marsupial hind limb, represented by two species of wombat, three species of wallaby, one species of tree kangaroo, the koala, Tasmanian Devil and the Thylacine. Specific morphological features are examined and their functional affinities explored. In addition to the extant fauna, specimens from two genera of extinct diprotodontids (*Diprotodon* and *Zygomaturus*) were included. Although these extinct forms are not the main focus of the study, some interesting features relating to their morphological relationships to the living forms are revealed.

From the results of bivariate and multivariate analyses, a number of distinct locomotor adaptations was established. The multivariate results displayed both subtle and gross differences between the extant species, for example; less pronounced discriminations appeared between two species of wallabies, while obvious differences were apparent between the saltatorial and non-saltatorial animals. The principal components and canonical variates analyses showed the two diprotodontids to be grouped quite distinctly from the extant species on both size related and non-size related axes. In some analyses *Diprotodon* and *Zygomaturus* were distinguished from each other and were each grouped with different extant species, perhaps suggesting slightly different adaptations.

Both *Diprotodon* and *Zygomaturus* have hind limbs which were adapted for power rather than speed. This suggests that they were not able to compete with the large fast moving grazers that were also evolving at the same time (namely, kangaroos). The results also indicate that *Zygomaturus* was both morphologically and functionally different from *Diprotodon*. If *Diprotodon* employed a grazing adaptation out on the Australian savanna, then perhaps *Zygomaturus* employed a more browsing adaptation in a wooded habitat.

A Late Pleistocene deposit at Rocky River, Kangaroo Island, South Australia

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Since 1908, Pleistocene vertebrates have been periodically recovered from the edge of Black Creek Swamp at Rocky River, Kangaroo Island. Tindale *et al.* (1935) first investigated the deposit and recorded the remains of *Zygomaturus*, *Diprotodon* and *Macropus*. Subsequent excavations west of Tindale's pit were undertaken by Hope *et al.* (1977), and more recently by Gröcke in 1996, and Wells and Prideaux in 1996 and 1997. We investigated subsurface stratigraphy by auguring a large area around the excavation, and confirmed the extensive nature of the fossil horizon. Preservation and arrangement of bones exposed in the pit suggest post-mortem disassociation, with subsequent hydraulic transport concentrating bones in small depressions of a palaeo-channel. Several species of megafauna occur in the deposit along with extant rodents and small to medium sized marsupials. Radiocarbon dates of ~19.5 kyr obtained previously (Hope *et al.* 1977) and the discovery of a new dwarf *Zygomaturus* species highlight Rocky River's potential as one of the last refuges of Australian megafauna.

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What was on the menu — avian extinction in New Zealand

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The North and South islands of New Zealand had 130 resident taxa of birds in the latest Holocene. Of these, 34 became extinct in the prehistoric period of the last 1000 years, and 6 more since then. An additional 30+ species are rare on the main islands or restricted to offshore islands. All extinct taxa are present and usually common in Late Holocene fossil deposits. The avifaunas of 174 archaeological sites have been surveyed from the literature and the number of sites individual taxa are present in, tabulated. Thirty-four extinct species are present in Maori sites. The absence of the remaining extinct species from the archaeological record is explicable as either they are recently described species whose bones are likely to have been misidentified, or they are small non-harvested species whose extinction is a result of predation by the Pacific rat (*Rattus exulans*). Moas of one sort or another were present in 102 of the sites (59%). The data reveal poor sampling of small bird species, with 57 resident taxa (44%) in five or fewer sites. There is also a geographic imbalance in available data as only 28% of sites are from the North Island. Few sites have been investigated with a prime purpose of obtaining a representative sample of the associated fauna. Despite these biases, the data indicate that predation by humans was a significant factor in the majority of Late Holocene avian extinctions in New Zealand. Further archaeological investigations aimed at recovering representative faunas from sites, rather than as incidental byproducts of other investigations, can only cement this conclusion.

Were propleopines carnivorous? *

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The interpretation of propleopine palaeobiology represents the focus of perennial debate in the literature. Were they or were they not carnivores? A general failure to clearly define what is meant by the term 'carnivorous' by contributors to the argument has, to some degree, confused the issue. Because various definitions of the term 'carnivore' are available it is essential that this semantic distinction be made if misinterpretation is to be avoided. Historically, terrestrial mammalian carnivores have long been defined on the basis of dental features (i.e., the development of high amplitude vertical shearing blades and the concomitant reduction of horizontal shearing/crushing elements in the dentition). These adaptations have arisen independently in numerous mammalian clades in response to similar selective forces. Recent studies have shown a direct correlation between the relative importance of these variables and the proportion of meat versus vegetable matter in the diet of carnivorans. The relative significance of high amplitude vertical shear versus horizontal shear among propleopines is not comparable to that of known carnivores and it is argued that propleopines were omnivorous.

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The Lapillopsidae, a new family of small temnospondyls from the Early Triassic of Australia

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Examination of the small and potentially juvenile temnospondyl material from the "Crater" in southeastern Queensland has revealed that most specimens are referable to one species, *Lapillopsis nana*. Originally described as a dissorophoid, the new material has allowed a reassement of the systematic position of this genus. To accomplish this a cladistic analysis was performed using 122 osteological characters and 38 terminal taxa, sampling a wide range of Mesozoic and Palaeozoic temnospondyl diversity. Far from being a dissorophoid *Lapillopsis* is shown to be closely related to the assemblage traditionally called the Stereospondyli. Monophyly of the Stereospondyli is well supported by this analysis. Amongst the Stereospondyli *Lapillopsis* is one of the most plesiomorphic and it appears to be a relictual taxon in the Early Triassic of Australia. The similarities between *Lapillopsis* and dissorophoids are interpreted as convergences caused by a similar terrestrial mode of life. A new genus and species from the Early Triassic of Tasmania shares a number of synapomorphies with *Lapillopsis*. These two genera are united in the new family, Lapillopsidae. Despite Australia having the world's highest diversity of Early Triassic temnospondyls, the Lapillopsidae is Australia's first recorded endemic family of temnospondyls.

New placoderm discoveries (Upper Devonian) in central N.S.W.: biostratigraphic and biogeographic significance

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