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GLOBAL CORRELATION OF THE TRIASSIC THEROPOD RECORD

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ABSTRACT: Theropod dinosaur body fossils are known from Upper Triassic (Carnian-Rhaetian) strata in North and South America, Greenland, Europe, and India. Theropod footprints, usually assigned to the ichnogenus *Grallator* HITCHCOCK and related ichnotaxa, have been described from the Upper Triassic of North America, Greenland, Europe, and Africa. These theropod occurrences are readily correlated as latest Carnian, Norian, and Rhaetian records. The earliest theropods are among the first dinosaurs and appear essentially synchronously in the Upper Triassic of the United States, the United Kingdom, Brazil, Argentina, and India. These theropods include herrerasaurs and ceratosaurs from the lower Chinle Group in the southwestern United States, the problematic theropod *Saltopus elginensis* HUENE from the Lossiemouth Sandstone in Scotland, the herrerasaurid *Staurikosaurus pricei* COLBERT from the Santa Maria Formation in Brazil, the herrerasaurid *Herrerasaurus ischigualastensis* REIG and the basal theropod *Eoraptor lunensis* SERENO, FORSTER, ROGERS & MONETTA from the Ischigualasto Formation in Argentina, and the probable basal theropod *Alwalkeria maleriensis* (CHATTERJEE) from the Maleri Formation in India. All of these occurrences are of late Carnian age, approximately 228 Ma. Thus, the oldest dinosaurs are not from South America, as commonly claimed, but instead appear synchronously across Pangea in the upper Carnian fossil record of four modern continents.
There are several ceratosaurs and herrerasaurs of Norian age, including the herrerasaur *Chindesaurus bryansmalli* LONG & MURRY, several unnamed herrerasaurs, and at least two ceratosaurs from the middle Chinle Group, USA, as well as the ceratosaurs *Procompsognathus triassicus* HUENE and *Liliensternus liliensterni* (HUENE), and problematic theropods such as *Halticosaurus* HUENE from the Middle Stubensandstein, Germany. The Rhaetian fossil record of theropods is characterized by abundant tracks, particularly of the ichnogenus *Grallator* HITCHCOCK, in the USA, Europe, and Africa, and numerous theropods, including the Whitaker quarry theropods *Coelophysis bauri* COPE and *Syntarsus*? RAATH from the United States, the ceratosaur *Liliensternus airelensis* CUNY & GALTON and other, indeterminate forms from France, and a poorly known theropod fauna from the Los Colorados Formation of Argentina. With the notable exception of the Whitaker Quarry at Ghost Ranch, which preserves dozens of theropod skeletons, Late Triassic theropods never dominated the tetrapod predator guild.

INTRODUCTION

In this paper, we document the stratigraphic succession of Triassic theropod dinosaurs worldwide. At this time, all Triassic theropods appear to be endemic, with the possible exception of the Rhaetian Whitaker quarry theropod(s). However, correlations based on other tetrapods, principally aetosaurs, allow us to order chronologically the appearance of theropod taxa. Because most of these taxa are known from relatively few specimens, often at a single locality, we cannot discuss their actual stratigraphic ranges in a quantifiable fashion, but we feel that detailed documentation of the lithostratigraphic and biostratigraphic superposition of these theropods provides important information regarding their early evolution and diversification.

Theropods are among the first dinosaurs, and their body fossils occur in Upper Triassic sediments in North and South America, Greenland, Europe, and India, with footprints known from North America,

Greenland, Europe, and Africa (Fig. 1). Theropod body fossils are known from rocks as old as Upper Carnian, and occur throughout rocks of Norian and Rhaetian age. The ichnogenus *Grallator* HITCHCOCK and related ichnotaxa are widely accepted as the footprints of theropod dinosaurs. These trace fossils are rare in pre-Rhaetian rocks, but are locally abundant in uppermost Triassic rocks in the Chinle Group and Newark Supergroup in North America and in the lower Elliot Group in South Africa.

For the purposes of this paper, we consider *Eoraptor lunensis* SERENO, FORSTER, ROGERS & MONETTA and herrerasaurids to be theropods. We are well aware of recent debate surrounding the origins and definition of dinosaurs. Specifically, we recognize that some consider *Eoraptor* and herrerasaurs, including *Herrerasaurus ischigualastensis* REIG and *Staurikosaurus pricei* COLBERT, to lie outside of the Dinosauria (e.g., Ornithischia + Saurischia) (e.g., PADIAN & MAY, 1993; HOLTZ, 1994, 1995; FRASER & PADIAN, 1995; HOLTZ & PADIAN, 1995). However, we agree with the ongoing work of Sereno and Novas (e.g., NOVAS, 1992, 1993, 1996; SERENO, 1993, 1995; SERENO & NOVAS, 1992, 1993; SERENO *et al*., 1993) and consider *Eoraptor* and herrerasaurids to represent dinosaurs, specifically basal theropods, and thus include them in our review of Triassic theropods.

WESTERN NORTH AMERICA

All Triassic theropod body fossils in North America are derived from the Upper Triassic Chinle Group, which encompasses nonmarine deposits from Texas to Idaho and Oklahoma to Nevada (LUCAS, 1993). To date, numerous theropod fossils have been reported from Triassic sediments in Texas, New Mexico, and Arizona, with isolated specimens known from Wyoming.

The first theropod reported from the Chinle Group was *Coelophysis* (COPE, 1887), with other notable theropod remains reported later by HUENE (1915), CASE (1922, 1927, 1932a), and CAMP (1930). Even after discovery of the Whitaker quarry in 1947 (COLBERT, 1947, 1989), other theropod sites were rare. Recently, intensive collection and study of the Chinle has greatly increased the number of known theropods from the Chinle Group. To date, only the Whitaker quarry theropod is named and well-known. Here, we briefly review recent Chinle Group theropod discoveries.

A fragmentary centrum from the Salitral Formation of northern New Mexico reported by HUNT & LUCAS (1990a) may represent a theropod dinosaur. This is the only putative theropod that co-occurs with the aetosaur *Longosuchus meadei* (SAWIN). *Longosuchus* is an index taxon of the Otischalkian landvertebrate faunachron (lvf) of LUCAS & HUNT (1993a, 1993b) and is of early late Carnian age. HUNT *et al*. (1998) reported a single theropod podial from the Popo Agie Formation of Wyoming, which is also considered Otischalkian based on the presence of the primitive phytosaur *Paleorhinus* (LUCAS, 1993, 1994).

Numerous theropods from the lower Chinle Group co-occur with the aetosaur *Stagonolepis robertsoni* AGASSIZ, the phytosaur *Rutiodon* EMMONS (*sensu* BALLEW, 1989), or both. *Stagonolepis* and *Rutiodon* are index taxa of the Adamanian (latest Carnian) lvf, so numerous latest Carnian dinosaurs are known from the lower Chinle.These include a herrerasaurid and a ceratosaur from the Placerias quarry in the Bluewater Creek Formation of Arizona (LUCAS, HUNT & LONG, 1992; LUCAS, HECKERT & HUNT, 1997; LONG & MURRY, 1995 - HUNT *et al*. [1998] named the ceratosaur *Camposaurus arizonensis*), two relatively derived (non-herrerasaurid) theropods from the Bluewater Creek Formation near Fort Wingate, New Mexico (HECKERT, 1997), a theropod of unknown affinities (CASE, 1922, 1927; HUENE, 1930; HUNT *et al*., 1998) named *Spinosuchus caseanus* by HUENE (1930), an herrerasaurid (CASE, 1922, 1927, 1932a; MURRY, 1989; LONG & MURRY, 1995) from the Tecovas Formation in Texas named *Caseosaurus crosbyensis* by HUNT *et al*. (1998), and a fragmentary theropod from the Garita Formation in New Mexico (HUNT & LUCAS, 1995). Recently, HUNT *et al*. (1996) reported two additional theropods from the Blue Mesa Member of the Petrified Forest Formation in the Petrified Forest National Park (PFNP) in eastern Arizona. Therefore, we document numerous theropods from the lower Chinle Group, including two herrerasaurs, a ceratosaur, and as many as four other theropods of unknown affinities.

Theropods from the middle Chinle Group in Arizona, New Mexico and Texas are generally more fragmentary than the late Carnian dinosaurs. Herrerasaurs include *Chindesaurus bryansmalli* LONG & MURRY from the Painted Desert Member of the Petrified Forest Formation in the PFNP (LONG & MURRY, 1995) and a number of fragmentary herrerasaurids from the Bull Canyon Formation in eastern New Mexico and West Texas (HUNT, 1994; HUNT *et al*., 1998). Ceratosaurs include *Gojirasaurus quayi* CARPENTER from eastern New Mexico, a new taxon from northern New Mexico, and at least one ceratosaur from the PFNP (PADIAN, 1986). Problematic theropod taxa from the middle Chinle Group include the putative bird *Protoavis texensis* CHATTERJEE and the putative ornithomimosaur *Shuvosaurus inexpectatus* CHATTERJEE.

LONG & MURRY (1995) named *Chindesaurus* based on a partial skeleton of an herrerasaur col-

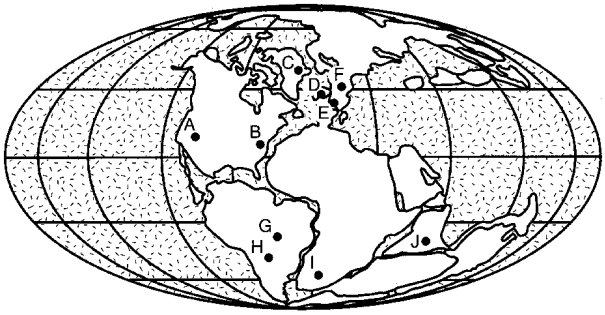

Fig. 1 - Upper Triassic theropod localities. **A** - Chinle Group, southwestern U.S.A. **B** - Newark Supergroup, eastern U.S.A. and Canada. **C** - Fleming Fjord Formation, Greenland. **D** - Lossiemouth Sandstone, Elgin, Scotland. **E** - Airel layer, Carentan Basin, Normandy, and Grés á *Avicula contorta*, Nancy, France. **F** - Keuper, Germany. **G** - Santa Maria Formation, Brazil. **H** - Ischigualasto Formation, Argentina. **I** - lower Elliot Formation, Stormberg Group, southern Africa. **J** - Maleri Formation, India.

lected from the Painted Desert Member of the Petrified Forest Formation in the PFNP. This moderately large (3 to 4 m long) herrerasaur is diagnosed on the basis of several features of the astragalus (LONG & MURRY, 1995: 173). Consequently, we disagree with LONG & MURRY (1995) and refer no specimens to this genus outside of the holotype, as the astragalus is not preserved in any of the specimens they refer to *Chindesaurus*, and many of these specimens are not even convincingly dinosaurian. Other herrerasaurs from the middle Chinle Group include three forms from the Bull Canyon Formation described, but not named, by HUNT (1994) and HUNT *et al*. (1998).

CARPENTER (1997) described a large ceratosaur, *Gojirasaurus quayi* CARPENTER, from the Bull Canyon Formation in eastern New Mexico. This theropod was previously described, but not named, by PARRISH & CARPENTER (1986), and also mentioned by CARPENTER & PARRISH (1985), HUNT & LUCAS, (1989), LUCAS & HUNT (1989), PARRISH (1989), and LONG & MURRY (1995). This theropod is known from fragmentary ribs, centra, a scapula, a pubis, a tibia, and a metatarsal (CARPENTER, 1997). Based on the tibia, CARPENTER (1997) estimated a body length of 5.5 m, which would make this one of the largest Upper Triassic theropods.

Ceratosaurs from the Painted Desert Member of the Petrified Forest Formation in northern New Mexico almost certainly represent the type material of *Coelophysis* COPE (SULLIVAN *et al*., 1996; SULLIVAN & LUCAS 1999). However, in 1996 the ICZN ruled in favor of COLBERT *et al*.'s (1992) petition and established a neotype for *Coelophysis bauri* COPE from the Whitaker quarry specimens, *contra* HUNT & LUCAS (1991a, 1993) and SULLIVAN *et al*. (1996). A new ceratosaur, to which at least one element of the original (COPE, 1887) type material of *Coelophysis* can be assigned, was recentlly described as *Eucoelophysis baldwini* (SULLIVAN & LUCAS, 1999). PADIAN (1986), LONG & MURRY (1995) and HUNT *et al.* (1996) have also reported ceratosaurs from the Painted Desert Member of the Petrified Forest Formation in the PFNP.

The type material of the putative bird *Protoavis texensis* CHATTERJEE (CHATTERJEE, 1991, 1995) includes bones of an aberrant, non-avian theropod (LONG & MURRY, 1995; HUNT *et al*., 1998). The putative ornithomimosaur *Shuvosaurus inexpectatus* CHATTERJEE exhibits no synapomorphies of the Dinosauria (*sensu* GAUTHIER, 1986; BENTON, 1990; SERENO, 1991, 1995; SERENO & NOVAS, 1992, 1993; NOVAS, 1993, 1996; SERENO *et al*., 1993). Further, we are not convinced that this specimen preserves any material diagnostic of the Theropoda, and the supposed synapomorphies of the Ornithomimosauria (CHATTERJEE, 1993a) are unconvincing because of poor preservation. Hence, we follow LONG & MURRY (1995) and consider *Shuvosaurus* to represent a problematic archosaur, perhaps the aberrant rauisuchian *Chatterjeea elegans* LONG & MURRY.

These theropods co-occur with the aetosaur *Typothorax coccinarum* COPE and the phytosaur *Pseudopalatus* MEHL, both of which are index taxa of the Revueltian lvf of LUCAS & HUNT (1993a, b) and thus of early-mid-Norian age (Fig. 2). Thus, preliminary analyses indicate the presence of at least three herrerasaurs, as many as three ceratosaurs, and several problematic theropods in the middle Chinle Group of early-mid-Norian age.

Unlike the underlying rocks, strata of Apachean (Rhaetian) age in the Chinle Group contain abundant tetrapod footprints and relatively few body fossils. Outside of the extremely prolific Whitaker quarry, which produces abundant ceratosaur skeletons, almost all theropod fossils from the upper Chinle Group are trace fossils assigned to the ichnogenus *Grallator* HITCHCOCK.

The Whitaker quarry produces abundant remains of the ceratosaur *Coelophysis* (COLBERT, 1989) and possible individuals of the genus *Syntarsus* (PAUL, 1993; SULLIVAN, 1994; HUNT *et al*., 1998). These are the most derived ceratosaurs and are among the most derived Triassic theropods known (e.g., ROWE & GAUTHIER, 1990; HOLTZ, 1994).

Various workers have assigned tridactyl tetrapod tracks in the Chinle to the ichnogenera *Grallator* HITCHCOCK, *Agialopous* BRANSON & MEHL, *Coelurosaurichnus* KUHN, and *Atreipus* OLSEN & BAIRD. With the possible exception of *Atreipus*, these tracks

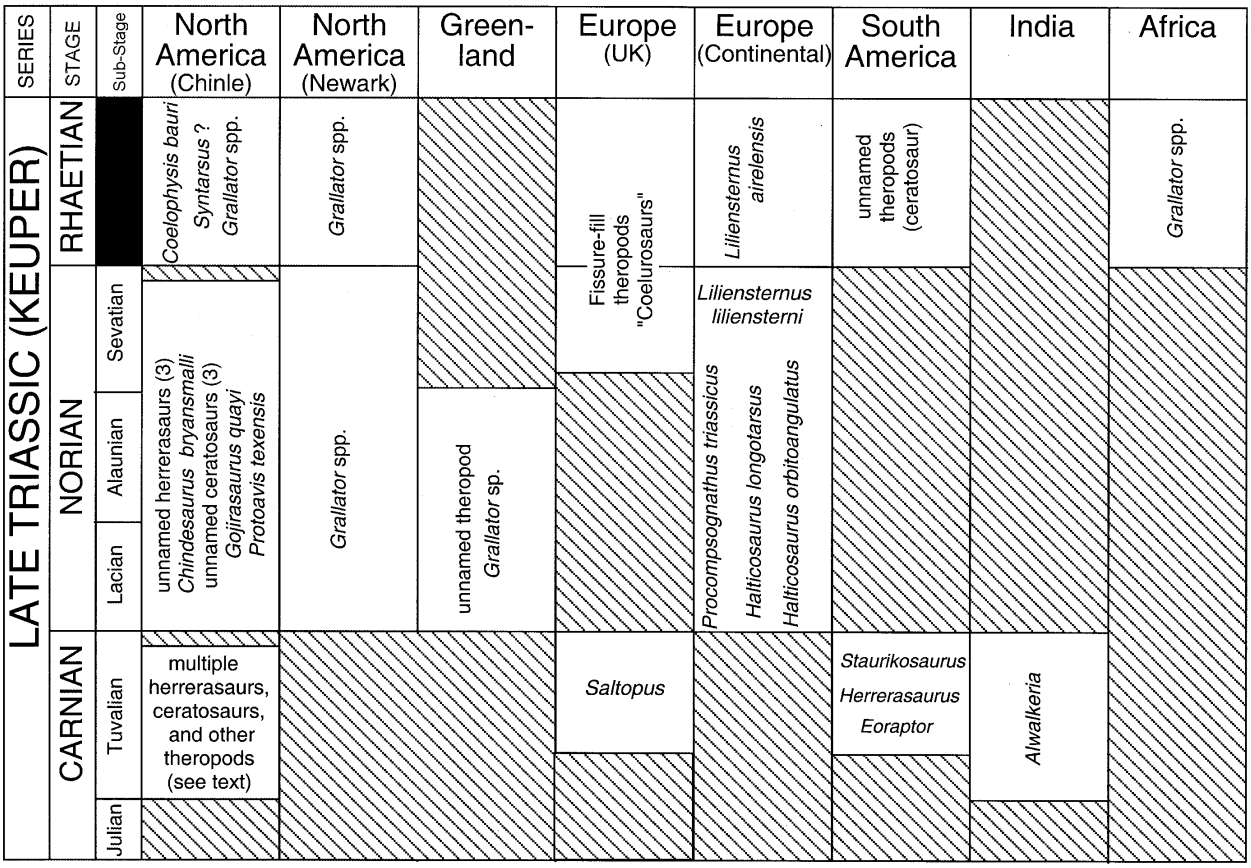

Fig. 2 - Biochronology of Late Triassic theropods.

represent theropods of varying sizes, and we agree with LEONARDI & LOCKLEY (1995) that *Agialopous* and *Coelurosaurichnus* are probably junior subjective synonyms of *Grallator*. OLSEN & BAIRD (1986) believe that the nature and association of manus prints with tridactyl pes prints of *Atreipus* indicate that the probable *Atreipus* trackmaker was an ornithischian(s). However, WEEMS (1992) believes that the manus prints are inconclusive and could represent occasional manus tracks by a theropod. The vast majority of Chinle Group theropod footprints occur in rocks of, or correlative to, the Rock Point Formation (LUCAS & HUNT, 1993a,1993b; LOCKLEY & HUNT, 1995). Therefore, the upper Chinle Group is depauperate in theropod body fossils outside of the Whitaker quarry, but has a rich ichnofossil record of theropod footprints.

EASTERN NORTH AMERICA

The Newark Supergroup in eastern North America yields no body fossils of Triassic theropods. The holotype of *Podokesaurus holyokensis* TALBOT and casts of theropod bones attributed to *Coelophysis* sp. (COLBERT & BAIRD, 1958), originally considered to be Triassic in age, were probably derived from the Portland Formation and thus are of Jurassic age (OLSEN, SCHLISCHE & GORE, 1989).

With the relatively recent recognition that much of the uppermost Newark Supergroup is of Jurassic, not Triassic age, most of the famous Newark Supergroup theropod footprint localities - are now part of the Early Jurassic ichnofauna (OLSEN, 1980; OLSEN, MCCUNE & THOMSON, 1982; OLSEN, SCHLISCHE & GORE, 1989; SILVESTRI & SZAJNA, 1993). However, unlike the Chinle Group, theropod footprints are known from nearly the entire stratigraphic section of the Newark Supergroup. Footprints of *Grallator* and related ichnotaxa occur in rocks of late Carnian to Rhaetian age throughout much of the Newark Supergroup and have been reported by numerous workers (e.g., BAIRD, 1957; OLSEN & BAIRD, 1986; WEEMS, 1987, 1992; OLSEN, 1980; OLSEN & FLYNN, 1989; OLSEN, SCHLISCHE & GORE, 1989) (Fig. 2).

A variety of names have been assigned to tridactyl tetrapod footprints in the Newark Supergroup. These include *Grallator* HITCHCOCK, *Eubrontes* HITCHCOCK, *Kayentapus* WELLES, *Anchisauripus* HITCHCOCK, *Atreipus* OLSEN & BAIRD, *Otouphepus*

CUSHMAN, and *Stenonyx* (LULL), many of which have multiple ichnospecies. Recently WEEMS (1992) argued that of these, only *Eubrontes*, *Grallator*, and *Kayentapus* are valid. In general, Triassic theropod footprint assemblages are dominated by *Grallator*, and Jurassic assemblages by *Eubrontes*, with a few *Kayentapus* known also from the Jurassic section.

Noteworthy recent additions to the ichnofossil record of the Newark Supergroup are the new dinosauromorph ichnogenus and ichnospecies *Banisterobates boisseaui* FRASER & OLSEN from the Dry Fork Formation in the Danville River Basin. This ichnogenus strongly resembles *Grallator* and has a probable theropod trackmaker (FRASER & OLSEN, 1996). SULLIVAN, RANDALL & HENDRICKS (1994) reported a new ichnofauna from the Lockatong Formation of Pennsylvania that includes *Atreipus* and *Grallator* (=*Coelurosaurichnus*). Thus, the entire Triassic theropod fossil record of the Newark Supergroup consists of a variety of *Grallator* and *Grallator*-like footprints from strata ranging from late Carnian to Rhaetian in age (Fig. 2).

GREENLAND

JENKINS *et al*. (1994) first documented the Upper Triassic tetrapod fauna of Greenland in detail. So far, the only theropod body fossil this assemblage contains is an indeterminate theropod consisting of "disassociated vertebrae and ribs, a partial pelvis and hindlimb, including a femur (length, 33 cm) and phalanges" (JENKINS *et al*., 1994: 14) from the upper Bjergkronerne beds in the Ørsted Dal Member of the Fleming Fjord Formation. They also reported numerous trackways assignable to *Grallator* sp. from the Ørsted Dal Member. The occurrence of *Aetosaurus* with the theropod fossils of the Ørsted Dal Member indicates an early-mid Norian age for this fauna (Fig. 2).

EUROPE

The Triassic theropod fossil record of Europe includes body fossils from the United Kingdom, France, and Germany, with numerous footprints from several localities. The Lossiemouth Sandstone of Elgin, Scotland, has produced theropod fossils assigned to *Saltopus elginensis* HUENE. The Lossiemouth Sandstone is the type stratum of the aetosaur *Stagonolepis robertsoni* AGASSIZ, which is of Adamanian (latest Carnian) age. OSTROM (1981) and NORMAN (1990) reviewed the problematic theropods, and NORMAN (1990) considered *Saltopus elginensis* to be a *nomen dubium*. Because of its strong theropod affinities and latest Carnian age, we include it in our review here as one of the oldest known theropods. The fissure-fill assemblages developed in Carboniferous limestone around the Bristol Channel area and in South Wales also produce fragmentary Triassic coelurosaurs (FRASER, 1994).

In Germany, the holotypes of the ceratosaur *Procompsognathus triassicus* HUENE and the problematic taxa *Halticosaurus longotarsus* HUENE and *H. orbitoangulatus* HUENE were found in a marly interval just above the Middle Stubensandstein (HUENE, 1908, 1921, 1932; SERENO & WILD, 1992), strata of undisputed Norian age (AIGNER & BACHMAN, 1992). Recently, SERENO & WILD (1992) dismembered the holotype of *Procompsognathus triassicus*, assigning the skull to the sphenosuchian *Saltoposuchus connectens* and retaining the postcrania in *Procompsognathus*. They then redescribed *Procompsognathus* as a moderately derived, "*Segisaurus*-like" ceratosaur (SERENO & WILD, 1992: 455). CHATTERJEE (1993b) argued that the skull is actually ceratosaurian. Thus, there is at least one ceratosaur in the Middle Stubensandstein.

Halticosaurus HUENE is a problematic Late Triassic taxon represented by several fragmentary specimens that Huene identified as three different species, *H. longotarsus*, *H. orbitoangulatus*, and *H. liliensterni* HUENE (HUENE, 1908, 1932,1934) Of these, *H. longotarsus* and *H. orbitoangulatus* are from the Middle Stubensandstein and *H. liliensterni* was found in the Knollenmergel of Germany (HUENE, 1908, 1932, 1934; SERENO & WILD, 1992). WELLES (1984) removed the type of *H. liliensterni* from the genus and designated it the type of his new genus *Liliensternus liliensterni* (HUENE). ROWE & GAUTHIER (1990) assigned *Liliensternus* to the Ceratosauria, and NORMAN (1990) considered the remaining species *nomina dubia*. Both *H. longotarsus* and *H. orbitoangulatus* are represented by fragmentary material (a partial jaw and fragmentary postcrania for *H. longotarsus* and a crushed skull for *H. orbitoangulatus*) that have thus far prevented workers from incorporating these taxa into a modern phylogenetic hypothesis of early dinosaur evolution (e.g., NORMAN, 1990; HOLTZ, 1994). Pending such studies, we retain the genus *Halticosaurus* as a problematic Norian theropod. The co-occurrence of these forms with numerous taxa, particularly the aetosaur *Aetosaurus*, indicates an early-mid Norian age for the Triassic theropods of the Keuper, with the ceratosaur *Liliensternus liliensterni* representing the youngest Keuper Norian theropod.

The holotype of the ceratosaur *Liliensternus airelensis* (LARSONNEUR & LAPPARENT, 1966; CUNY & GALTON, 1993) was derived from the Airel layer of the Carentan Basin in Normandy, France. This locality and the Saint-Nicolas-de-Port locality near Nancy, in the "Grés á *Avicula contorta*", which has also produced fragmentary theropod material, are of Rhaetian age (LUCAS & HUBER, 2000).

SOUTH AMERICA

The Triassic theropods of South America are very well-studied, and consist of the herrerasaurids *Staurikosaurus pricei* COLBERT from the Santa Maria Formation of Brazil and *Herrerasaurus ischigualastensis* REIG from the Ischigualasto Formation of Argentina, which co-occurs with the basal theropod *Eoraptor lunensis* SERENO, FORSTER, ROGERS & MONETTA, 1993. *Ischisaurus cattoi* REIG is a junior subjective synonym of *Herrerasaurus* (NOVAS, 1992, 1993; SERENO & NOVAS, 1992, 1993). Some fragmentary theropods are known from the Los Colorados Formation in Argentina (A. Arcucci, pers. comm., 1996).

In the Santa Maria Formation of Brazil, *Staurikosaurus* COLBERT co-occurs with the rhynchosaur *Scaphonyx* WOODWARD and the aetosaur *Stagonolepis* AGASSIZ (=*Aetosauroides* CASAMIQUELA) and thus is the same age as the Ischigualasto fauna, which also includes *Scaphonyx* and *Stagonolepis* (=*Aetosauroides*) (BRINKMAN & SUES, 1987; SUES, 1990). Recently, we have determined that *Aetosauroides* is a junior subjective synonym of the aetosaur *Stagonolepis*. *Stagonolepis* is known to occur in rocks of latest Carnian age (Adamanian lvf of LUCAS & HUNT, 1993a, 1993b) in the Chinle Group and the Lossiemouth Sandstone (WALKER, 1961). Therefore, we correlate the Ischigualasto and Santa Maria Formations with these units (LUCAS & HECKERT, 1996). ROGERS *et al*. (1993) reported a date of 227.8 ± 0.3 Ma from an ash 80 m below the dinosaur occurrences in the Ischigualasto Formation. Therefore, we consider 228 Ma to be a useful date for both the lower Chinle and for the Lossiemouth Sandstone, indicating that a diverse theropod assemblage existed on several continents by this time.

The Los Colorados Formation produces fragmentary theropods, none of which are named. At least one of these theropods appears to represent a ceratosaur (A. Arcucci, pers. comm., 1996).

AFRICA

Africa, like eastern North America, has a depauperate fossil record of Triassic theropods. There are no body fossils of Late Triassic theropods known from Africa, and the entire Late Triassic theropod record consists of footprints from the lower Elliot Formation in the Stormberg Group. ELLENBERGER (1970, 1972, 1974), originally described this theropod ichnofauna of footprints, recognizing at least three ichnogenera and at least nine ichnospecies. OLSEN & GALTON (1984) re-examined this assemblage and considered all of the tracks to pertain to *Grallator* spp. Precise correlation of the lower Elliot to other Triassic strata is problematic due to a high degree of endemism in the fauna, although preliminary lines of evidence indicate that it is probably of late Norian age (COOPER, 1982; LUCAS & HUBER, 2000), not late Carnian age, as argued by GAUFFRE (1993a), who mistakenly thought that traversodontids, present in the upper Elliot, do not occur in post-Carnian strata.

INDIA

CHATTERJEE (1987, 1994) described the primitive theropod *Alwalkeria maleriensis* (CHATTERJEE) from the lower Maleri Formation in India. NORMAN (1990) considered *Alwalkeria* to be a problematic possible dinosaur. For purposes of this analysis, we consider it a theropod, although we recognize that it may represent a lagosuchid. JAIN & ROYCHOWDHURY (1987) summarized the lower Maleri Fauna and listed among its constituents the phytosaur *Paleorhinus* WILLISTON (=*Parasuchus* LYDEKKER) and the aetosaur "*Typothorax*." Prior to 1990, many workers identified "*Typothorax*" based on material referable to "*T." meadei*. HUNT & LUCAS (1990b) demonstrated that the holotype skeleton of "*Typothorax*" *meadei* is generically distinct from *Typothorax coccinarum* COPE, and recognized it as the holotype for the type species of the genus *Longosuchus* HUNT & LUCAS. The presence of *Paleorhinus* and, possibly, *Longosuchus* indicates a late Carnian (Tuvalian) age (HUNT & LUCAS, 1990b, 1991b; LUCAS & HUNT, 1993a, 1993b). Therefore, *Alwalkeria* CHATTERJEE is one of the oldest named dinosaurs. No other theropod fossils of Triassic age are known from Asia.

DISCUSSION

Because almost all Triassic theropods appear to be endemic, there are no direct correlations based on theropod dinosaurs. However, other tetrapods, principally aetosaurs, provide a robust biostratigraphy which allows us to divide the Upper Triassic theropod record into three distinct zones, a lower, late Carnian zone that is primarily latest Carnian in age, a Norian zone, and a latest Triassic (Rhaetian) zone (Fig. 3).

Historically, most workers have considered the dinosaurs from the Ischigualasto and Santa Maria Formation in South America to be the oldest known dinosaurs, a concept that has been widely disseminated (COLBERT, 1970; BENTON, 1990; NOVAS, 1992, 1993, 1996; SERENO & NOVAS, 1992, 1993; ROGERS *et al*., 1993; SERENO, 1993, 1995; SERENO *et al*., 1993). This concept dates back to ROMER (1962), who originally considered the abundant rhynchosaurs of the Ischigualasto Formation to indicate a Middle Triassic age. However, a detailed examination of the Ischigualasto and Santa Maria Formation faunas demonstrates that there is no compelling reason to consider them older than late

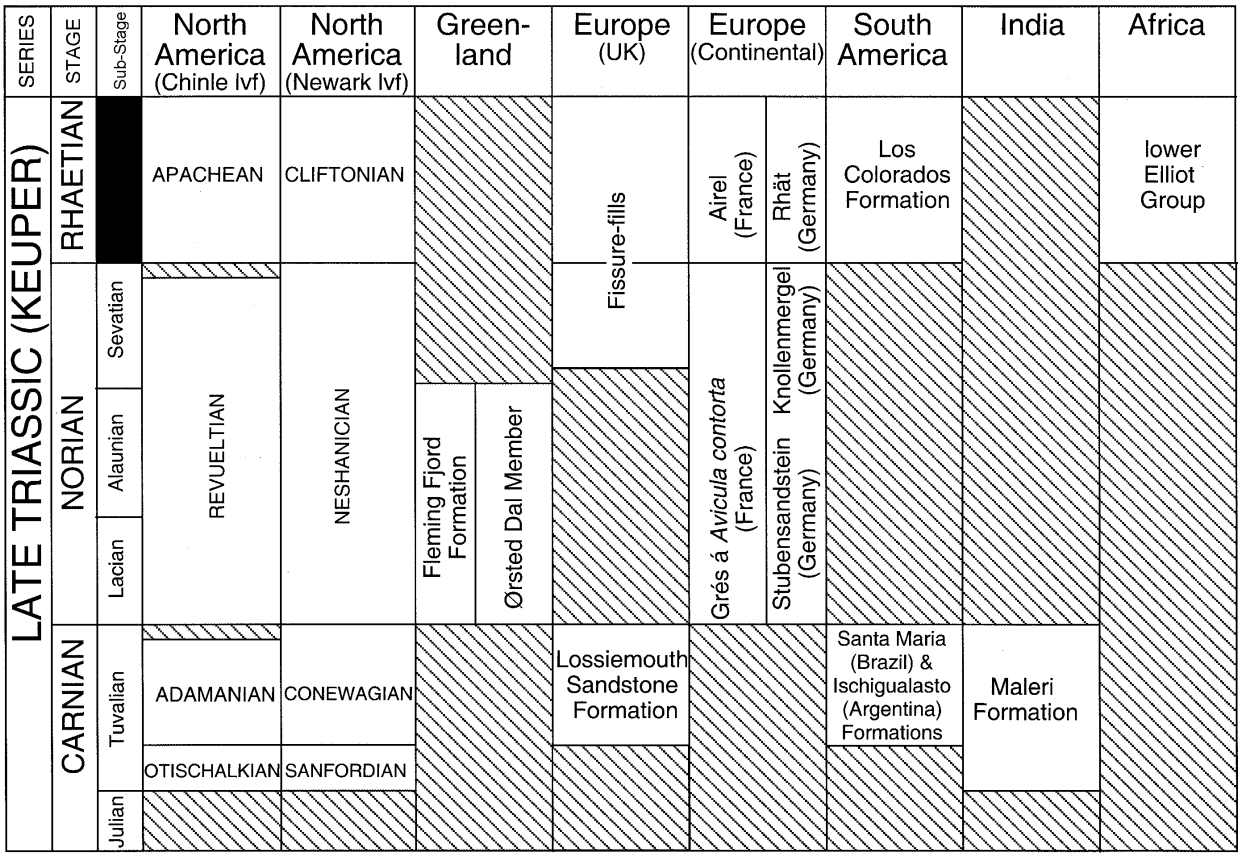

Fig. 3 - Correlation of Upper Triassic theropod-bearing units. Chinle and Newark Supergroup faunachrons follow LUCAS & HUNT (1993a), LUCAS (1998) and LUCAS & HUBER (2000).

Carnian, and that there is strong evidence supporting correlation of these units with parts of the lower Chinle Group and the Lossiemouth Sandstone, both of latest Carnian age (LUCAS & HUBER, 2000).

The Ischigualasto and Santa Maria Formations are readily correlated based on the occurrence of the rhynchosaur *Scaphonyx* in both the Santa Maria (BARBARENA, ARAÚJO & LAVINA, 1985) and Ischigualasto Formations (SILL, 1970; BONAPARTE, 1978) and the aetosaur *Aetosauroides* in the Ischigualasto (CASAMIQUELA, 1960, 1961) and Santa Maria (ZACARIAS, 1982). Recently, we have examined the type material of *Aetosauroides* and concluded that it is congeneric with *Stagonolepis* (HECKERT & LUCAS,1996). *Stagonolepis* was originally described from the Lossiemouth Sandstone (AGASSIZ, 1844) and has long been known (e.g. "new phytosaur," CASE, 1932b; = *Calyptosuchus* LONG & BALLEW, 1985), if only recently recognized, from the Chinle Group (MURRY & LONG, 1989; LONG & MURRY, 1995; LUCAS & HUNT, 1993a, b). Therefore, the occurrence of *Stagonolepis* in the Ischigualasto and Santa Maria Formations provides a direct correlation of these units to the Lossiemouth Sandstone and much of the lower, although not lowermost, Chinle Group. Consequently, the South American late Carnian dinosaurs *Eoraptor*, *Herrerasaurus* and *Staurikosaurus* are as old as *Saltopus* from the Lossiemouth and the Adamanian theropods from the Chinle. Detailed biochronology (HUNT & LUCAS, 1991b; LUCAS & HUNT, 1993a,b) indicates that *Stagonolepis* occurs in rocks of latest Carnian age.

ROGERS *et al*. (1993) reported an Ar/Ar age of 227.8 ± 0.3 for a tuff approximately 60 m below the lowest occurrence of *Stagonolepis* (=*Aetosauroides*) and concluded that the Ischigualasto fauna was thus of middle Carnian age. However, we and others have noted that: (1) there is no official "middle" subdivision of the Carnian; (2) on most recent timescales, including that of HARLAND *et al*. (1990) the Carnian spans approximately 235 to 225 Ma, so 228 Ma is a late Carnian age, and (3) the ROGERS *et al*. (1993) date is necessarily a maximum constraint, indicating that the Ischigualasto fauna is slightly less than 228 Ma old. Although GRADSTEIN *et al*. (1995) have published a timescale with a Ladinian-Carnian boundary at 227.4 ± 4.5 Ma. This date differs from the HARLAND *et al*. (1990) timescale because of the different methods of interpolation used by the two

groups. Regardless of this inconsistency, we note here that in the Chinle Group the aetosaur *Stagonolepis* occurs above strata bearing the phytosaur *Paleorhinus*, known from marine strata of undisputed late Carnian age in Germany (HUNT & LUCAS, 1991b). Therefore, by the correlation we propose here, the co-occurrence of early theropods with *Stagonolepis* indicates that those theropods are of late Carnian age.

We note here that the oldest well-known theropods, *Staurikosaurus*, *Eoraptor*, and *Herrerasaurus*, appear at the same time as more fragmentary, yet more derived forms in the Chinle Group and *Saltopus* from the Lossiemouth Sandstone. Accordingly, the oldest known probable theropods are actually those of early late Carnian (Otischalkian) age, including fragmentary remains such as those published by HUNT & LUCAS (1990a) and LUCAS (1994) from the Chinle and, possibly, *Alwalkeria* from the Maleri Formation in India. These theropods co-occur with the phytosaur *Paleorhinus*, and are thus of late Carnian age.

Refining the biostratigraphy of Triassic theropods enables us to make several observations about the nature of the original dinosaur diversification. In addition to the oldest theropods reviewed here, several ornithischians and prosauropods are known from the same or correlative strata. These include the ornithischians *Pisanosaurus* from the Ischigualasto Formation in Argentina (CASAMIQUELA, 1967), *Pekinosaurus* from the Pekin Formation in North Carolina (HUNT & LUCAS, 1994) and the prosauropod *Azendohsaurus* from the Argana series in Morocco (DUTUIT, 1972; GAUFFRE, 1993b). Consequently, we recognize that dinosaurs comprise a very small, yet diverse, component of late Carnian tetrapod faunas. These first dinosaurs had already diversified and included representatives of the ornithischian, prosauropod, and theropod clades. Furthermore, by the latest Carnian the theropods had already diverged from other dinosaurs and included numerous basal forms (*Eoraptor* and many of the problematic taxa), herrerasaurids, and, rarely, ceratosaurs, as well as several problematic, but apparently derived, forms. This divergence suggests that tetanurine theropods should also be present at this time, although none have been identified from Triassic strata at this time. Almost all of these taxa were small, usually considerably less than 2 m long, with the exception of *Azendohsaurus* and some herrerasaurs, which may have reached lengths of 3 - 4 m.

By Norian time, prosauropod dinosaurs dominated the more terrestrial, dry ecosystems, as evidenced by the abundant specimens of prosauropods known from the Norian portion of the Keuper (HUNT, 1991). The theropods, however, remained a minor component of all faunas. Ceratosaurs are the best-represented theropod group, although some of the remaining herrerasaurs are the largest known Norian theropods, approximately 5-6 m in length (HUNT, 1994; HUNT *et al*., 1998).

By the end of the Triassic (Rhaetian), the herrerasaurs had apparently become extinct, and the vast majority of the theropod fauna consists of moderately to highly derived ceratosaurs, such as *Liliensternus airelensis* and *Coelophysis*. Abundant footprint evidence indicates that small- to medium-sized theropods (1-3 m long) had become common, although, with the exception of the Whitaker quarry, theropods never dominated the Late Triassic body fossil record to the extent that prosauropods did, and they remained a conspicuously rare element in prosauropod-dominated faunas.

CONCLUSIONS

The oldest theropods include several fragmentary theropods, including the ceratosaur *Camposaurus arizonensis*, from the lower Chinle Group, *Eoraptor lunensis* and *Herrerasaurus ischigualastensis* from the Ischigualasto Formation in Argentina, *Staurikosaurus pricei* from the Santa Maria Formation in Brazil, the problematic, fragmentary, *Saltopus elginensis* from the Lossiemouth Sandstone in Scotland, and possibly, *Alwalkeria maleriensis* from the lower Maleri Formation of India. These dinosaurs have a nearly synchronous first appearance during the late Carnian and are among the oldest known dinosaurs. By Norian time, the theropod dinosaur fauna was dominated by ceratosaurs at the expense of herre- rasaurs. The Norian theropod fossil record includes the herrerasaur *Chindesaurus bryansmalli* and other herrerasaurs and ceratosaurs from the middle Chinle Group, the ceratosaurs *Procompsognathus triassicus* and *Liliensternus liliensterni* and the problematic theropod *Halticosaurus* from units of Norian age in Germany. Of these, *Liliensternus* appears to be the youngest, making its first appearance in the Knollenmergel, whereas the other Norian theropods in Germany are found in the Middle Stubensandstein. Rhaetian and probable Rhaetian theropods include *Coelophysis bauri* from the upper Chinle Group, *Liliensternus airelensis* from the Triassic of Normandy, a poorly known theropod from the Grés á *Avicula contorta* in France, and poorly known theropods from the Los Colorados Formation in Argentina. All known Rhaetian theropods are at least of ceratosaur-grade, and the herrerasaurids had apparently gone extinct by the Rhaetian. The most significant implications of the ichnofossil record of early theropods is the documentation of their increasing abundance, particularly at the end of the Triassic and into the Early Jurassic.

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