

## Late Triassic Faunal Successions of Central Pangaea

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### ABSTRACT

Mass extinctions have long been recognized in the fossil record. The end Permian extinction was by far the greatest of these, and the terminal Cretaceous extinction is well known for the demise of the dinosaurs. However the exact nature, timing and causes of such events are still disputed. Large scale global extinctions are known to have occurred at the end of the Triassic period. The Triassic period is a key period in the evolution of modern terrestrial vertebrates. Triassic sediments in Virginia are producing rich and varied faunas which are beginning to shed considerable light on global events at this time.

Key Words: Triassic, Carnian, Norian, Pangaea, Virginia, tetrapods, extinctions, Newark Supergroup.

### INTRODUCTION

Extinction is an integral part of macroevolution, and in some ways it can be viewed as a balancing effect on mechanisms of species origination. In recent years interest in extinctions has centered upon two aspects. 1) Man's ability to alter population numbers drastically in a very short period of time has generated increasing debate. 2) No less a controversial subject is the nature of extinctions throughout the history of life. In the case of the former we have difficulty assessing the impact of man over a relatively prolonged period of time since the database has only been accumulated over the last few decades. In the case of the latter the reverse is true: we know the effect over a long period of time, but we have difficulty in resolving the exact pattern and tempo of extinctions.

Major crises in the earth's biota are often viewed as a departure from the "normal" process of evolution. Yet mass extinctions, whilst decreasing diversity in the short term, may have operated to maintain the ecological diversity of life on a geologic time-scale. Initial analyses of global mass extinctions (and radiations) were at the stratigraphic level of stage and the taxonomic level of family (e.g. Sepkoski, 1982; Benton, 1985a), but such studies have proved too general to be able to resolve many of the more critical questions. There is a need for more detailed analyses using data at least at the regional, generic (and preferably species) and zonal levels.

The controversial proposal that a meteorite impact may have caused mass extinctions at the close of the Cretaceous period (Alvarez et al., 1980) produced a resurgence of interest in the demise of the dinosaurs. While the evidence for an impact is now very compelling, whether it was responsible for the sudden extinction of groups such as the dinosaurs is equivocal. Part of the dispute lies in the difficulty of dating sediments to within less than  $\pm 1$  million years, and then correlating these sediments to other areas worldwide. Assessing the nature, timing and causes of other so-called mass extinction events, such as the great end Permian extinction, are subject to the same problems. Likewise, although the proposal of Raup and Sepkoski (1984) that there is a 26 million year periodicity in mass extinctions has

received some support, once again the evidence is inconclusive when the inadequacy of the geological time scale is taken into account.

A mass extinction at the end of the Triassic has been recognized by many authors (Colbert, 1958; Newell, 1967; Hallam, 1981; Raup and Sepkoski, 1982) although it is not widely cited in the popular literature because it does not mark the disappearance of any well known group. Recent work by Olsen and colleagues (Olsen et al., 1978; Olsen, 1986, 1988; Olsen et al., 1987) on Triassic - Jurassic deposits of eastern North America strongly suggest that very fine temporal control is provided by sedimentary cycles produced by the rise and fall in the levels of Triassic lake systems. Many of these deposits contain rich vertebrate remains and there is therefore a potential to examine faunal change at the end of the Triassic to a remarkably fine resolution of time.

#### TERRESTRIAL VERTEBRATE EVOLUTION IN THE TRIASSIC

The Triassic period is perhaps the most important time in the evolution of terrestrial vertebrates. The end of the period saw the evolution of most modern terrestrial vertebrates, so that the first fossil mammals, crocodiles, turtles, sphenodontians, lissamphibians, and reportedly birds (Chatterjee, 1991, but see Ostrom, 1991) are known from Triassic deposits. Furthermore if sphenodontians are the closest sister group to lizards (Gardiner, 1982; Evans, 1984, 1988; Benton, 1985b), then by implication early lizards must also have been present by the end of the Triassic. In addition to these "modern" groups the Triassic also witnessed the appearance of the first dinosaurs and pterosaurs.

The marine fossil record shows that there were three putative mass extinctions in the Triassic. Firstly the beginning of the period is marked by the greatest of all recognised extinctions, the so-called end Permian event. It has even been suggested that as few as 4% of all species present in the Permian world survived into the Triassic (McGhee, 1989). Secondly the period closes with another major extinction episode marking the beginning of the Jurassic. The third Triassic extinction occurs at the end of the Carnian stage. Some authors regard this as a relatively minor event (Olsen and Sues, 1986), whereas others argue that this is the most pronounced Upper Triassic mass extinction with a drastic decrease in diversity of many groups (Benton, 1992), and that the episode that followed at the close of the period (i.e. at the Norian-Hettangian boundary) was little more than the final disappearance of these depauperate taxa.

#### Causes of Triassic extinctions

At the close of the Permian period the continents came together to form the supercontinent Pangaea (Figure 1). This major palaeogeographical change may have been responsible for many of the extinctions, particularly the drastic reduction in species from coastal waters. However the exact causes and timing are unknown and it may well have been the result of a number of complex factors occurring over a period of thousands or millions of years. There is little evidence in favor of a sudden drastic decline in the biota taking place in a matter of months or years, but an extinction over a much shorter period of time cannot be ruled out.

Throughout Triassic times the continents remained united, but the rifting which preceded the separation of North America from Europe and Africa in the Jurassic

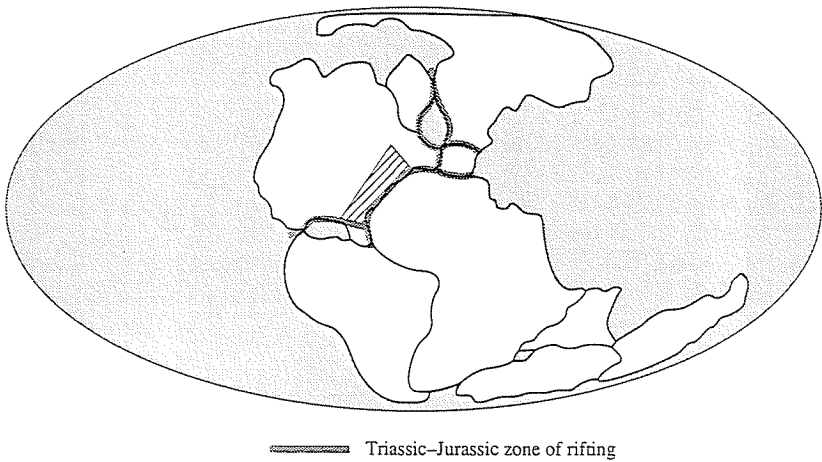


FIGURE 1. The relative position of the continental land masses towards the end of the Triassic period. The location of the Newark Supergroup is cross-hatched.

had begun (Figure 1). Evidence suggests that reptiles and amphibians migrated extensively, for there was a fairly homogeneous vertebrate fauna worldwide.

Major faunal changes occurred on land during Triassic times. As a result of the end Permian mass extinction the faunas were restricted at the beginning of the period, but the mammal-like reptiles re-radiated and the archosaurs ("thecondontians") and rhynchosaurs flourished. The end of the period saw the initial radiations of the dinosaurs and pterosaurs as well as the modern terrestrial vertebrate groups. However the transition from Middle to Late Triassic assemblages is poorly understood. There are two alternative theories accounting for the demise of the rhynchosaurs, the early archosaurs and many mammal-like reptile groups during the Triassic. Either they gradually died out through late Middle and early Late Triassic times through competitive replacement with the dinosaurs (Charig, 1984), or they disappeared suddenly at the end of the Carnian stage (early Late Triassic) allowing the dinosaurs to radiate opportunistically (Benton, 1983). It is difficult to reconcile the notion that families or orders of animals can compete with each other with the ecological concept of competition within or between species. In addition the role of competition in shaping ecological communities and its effects on evolutionary changes in species distribution or adaptation have been questioned by some authors (Connell, 1980; Simberloff, 1983; Price et al., 1984). Consequently I favor opportunistic replacement over the competitive replacement model. At the same time the evidence for a mass extinction of land vertebrates at the end of the Carnian stage is inconclusive and it has been suggested that it may in part merely represent a temporal discontinuity between the geographically disjunct Middle Triassic synapsid dominated assemblages characteristic of Gondwana (southern hemisphere), and the archosaur dominated assemblages typifying the Upper Triassic of Laurasia (northern hemisphere) (Sues and Olsen, 1991).

## THE TRIASSIC OF VIRGINIA

Late Triassic vertebrate localities in Virginia are particularly important and this survey follows the reviews by Olsen et al. (1978), Olsen (1988) and Sues and Olsen (1991). The early Mesozoic sediments of Virginia are part of what is known as the Newark Supergroup (Figure 2). The Newark Supergroup consists of a series of sediments deposited in rift basins running down the eastern part of North America. These rift basins formed during a 45 million year episode of crustal thinning and stretching which preceded the breakup of Pangaea during early Jurassic times. Within Virginia there are six main basins: Danville/ Dan River, Farmville, Scottsville, Richmond, Taylorsville, and the Culpeper basins (Figure 2). Recent research on these features has shown that their contained sediments sometimes contain abundant vertebrate remains.

A locality in the Richmond basin (Figure 2), which is of early to middle Carnian age, is yielding a diverse fauna of small tetrapods. To date it has produced abundant remains of a new traversodont eucynodont, *Boreogomphodon jeffersoni* (Sues and Olsen, 1991), which is very similar to *Luangwa* from the Anisian of Zambia and *Traversodon* from the Carnian of Brazil. Another eucynodont in the assemblage resembles *Microconodon* and *Pseudotriconodon* from the Carnian of North Carolina and the Norian of western Europe respectively.

Archosaurian remains at the Richmond locality consist of a number of isolated phytosaur teeth, and armor and postcranial elements of an unusual new species which shows at least a superficial resemblance in its armor to *Doswellia* from the adjacent Taylorsville basin (Weems, 1980). The structure of recently described venom-conducting teeth is also most consistent with an archosaur (Sues, 1991).

The abundant eucynodont synapsids are consistent with Gondwanan faunas whilst the phytosaurs show affinity to Upper Triassic Laurasian assemblages. Triassic sediments in the Deep River Basin (Figure 2) of North Carolina are slightly younger (middle Carnian) than the Richmond deposits, and they have produced tetrapod assemblages containing mostly phytosaurs and suchian archosaurs. Synapsids, including *Microconodon*, are rare. The occurrence of a dominantly "Gondwanan" type fauna from an early to middle Carnian locality in the Northern hemisphere suggests that previous distinctions between tetrapod assemblages of Gondwana and Laurasia may actually reflect age differences rather than a basic geographic separation. Furthermore, Sues (1991) has suggested that the rare occurrence of synapsids in the phytosaur and suchian archosaur dominated Middle Carnian assemblages of the Deep River basin in North Carolina indicates a Carnian faunal turnover rather than a major extinction at the Carnian-Norian boundary.

A second vertebrate-bearing locality in the Virginian Triassic occurs in the Late Carnian Cow Branch Formation. It is situated in the Danville/ Dan River basin (Figure 2), and it contains an exceptional flora and fauna (Olsen et al., 1978; Olsen, 1979). The vertebrate fauna described to date includes articulated fish and abundant beautifully preserved skeletons of the tanytropheid, *Tanytrachelos*, with some preservation of soft tissues. However the invertebrate fauna (which includes a diverse number of insects) and the flora are still to be described fully.

Disarticulated remains of *Tanytrachelos* are also known from a number of other Triassic localities in the Newark Supergroup, in particular from Norian sediments (Olsen and Flynn, 1989). On the other hand lithologically similar sediments to those

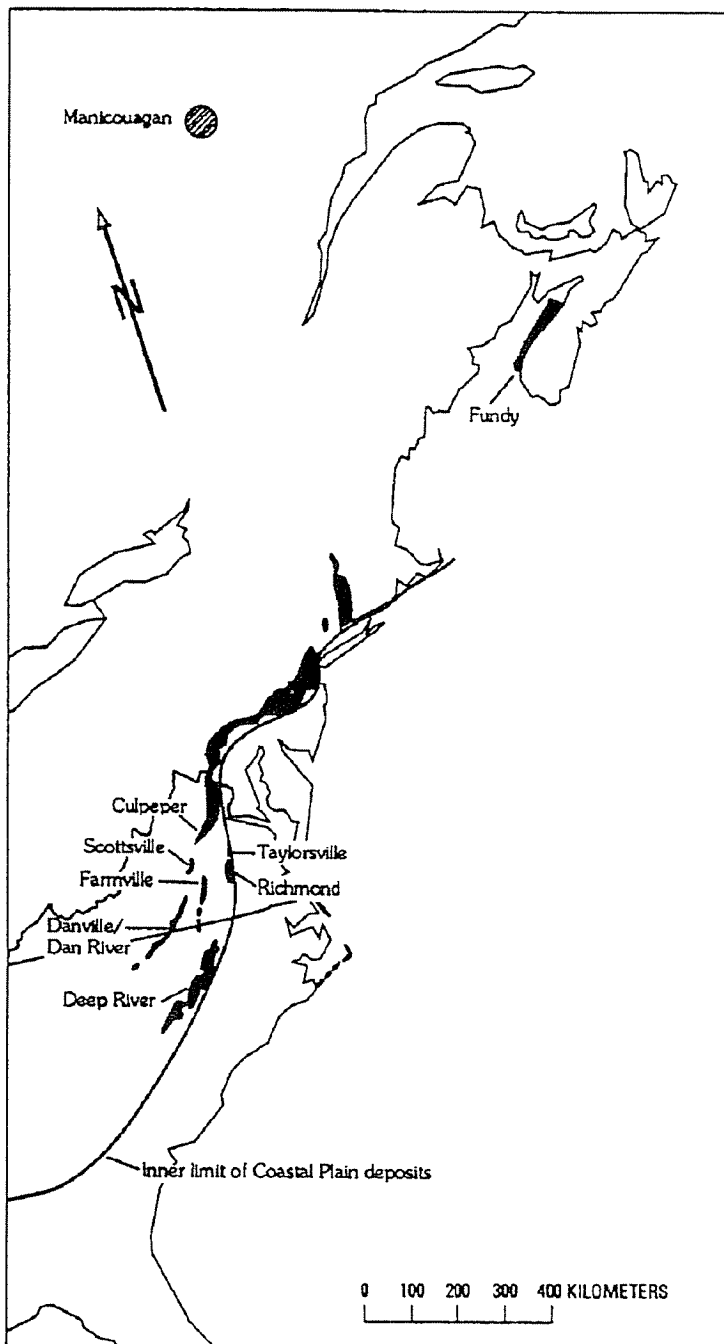


FIGURE 2. Occurrence of the Newark Supergroup sedimentary basins. After Olsen et al. (1987).

of the Cow Branch Formation in the Newark Supergroup which are Early Jurassic in age completely lack *Tanytrachelos*, despite the presence of articulated fish. Olsen (1992) has suggested that the lack of articulated *Tanytrachelos* specimens in the Norian of the Newark Supergroup is a function of the absence of units bearing articulated fish, but that the absence of any *Tanytrachelos* material in the Jurassic sections is a real phenomenon and reflects a Triassic-Jurassic extinction event.

The Danville/ Dan River locality also serves to illustrate an extremely important facet of the research into many of the sedimentary basins of the Newark Supergroup. Olsen (1986) showed that the sediments consist of repetitive sequences representing fluctuations in the levels of very large lakes. Changes in precipitation resulted in large scale increases and decreases in lake depth. Thus at localities such as the Dan River site and also at the Culpeper Stone Company Quarry in the Culpeper basin (Figure 2), repetitive sequences of massive mudcracked mudstones (deposited during lowstands) grade into deep water microlaminated muds (deposited during highstands). There is a sharp contact between cycles, but only a gradational change in lithology within cycles. This cyclic pattern has been compared with Quarternary sections exhibiting major climate cycles apparently controlled by variations in the earth's orbit (Olsen, 1986). Studies of Quarternary sections indicate that there are 21,000 year climate cycles corresponding to the precession of the equinoxes, 41,000 year climate cycles resulting from the variation of the tilt of the earth's axis relative to an axis perpendicular to the orbital plane, and approximately 95,000, 123,000 and 413,000 year climate cycles resulting from eccentricity cycles. Van Houten recognised several orders of cycles in the Newark Supergroup sedimentary sequences, and Olsen (1986) argued that such Van Houten cycles corresponded to 25,000 (precession of the equinoxes), 45,000 (obliquity cycle), 100,000, 133,000 and 400,000 years (eccentricity cycles). Repetition of these cycles appear to have continued throughout the 45 million year period during which the Newark Supergroup sediments were deposited. Since such sequences are widespread throughout the Newark Supergroup it is possible to determine the relative ages of sediments at any extensive quarry outcrop to within a few thousand years. In addition, on the basis of these characteristic cycles it may now be possible in some cases to cross-correlate sections within the Newark basins.

#### **Absolute Dating of the Triassic-Jurassic Boundary in the Newark Supergroup**

In the northern part of the Newark Supergroup, vertebrate-bearing assemblages of Jurassic age are yielding further valuable information (Sues et al., 1987) which may eventually allow a detailed age correlation of the entire Newark Supergroup. In the Fundy basin the age of the faunas is constrained by two separate lines of evidence. Firstly pollen and spore data strongly indicate a maximum of a Hettangian age (i.e immediately post-dating the Triassic-Jurassic boundary) (Olsen et al., 1987). Secondly the bone-bearing units are underlain by the extrusive North Mountain Basalt. The upper layers of this basalt unit are discontinuous in some areas, and interbed with the bone-bearing units. Conventional Potassium-Argon and Potassium-Argon isochron dates from the North Mountain Basalt, and therefore the vertebrate-bearing sediments, are consistent with an Early Jurassic age. The North Mountain Basalt in the Fundy basin correlates with the oldest of the extrusives known in the more southern Newark basins. The Triassic-Jurassic

boundary is palynologically fixed at about 30m below the oldest basalt (Orange Mountain in the Newark basin), which on the basis of climate cycles is about 100,000 years older than the oldest basalts. Typical lacustrine cycles occur interbedded with and underlying the basalt flows in the Newark basin. From these cycles, as well as other lines of evidence, the duration of the Newark extrusive episode has been estimated to be as short as 600,000 years (Olsen et al., 1987). Furthermore the vertebrate-bearing sediments immediately overlying the North Mountain Basalt in the Fundy basin are no more than 300,000 years younger than the boundary.

The Newark Supergroup therefore offers the opportunity to assess terrestrial vertebrate faunal turnover over a period of 45 million years (including the Triassic-Jurassic boundary), but at a much finer time resolution than is normally possible in Mesozoic sequences. Within the Newark Supergroup the data support an extinction event at the Triassic-Jurassic boundary with the sudden loss of taxa such as *Tanytrachelos*, various procolophonids and phytosaurs, which are abundant and ubiquitous to that point. In addition the evidence suggests a zero origination rate throughout the Hettangian (Olsen et al., 1987). Supposed originations in the Hettangian are equivocal. For instance the Gephyrosauridae have been recorded as an example of a Hettangian origination (Olsen and Sues, 1986), yet the relationships of basal sphenodontids remains unresolved (Fraser and Benton, 1989), and Fraser (1988) suggested that *Gephyrosaurus* together with the Triassic genera *Planocephalosaurus* and *Diphydontosaurus* may form a monophyletic taxon. Similarly, certain ichnotaxa, such as *Anomoepus*, might be cited as examples of Hettangian origination. Unfortunately the criteria for describing prints and trackways are not sufficiently well established to allow for age determinations based solely on ichnotaxa; but I have observed *Anomoepus*-like trackways in Triassic sediments in Virginia. Thus within the Newark Supergroup Early Jurassic faunas are characterised by the absence of certain Triassic taxa and, at present, no substantive evidence for the origination of new taxa. This is consistent with the proposal of a dramatic extinction event, at least locally. On the other hand the Newark Supergroup sequences do not suggest any major extinction event at the Carnian-Norian boundary.

#### GLOBAL TERRESTRIAL VERTEBRATE TURNOVER ACROSS THE TRIASSIC-JURASSIC BOUNDARY

The majority of Triassic and Jurassic vertebrate-bearing sequences in the rest of the world do not permit such a high resolution dating of the sediments. Therefore a global picture of faunal change across the Triassic-Jurassic boundary has been difficult to assess with any degree of confidence resulting in conflicting hypotheses regarding faunal turnover at the Triassic-Jurassic boundary (Olsen and Sues, 1986; Benton, 1992). Many of the classic vertebrate-bearing localities of the world are notoriously difficult to date. For instance the diverse range of British Mesozoic fissure deposits contain abundant and exceptionally preserved assemblages of reptiles and early mammals (Fraser, 1985), yet because of their isolation from normally bedded sequences it is generally only possible to assign a very approximate age to each assemblage. Even where vertebrates occur in well-bedded sediments such as the Lufeng Series of Yunnan, China, or the Stormberg Series of South

Africa, there are few unequivocal data to constrain the ages of the deposits (Colbert 1986).

Colbert (1958) exemplifies an early view that there was a catastrophic extinction marking the close of the Triassic period. However Olsen and Galton (1977) showed that many of the deposits which had previously been regarded as uppermost Triassic were in fact Early Jurassic in age. As a result many taxa thought to have disappeared at the end of the Triassic did in fact persist into the Jurassic, which in turn led Olsen and Galton to suggest that faunal turnover across the Triassic-Jurassic boundary followed a much more gradual pattern. However in recent years many more Early Mesozoic fossil discoveries have been made, and the opinion has once more shifted towards a catastrophic extinction event among terrestrial tetrapods in the Late Triassic, although, as mentioned earlier, there is some dispute with regard to the precise timing.

Although the Newark basins only give a picture of faunal turnover in the eastern part of the North American continent, Early Mesozoic faunas worldwide show a remarkable homogeneity, and many of the taxa in the Newark basins are now known from other Late Triassic and early Jurassic localities worldwide. Although some of these taxa appear to be relatively long ranging in time, research on the British fissure deposits indicates that some widespread forms may be very restricted (Fraser, 1992). Where such taxa occur in the Newark Supergroup it would be possible to use them as biostratigraphic indicators to date more accurately the sediments where they occur elsewhere.

Currently, research on the sphenodontids in the British fissure deposits indicates that the genus *Clevosaurus* (Figure 3) may be useful biostratigraphically (Fraser, 1992). At least three species are known in the fissure deposits, and apparently none of them have overlapping ranges (Fraser, 1988). The same (or at least a closely related) genus occurs in restricted sections of the Newark Supergroup (Sues, pers. comm.) and the Lufeng series of Yunnan, China (Wu, 1991). In some cases there even seems to be a very close resemblance at the species level in what are today disjunct occurrences of fossil sphenodontids.

The procolophonids, although widespread and abundant in Triassic rocks worldwide, are poorly known. However there has been renewed interest in the group recently. I have observed that some of the forms which occur in the Newark Supergroup and in British Triassic sediments appear to be very closely related indeed, and may prove to be congeneric. As mentioned above, within the Newark basins procolophonids occur right up to the Triassic-Jurassic boundary, but are completely absent above it. Elsewhere, although the position of the boundary may not be as well documented, procolophonids do not appear to extend beyond the end of the Triassic. Additional taxa which apparently do not survive beyond the Triassic include the phytosaurs and aetosaurs. Together with groups such as the sphenosuchid crocodiles, which do extend beyond the Triassic and also occur in the Newark Supergroup, it may be possible to develop a high resolution biostratigraphy for Early Mesozoic terrestrial vertebrates.

This work on the biostratigraphy is only in the preliminary stages, and to date the results are insufficient to indicate whether there was a catastrophic extinction episode at the Carnian-Norian or the Norian-Hettangian boundaries. However it is interesting to note that the Manicouagan impact structure in Quebec, Canada is



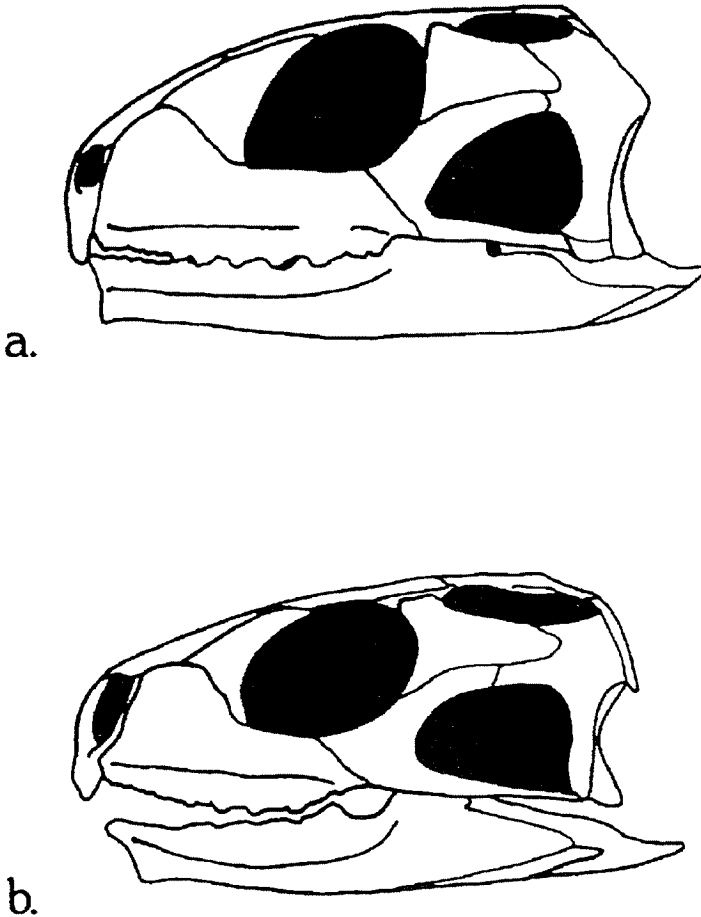


FIGURE 3. Skulls of clevosaur (Sphenodontida) in lateral view. a) *Clevosaurus wangi* and b) *Clevosaurus hudsoni*. ((a) after Carroll and Wild, 1992 and (b) after Fraser, 1988.)

a potential candidate for the cause of extinctions at the end of the Triassic. It has not proved possible to obtain a precise age for this structure, and dates range from 220 to 200 million years old. Accordingly either an end Carnian or an end Norian extinction episode could conceivably be attributed to the Manicouagan impact. Olsen et al. (1987) made the observation that the Triassic-Jurassic extinctions seem to parallel those at the Cretaceous-Tertiary boundary, and that, with the exception of dinosaurs (excluding birds), pterosaurs and a few mammal-like reptiles, the terrestrial vertebrate groups that survived the Triassic also survived the Cretaceous.

The recent research on the Triassic vertebrates of Virginia and eastern North America has added to our knowledge of the nature of Late Triassic terrestrial tetrapods. Further comparison of the Newark Supergroup fossil assemblages with contemporaneous faunas from elsewhere in the world may ultimately provide the answers to the nature of Early Mesozoic extinctions.

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