FAUNA *of* AUSTRALIA

12. GENERAL DESCRIPTION AND DEFINITION OF THE CLASS REPTILIA

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Both in numbers and taxonomic diversity, living reptiles represent but a remnant of the enormous variety of reptiles which we know from the fossil record have previously inhabited the earth. While these earlier radiations consisted mostly of groups of reptiles which were not significantly different in size range from extant reptilian groups, popular knowledge and culture has emphasised one or two fossil groups containing megareptiles—the orders Saurischia and Ornithischia. A general overview of this past diversity, and of the classification of fossil reptiles, can be found in Romer (1956) and Carroll (1988b).

The first recognisable reptiles appeared in the Carboniferous, some 340 million years ago. By the middle of the Mesozoic, about 170 million years ago, they had evolved and adapted to occupy most of the world's ecotopes. In terms of species richness, biomass and physical dominance, they became the dominant vertebrates during this period.

Reptiles are amniotes, a group containing the reptiles, birds and mammals and characterised by the presence of a series of three extra-embryonic membranes. The amnion and chorion start as two-layered outgrowths of the body wall at each end of the embryo and grow around the embryo to eventually meet and fuse; the allantois begins as an outgrowth of the lower gut. The amnion forms a fluid-filled sac in which the embryo develops, cushioned from the external world and largely safe from dehydration. The chorion is a vascularised membrane lying just beneath the egg shell where its primary function is gas exchange. The allantois stores the embryo's metabolic wastes. These membranes first evolved in conjunction with a shelled egg, allowing reptiles to breed in less-humid areas than their amphibian progenitors, or even in areas without free water. Later amniotes have retained these membranes, albeit often in a form modified for viviparity. The reptiles were the first vertebrates to be freed from reproductive dependence on water, by providing a 'pond' inside a relatively impervious eggshell, within which the developing embryo could be cushioned from the outside world, it could avoid desiccation, and into which it could safely void the poisonous waste products of metabolism.

The amniotes are believed to represent a true clade. They are a monophyletic group containing an ancestral species and all of its descendant species of reptiles, birds and mammals.

The Class Reptilia, the 'reptiles', has for nearly two centuries had a clear meaning to neontologists. Living reptiles are readily distinguished from the other amniote tetrapod vertebrates—the birds and mammals—simply by virtue of the combination of ectothermy (often known colloquially as being 'cold-blooded'), scaly (rather than furred or feathered) skins and the possession of intromittent sex organs for internal fertilisation.

For palaeontologists, struggling with a disjointed and discontinuous record of mostly bony fragments extending over 450 million years, assigning a given fragment to the Reptilia has often proved surprisingly difficult. The distinctions between many early reptiles and contemporaneous amphibians, or between reptiles and the early ancestors of birds and mammals, are often blurred in the fossil record.

Consequently, for nearly two centuries three living Classes have been recognised within the amniotes—mammals (Mammalia), birds (Aves) and reptiles (Reptilia). Indeed, this Volume implicitly supports this conventional classification. However, under this traditional treatment of the Class Reptilia, the group is clearly paraphyletic, as it excludes one of its descendant groups, the birds.

In his classic work on the osteology of the reptiles, Romer (1956) provided a brief, but highly informative account of the history of the classification of the Reptilia. The classification Romer adopted in this work has remained in place with minor modifications until the present day, although recently it has been overtaken by new studies of fossil forms and their relationships, and by the cladistic methods of analysis of Hennig (1966) and his successors. This essentially phenetic classification is represented in Figure 12.1 (after Bellairs 1969).

Whereas earlier methods of classification tended to give more or less equal weight in phylogenetic analysis to both primitive (plesiomorphic) and advanced (apomorphic, or derived) features, cladistics is based on the use of shared derived characters (synapomorphies). While theoretically rigourous, cladistics depends absolutely on the ability to assign polarity to a character, that is, to determine whether the expression of that character in any given taxon is closer to its primitive or advanced condition. Carroll (1988b) discussed the problems of applying cladistic methodologies and criteria to groups whose phylogenies are primarily constructed from the fossil record.

Romer recognised seven subclasses of reptiles (Table 12.1), three of which are represented by modern reptiles: Anapsida (turtles), Lepidosauria (tuataras, lizards and snakes) and Archosauria (crocodilians). One of the remaining subclasses was tentatively erected for one major fossil group, the mesosaurs. The remaining two subclasses, the Euryapsida and Synapsida, contained only fossil forms, including (in the Synapsida) the ancestors of mammals.

Because of the great diversity of fossil reptiles, which reached a peak during the Mesozoic, early classifications tended to be based on cranial features which are evident in the fossil record. The higher classification of reptiles has long been based on the number and location of openings in the skull. In modern reptiles only the anapsid (turtles) and diapsid (lizards, snakes, tuataras and crocodilians) conditions persist, albeit in a modified form.

Though the evolutionary relationships of many fossil forms continue to be debated, the above higher classification of extant reptiles has varied surprisingly little during the past century. Not until the post-1960s application of methods of phylogenetic systematics (cladistics), with its rejection of paraphyletic groups,

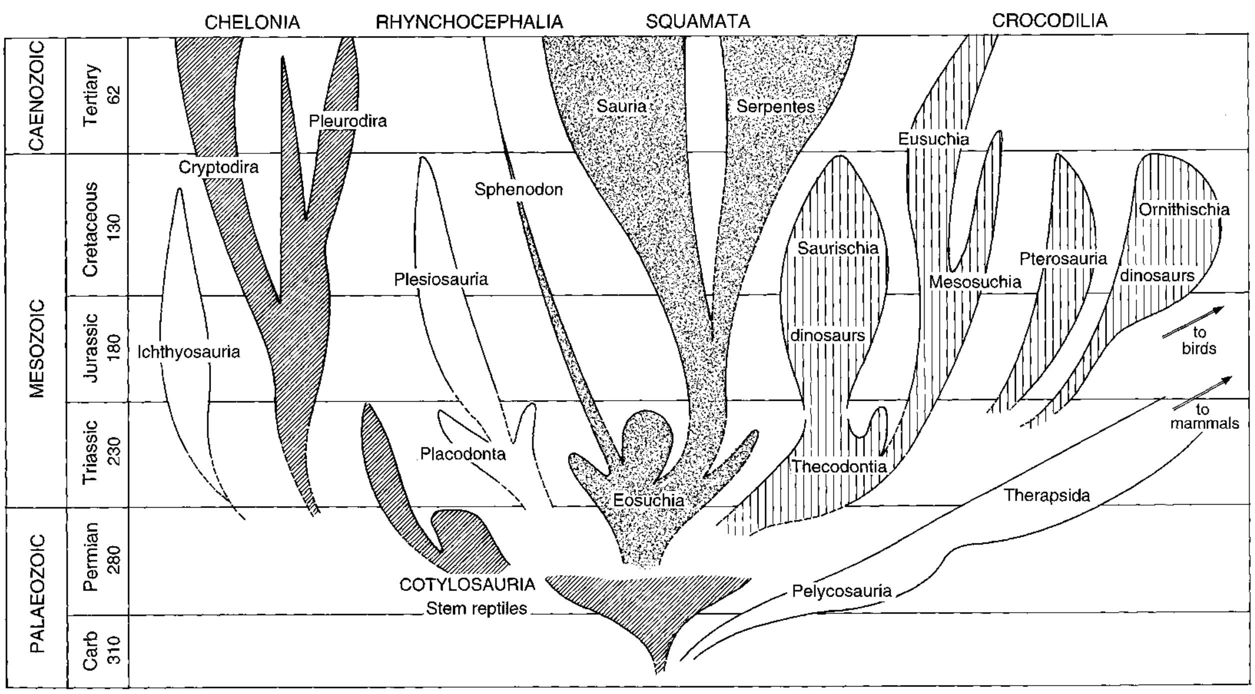

Figure 12.1 The evolutionary history and relationships of the Class Reptilia. The diversity of each subclass through time is indicated by its relative width in the diagram. (Modified after Bellairs 1969) [W. Mumford]

was the traditional view of modern reptilian relationships challenged (for example, Gauthier, Estes and de Quieroz 1988). This revised classification removed the synapsids entirely from the Reptilia, retained the anapsid turtles within the order Chelonia, and placed the birds, with crocodilians, in the subclass Archosauria. The remaining extant reptiles were assigned to the subclass Lepidosauria.

Table 12.1 The higher classification of the Class Reptilia. (After Romer 1956)

	Subclass Anapsida
	Order Cotylosauria
	Order Chelonia
	Subclass Lepidosauria
	Order Eosuchia
	Order Rhynchocephalia
	Order Squamata
'Sauropsid' orders	Subclass Archosauria
	Order Thecodontia
	Order Crocodilia
	Order Saurischia
	Order Ornithischia
	Order Pterosauria
	Subclass Uncertain
	Order Mesosauria
	Subclass Ichthyopterygia
	Order Ichthyosauria
'Theropsid' orders	Subclass Euryapsida
	Order Protorosauria
	Order Sauropterygia
	Subclass Synapsida
	Order Pelycosauria
	Order Therapsida

A key element of recent studies of reptilian evolutionary relationships has been the issue of the monophyly of the diapsid reptiles (the subclass Diapsida of some classifications). Romer (1956) and others believed that the diapsid condition of the skull had evolved independently in archosaurs and lepidosaurs. Gauthier (1984), Gauthier *et al*. (1988), and others have argued for the monophyly of the Diapsida.

The following key distinguishes the living orders of reptiles found in Australia. These orders include all extant reptiles except the sphenodontid tuataras of New Zealand. The latter have had a chequered classificatory history, being long regarded as members of the lepidosaurian order (or sometimes superorder) Rhynchocephalia, from which they were removed (Carroll 1977a), but to which they have been returned recently (Gauthier *et al*. 1988).

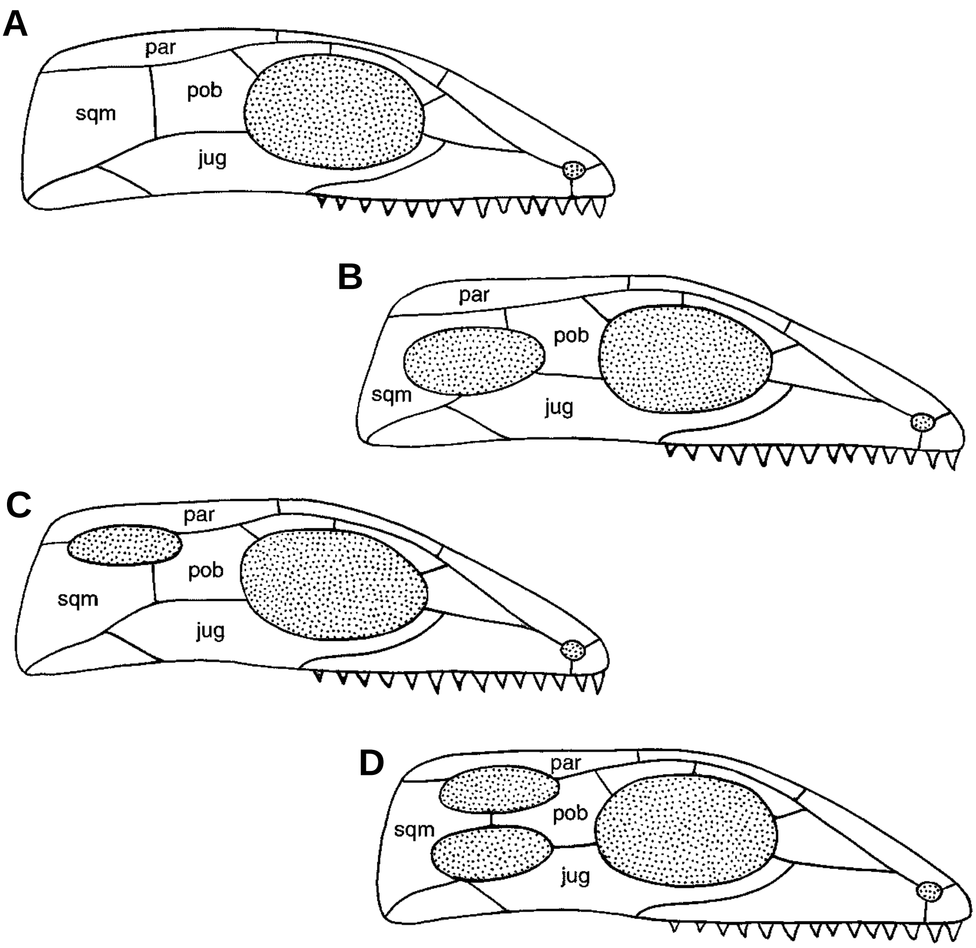

Figure 12.2 The arrangement of the temporal openings in four reptilian subclasses. **A**, Anapsida; **B**, Parapsida; **C**, Synapsida; **D**, Diapsida. **jug**, jugal; **par**, parietal; **pob**, postorbital; **sqm**, squamosal. (After Romer 1945) [D. Wahl]

Key to the orders of Australian reptiles

1 (a) Head/neck and limbs protruding from a hard, bony shell to which the underlying vertebrae and ribs are fused; no teeth, the jaws covered by a horny sheath; anapsid skull, without any temporal opening; single copulatory organChelonia

(b) No bony shell, the neck and limbs attached to a scaly body with a flexible vertebral column; jaws with teeth; diapsid skull, usually with two temporal openings on each side; single or paired copulatory organs2

2 (a) Thecodont teeth; a fully developed secondary palate; well-developed gastralia present; cloacal opening longitudinal Crocodylia

(b) Acrodont or pleurodont teeth; no fully-developed secondary palate; gastralia absent; cloacal opening transverseSquamata

The brief diagnoses in this key are extended in the individual chapters on each of these orders. In summary, modern reptiles (Class Reptilia) may be characterised by a combination of general features, though the adaptations of individual groups or species have led to full or partial loss of limbs, viviparous modes of reproduction and so forth. The bony skeleton is well-ossified. The well-developed limbs articulate with the large pectoral and pelvic girdles. The skin is dry and scaly, and its outer horny layer is periodically shed (sloughed). Skin glands are generally absent, and the vomero-nasal (Jacobson's) organ is well-developed, though not in adult crocodilians. Osteoderms are often present under the skin. The egg is cleidoic. The skull moves freely on a single condyle, and the first two vertebrae are modified to form an atlas and axis.