

because 'demon nuclei' are produced.

Even more recently, important difficulties with this suggestion have been raised by H.J. Lipkin of the Weizmann Institute. Crucial in creating a demon deuteron from three di-quarks is the role of the Pauli principle. Having all three di-quarks in s orbitals violates the Pauli principle and so the authors suggest each di-quark is in a p orbital, the three of them coupling to a total  $L = 0$  state with negative parity.

Lipkin points out that as there are only two independent orbital angular moments in a three-body system, then the  $J^P = 0^-$  object made from three  $J^P = 0^+$  di-quarks cannot exist. The so-called demon state is a spurious state of centre-of-mass motion in which the centre-of-mass of the three di-quarks is oscillating in a p-wave. When this

spurious excitation is removed by putting the centre-of-mass in an S-state then one obtains an allowed state with total angular momentum of one. This isoscalar  $J^P = 1^+$  has the same quantum numbers as the deuteron, might very well be mixed into the deuteron's wave function and be detectable in measurements of the deuteron's form factors. However it would not be expected to occur as a separate metastable state.

Thus the observation of anomalous nuclear processes on the one hand and the possible occurrence of new multi-quark configurations in nuclear matter on the other remain, for the moment, unconnected. If demon nuclei do exist it seems that they do not occur in the way that the Swedish group claim. □

noted the resemblance of many features of the skull and skeleton of the thecodontian *Chasmatosaurus (Proterosuchus)* to those of rhynchosaurs. Carroll<sup>4,5</sup> developed these ideas further and demonstrated close similarities between *Heleosaurus*, a late Permian eosuchian, and the early Triassic thecodontian *Euparkeria*. Although clearly similar to *Youngina*, *Heleosaurus* had a dentition very like that of *Euparkeria* and it may have been capable of an upright posture, an advanced feature of many archosaurs. Gow<sup>6</sup> redescribed *Youngina*, and also suggested that it was close to the ancestry of archosaurs.

New information on the affinities of rhynchosaurs and sphenodontids is also damaging to the integrity of Romer's Lepidosauria for it is believed that these two groups are particularly closely related. Carroll<sup>7</sup> redescribed *Noteosuchus*, a partial skeleton from the early Triassic of South Africa, and interpreted it as the oldest known rhynchosaur. Its ankle structure is similar to that of *Chasmatosaurus (Proterosuchus)*. Carroll stressed that there is no evidence for a close relationship between rhynchosaurs and sphenodontids and that supposed shared characters are either primitive features of all diapsids, or they have been wrongly interpreted. For example, the living *Sphenodon* has acrodont teeth (fused to the summit of the jaw bone), while rhynchosaurs had deeply rooted teeth. *Sphenodon* has a row of teeth on two

## The Diapsida: revolution in reptile relationships

from Michael J. Benton

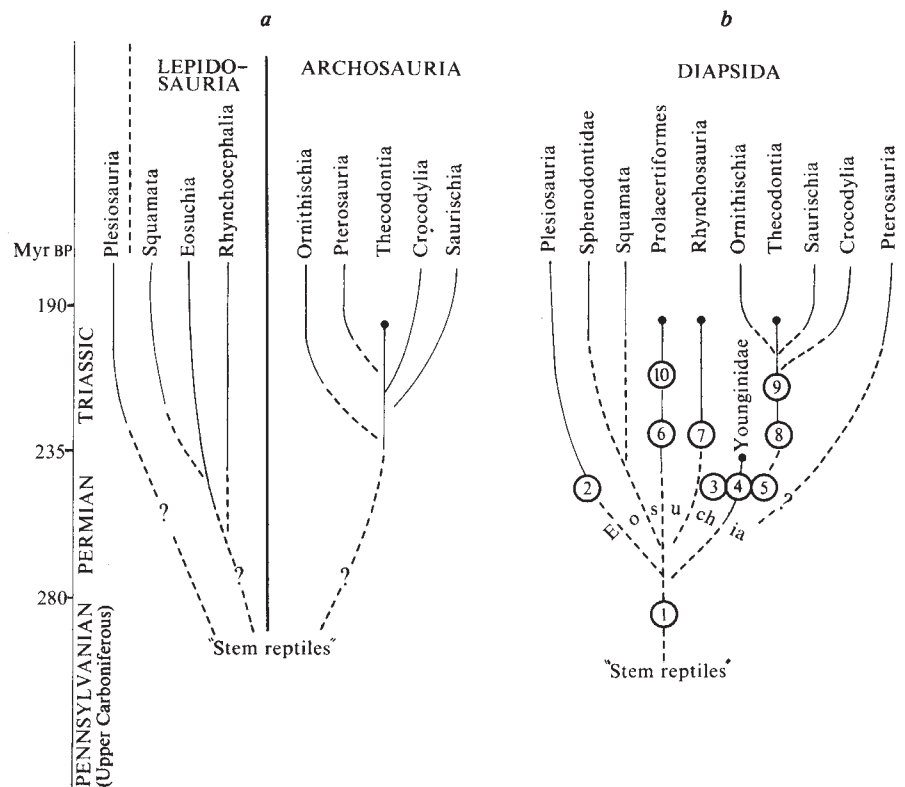
DISCOVERIES of new fossils and reinterpretation of existing data suggest the need for a major change in the traditional view of the relationships and ancestry of the lizards, snakes, crocodiles, dinosaurs and many extinct groups of reptiles. In standard textbooks (for example, Romer's *Vertebrate Paleontology*), the reptiles are divided into subclasses according to the number of openings behind the eye sockets. Those with two openings, the Diapsida, are further divided into two groups, the Lepidosauria (including lizards, snakes, sphenodontids, rhynchosaurs and eosuchians) and the Archosauria (including the thecodontians, crocodiles, dinosaurs and pterosaurs), that are thought to have diverged from separate ancestors as early as the Upper Carboniferous (Pennsylvanian; see Fig. 1a). The new view (summarized in Fig. 1b) is that all diapsids have a common ancestry and that their classification will have to be completely revised.

Romer<sup>1</sup> considered that lepidosaur groups, including the lizards, snakes, sphenodontids and rhynchosaurs (medium-sized 'beaked' and probably herbivorous reptiles of the Triassic), all derived from the eosuchians, a mixed group of primitive forms, of which *Youngina* from the late Permian of South Africa is usually regarded as typical. In contrast, archosaur groups, including the crocodiles, dinosaurs and pterosaurs, were considered to be derived from thecodon-

tians, such as the early Triassic *Chasmatosaurus (Proterosuchus)*.

More recent results now suggest that both lepidosaurs and archosaurs had common ancestors among the eosuchians<sup>2,3</sup>. Cruickshank<sup>3</sup> particularly

Fig. 1 Evolution of some major groups of reptiles, according to Romer<sup>1</sup> (a) and to recent work (b). Animals mentioned in the text are shown in b as follows: 1, *Petrolacosaurus*; 2, *Claudiosaurus*; 3, *Youngina*; 4, *Thadeosaurus*; 5, *Heleosaurus*; 6, *Prolacerta*; 7, *Noteosuchus*; 8, *Chasmatosaurus (Proterosuchus)*; 9, *Euparkeria*; and 10, *Tanystropheus*.



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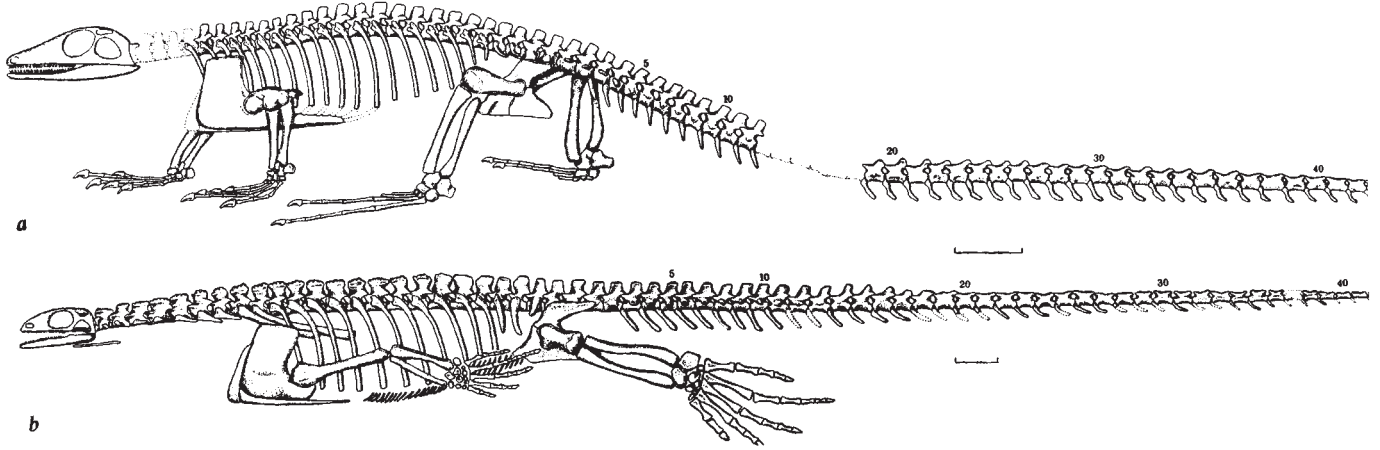


Fig. 2 Restorations of the skeletons of *Thadeosaurus* (a) and *Claudiosaurus* (b) in side view. *Claudiosaurus* is shown in a swimming pose. Scale bars are 2 cm. The similarities between *Claudiosaurus*, supposedly the earliest plesiosaur, and *Thadeosaurus*, a contemporary eosuchian from Madagascar, suggest a close relationship. After Carroll<sup>14</sup>.

separate bones of the palate (the maxilla and the palatine), while the multiple rows of teeth in rhynchosaurs are all on the maxilla. *Sphenodon* appears to show more affinity with ancestral lizards.

New evidence also suggests that the Pterosauria should be removed from the Archosauria and recognized as a distinct group. As early as the late Triassic, pterosaurs from Italy, described by Wild<sup>8</sup>, had all the special adaptations of the group for flight and had diversified into two quite different stocks. Wild suggested that pterosaurs originated directly from the eosuchians in the early Triassic since their anatomy suggests that they derived from small running insectivorous forms. The thecodontians of the Triassic were generally too large or otherwise unsuitable as ancestors, and there would probably have been insufficient time for a radiation from them to have occurred.

We can now discern four separate lineages of diapsid reptiles that radiated from the Eosuchia in the late Permian: pterosaurs, thecodontians, rhynchosaurs, and a group made up of lizards, snakes and perhaps sphenodontids. But how do we define the Eosuchia?

Romer<sup>1</sup> included a broad group of Younginiformes, the Prolacertiformes (centred on *Prolacerta*, an advanced form from the early Triassic of South Africa, that shows some parallel features to lizards) as well as some later aquatic forms. Evans<sup>9</sup> noted that the Eosuchia have no diagnostic advanced characters and can only be defined by the absence of features typical of other groups. Thus, she broadened the Eosuchia to include all diapsid reptiles except the archosaurs, the lizards and snakes. Further work may enable us to extract some of the motley collection of reptile families from the eosuchian rag-bag when we understand more about the diapsid radiations in the Permian and Triassic.

The confusion over the definition and limits of the Eosuchia makes it difficult to decide whether the Eosuchia had a

common ancestor, but an apparently suitable form exists. *Petrolacosaurus* from the late Pennsylvanian (260 million years ago) of Kansas has been redescribed recently on the basis of much new material<sup>10</sup>. It was clearly a diapsid, but certain features also indicate its ancestry among the 'stem reptiles'. Chatterjee<sup>11</sup> has included *Petrolacosaurus* in the Prolacertiformes, together with several Permian and Triassic reptiles. He regards the enlarged prolacertiform group as a lineage evolving separately from other eosuchians. Wild<sup>12</sup> has independently come to a similar conclusion on the basis of a re-study of the curious long-necked *Tanystropheus* from the middle Triassic

period of Switzerland.

One recent study adds a further dimension to the diapsid reptiles by suggesting that the aquatic plesiosaurs, previously of uncertain affinities, derived from the Eosuchia. Carroll<sup>13</sup> described two reptiles from the late Permian of Madagascar: *Thadeosaurus*, a younginid eosuchian, and *Claudiosaurus*, which he interprets as the first plesiosaur (see Figs 2,3). *Claudiosaurus* resembles younginids in its general anatomy, but it lacks the lower temporal bar and has a closed palate — typical plesiosaur features. Although it does not show all of the particular adaptations for aquatic locomotion that plesiosaurs had (paddle-like limbs, streamlined body, strong tail), certain features suggest that it was a swimmer (poorly ossified wrist and ankle, proportions of the limbs, small skull, long neck). The ancestry of plesiosaurs has been problematical, but Carroll makes a strong case for their derivation directly from diapsid reptiles during the Permian.

There now seems to be little evidence for the separate status of the Lepidosauria and the Archosauria, and it appears that all diapsid reptiles can be derived from *Petrolacosaurus*. Thus, we may re-instate the Subclass Diapsida, established by Osborn<sup>14</sup> in 1903. This group will now contain a large number of forms, many of them poorly known, and future work must concentrate on sorting out their relationships. □

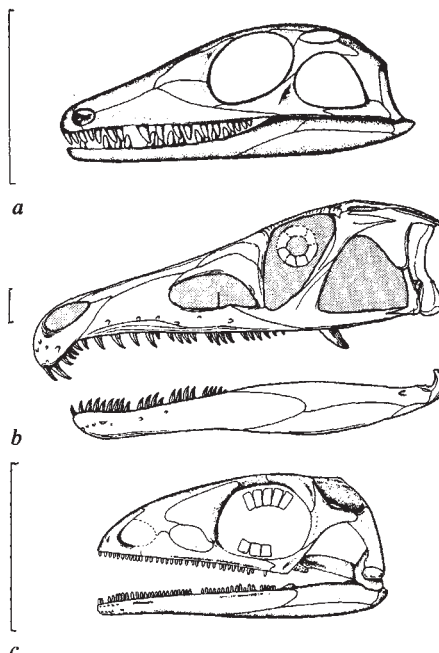


Fig. 3 Side views of the skulls of *Youngina* (a), *Chasmatosaurus* (*Proterosuchus*) (b) and *Claudiosaurus* (c), an eosuchian, a thecodontian and what may be the earliest plesiosaur respectively. These early representatives of the groups show considerable similarity. Scale bars are 2 cm. After Carroll<sup>14</sup> and Cruickshank<sup>3</sup>.

1. Romer *Vertebrate Paleontology* (Chicago, 1966).
2. Hughes *J. Zool., Lond.* 156, 457 (1968).
3. Cruickshank *Studies in Vertebrate Evolution*, 89 (Oliver & Boyd, 1982).
4. Carroll *Colloque int. C.N.R.S.* 218, 433 (1975).
5. Carroll *Athlon*, 58 (Royal Ontario Museum, 1976).
6. Gow *Palaont. afr.* 18, 89 (1975).
7. Carroll *Ann. S. Afr. Mus.* 72, 37 (1976).
8. Wild *Bull. Soc. paleont. Italiana* 17, 176 (1978), and see Cox, B. *Nature, News and Views* 284, 400 (1980).
9. Evans *Zool. J. Linn. Soc.* 70, 203 (1980).
10. Reisz *Univ. Kansas Mus. nat. Hist. spec. Publ.* 7, 1 (1981).
11. Chatterjee *Phil. Trans. R. Soc. B* 291, 163 (1980), and see Cox, B. *Nature, News and Views* 289, 745 (1981).
12. Wild *Schweiz. paläont. Abh.* 102, 1 (1980).
13. Carroll *Phil. Trans. R. Soc. B* 293, 315 (1981).
14. Osborn *Mem. Am. Mus. nat. Hist.* 1, 451 (1903).