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Fossil reptiles of the German Late Triassic and the Origin of the Dinosaurs

By Michael J. BENTON (Oxford)

The first dinosaurs are known from the late Triassic (Carnian/ Norian) of several localities around the world. It has commonly been believed that dinosaurs came onto the scene gradually, over many millions of years, during the middle and late Triassic, and that their radiation to dominate latest Triassic terrestrial faunas was the result of successful competition with mammal-like reptiles and thecodontians. An opposing view, that dinosaurs radiated to dominance rapidly in the middle Norian after a mass extinction has been proposed recently (BENTON 1983a, b, 1984). The middle and late Triassic terrestrial sedimentary sequences of Germany provide evidence about the evolution of the reptiles, and about the nature of the initial great radiation of the dinosaurs. This evidence is presented here, and it supports the view of a mass extinction of reptiles in the middle Norian, and the subsequent opportunistic radiation of dinosaurs in the middle-late Norian.

What is a dinosaur?

The term "dinosaur" is commonly regarded as a useful summary term for a polyphyletic group consisting of the Orders Saurischia and Ornithischia, which are supposed to have arisen from two, three or four ancestors (CHARIG 1982). However, it seems highly probable that the dinosaurs, as commonly understood, do in fact form a monophyletic group, the Dinosauria (BAKKER & GALTON 1974, BENTON & NORMAN, in prep.), defined by several synapomorphies, in comparison with "thecodontians", and with the Family Ornithosuchidae as the sister-group of the Dinosauria:

(1) Loss of the postfrontal.
(2) Deltopectoral crest runs far down the shaft of the humerus.
(3) Arm is about half as long as the leg.

(4) Reduced pubis/ ischium contact.
(5) Lesser trochanter on the femur is a spike or crest.
(6) Trochanter 4 is prominent and low on the femur.
(7) Proximal head of the femur is set off from the shaft.
(8) Twisted tibia.
(9) Reduced roller-like astragalus with an ascending process.
(10) Calcaneum is reduced or absent.
(11) Advanced mesotarsal ankle joint.
(12) Pes digits II-IV are in a bundle, elongate and subequal in length.
(13) Pes digits I and V are reduced and divergent.
(14) Foot has a digitigrade pose.

What is the oldest dinosaur?

Many authors still assume that the oldest known dinosaurs are middle, or even early Triassic in age. This assertion is based on two sets of data which I regard as incorrect: (1) thecodontian remains wrongly ascribed to dinosaurs; (2) incorrectly dated geological formations.

(1) HUENE (1908, 1932) and others listed dozens of so-called dinosaur remains from the middle and late Triassic of Germany and England which have subsequently turned out to belong to thecodontians, prolacertiforms, or placodonts, or to be indeterminate. Many middle Triassic remains that were called Procerosaurus, Thecodontosaurus or Zanclodon belong to the prolacertiform Tanystropheus (WILD 1973). The type jaw of Teratosaurus, and other "teratosaurid" teeth belong to rauisuchid thecodontians, or their close relatives, or they are indeterminate "archosaurian". The remaining middle Triassic "dinosaurs" include two "coelurosaur femora" from the Unteren Muschelkalk (Anisian) of SE Baden (HUENE 1914) - possibly placodont humeri; Avipes, a bunch of three incomplete metatarsals(?) from the Lettenkeuper (Upper Ladinian) of E Germany (HUENE 1932) - indeterminate metatarsals or ribs; and two "Coelurosaurierzähne" from the Lettenkeuper (Upper Ladinian) of Erfurt (HUENE 1932) - prolacertiform or archosaur teeth (?). HUENE (1908, 1932) also described two "dinosaur" teeth from the Schilfsandstein of Stuttgart and from a Blasensandstein equivalent of Lubetzko (both of Carnian age), but these are again indeterminate.

(2) Certain fossiliferous formations in South America that include rare early dinosaurs (e.g. Santa Maria Formation of Brazil, Ischigualasto Formation of Argentina) have been dated as middle Triassic in age. However, a variety of evidence now shows that both of these formations are late Triassic in age (Santa Maria Formation: Carnian/ Norian boundary (?); Ischigualasto Formation: Lower Norian (?)) (ANDERSON & CRUICKSHANK 1978, ANDERSON 1981; TUCKER & BENTON 1982, BENTON 1983a). Thus, the "middle Triassic" dinosaurs from these two formations are in fact upper Triassic in age.

The oldest dinosaurs, then, are known from the Upper Carnian - Lower Norian interval of the Upper Triassic from several localities around the world: Staurikosaurus (Santa Maria Formation, Brazil); Herrerasaurus, Ischisaurus, Pisanosaurus (Ischigualasto Formation, Argentina); Saltopus (Lossiemouth Sandstone Formation, Scotland), and unnamed forms (Maleri Formation, India). In the middle Norian

of Germany (Stubensandstein) and North America (Upper Chinle Formation), dinosaurs became more abundant, and they came to dominate latest Triassic faunas (BENTON 1983a).

Stratigraphy of the latest Triassic in Germany

The lithostratigraphic subdivisions of the Mittelkeuper of SW Germany are well established (e.g. BRENNER 1973, BRENNER & VILLINGER 1981, GWINNER 1981). However, these terrestrial sequences have not been clearly correlated with the standard Alpine marine sequences, dated with ammonites (TOZER 1974, 1979), or with palynologically dated horizons in Central Europe (e.g. VISSCHER & BRUGMAN 1981). Stratigraphic questions are further complicated by recent redefinitions of the late Triassic stages (c.f. TOZER 1979, FISHER & DUNAY 1981), and by considerable diagreement in radiometric dating of the stage boundaries (c.f. HARLAND et al. 1982, ODIN 1982, PALMER 1983). The sequence in Baden-Württemberg (SW Germany) is (Table 1):

Table 1. Stratigraphy of the SW German Keuper, with approximate stratigraphic assignments (ANDERSON 1981) and exact ages in Ma from (1) HARLAND et al. 1982, (2) ODIN 1982, (3) PALMER 1983).

			(1)	(2)	(3)
Lias		HETTANGIAN			
			213	204	208
Rät		(RHAETIAN)			
Knollenmergel	Upper				
Stubensandstein (1-4)	Middle	NORIAN			
Kieselsandstein					
Rote Wand	Lower				
			225	220	225
Schilfsandstein	Upper	CARNIAN			
Gipskeuper	Lower				
			231	229	230
Lettenkeuper	Upper	LADINIAN			

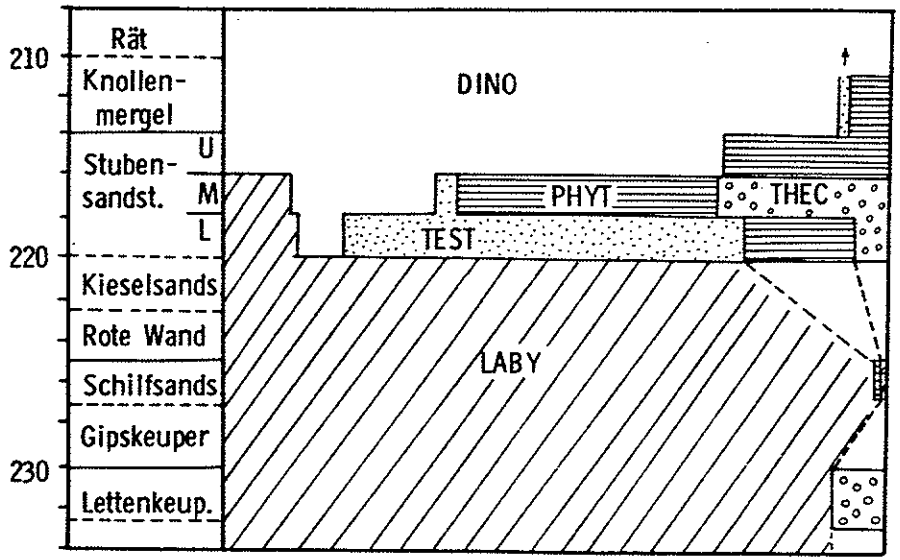
The appearance of dinosaurs in Germany

The earliest dinosaurs known from Germany occur in the Unterer Stubensandstein of Ochsenbach on the Stromberg ("plateosaur"), and Ebersbach, near Göppingen (?Plateosaurus). In the Mittlerer Stubensandstein, Plateosaurus and other prosauropod dinosaurs became more abundant, and specimens of the coelurosaurs Procompsognathus and Halticosaurus occur. In the Oberer Stubensandstein and the Knollenmergel, the prosauropod dinosaurs came to dominate the faunas of SW Germany.

A crude approximation of the pattern of the faunal changes that occurred in the late Triassic of SW Germany was obtained by studying the two largest representative museum collections, in Stuttgart and

in Tübingen. Numbers of specimens of each genus were recorded for each geological formation, and these were converted to percentages of the totals (Fig. 1). It can be seen that the labyrinthodont amphibians declined in abundance and disappeared at the end of the Mittlerer Stubensandstein. Early turtles (Proganochelys) were abundant in the Unterer Stubensandstein. Thecodontians (rauisuchians, aetosaurs) disappeared at the end of the Mittlerer Stubensandstein, while phytosaurs disappeared probably at the very end of the Triassic. Dinosaurs, particularly prosauropods, rose in abundance from 7% of all specimens in the Unterer Stubensandstein, to 20% in the Mittlerer, 77% in the Oberer, and 95% in the Knollenmergel.

Fig. 1. Approximate relative abundances of different groups of tetrapods in the Keuper (Upper Ladinian - Upper Norian) of SW Germany. Data compiled from the Stuttgart and Tübingen collections. Abbreviations: DINO dinosaurs, LABY labyrinthodonts, PHYT phytosaurs, TEST turtles, THEC thecodontians (excluding phytosaurs).



The pattern of the increase in the relative abundance of dinosaurs that occurred between the Unterer Stubensandstein and the Knollenmergel shows the approximate shape of their initial "adaptive radiation" in SW Germany. This radiation occupied a span of approximately 8 million years in total, according to the very crude stratigraphic information that is available. The greatest increase in dinosaur abundance, which occurred between the Mittlerer and Oberer Stubensandstein, occupied a span of perhaps 2-4 million years.

The evidence from SW Germany supports the view, expressed in general terms elsewhere (BENTON 1983a, b, 1984) that the dinosaurs

initially radiated much more rapidly than has previously been recognised, and that this radiation probably followed opportunistically after a mass extinction event in the middle Norian (?end of the Mittlerer Stubensandstein). The German data give little support to the commonly held view that the dinosaurs succeeded after a drawn-out process of competition with the thecodontians and other reptiles.

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