

ARE *SYNTARSUS* AND THE WHITAKER QUARRY THEROPOD THE SAME GENUS?

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ABSTRACT: The skeletons of *Syntarsus* and the Whitaker quarry theropods are very similar and belong in the same genus. If *Coelophysis* is a *nomen dubium*, then *Rioarribasaurus* is a junior synonym of *Syntarsus*.

INTRODUCTION

The taxonomic status of the small Late Triassic theropod from the Whitaker quarry at Ghost Ranch New Mexico has received considerable attention in recent years (Padian, 1986; Colbert, 1989; Hunt & Lucas, 1991; Colbert et al., 1992). Originally assigned by Colbert (1947) to the genus *Coelophysis* (Cope, 1889), the Whitaker remains have been given the new generic name *Rioarribasaurus* (Hunt & Lucas, 1991). Colbert et al. (1992) have applied to the ICZN (Colbert et al., 1992) for reinstatement of the better known name.

The small Early Jurassic theropod *Syntarsus* (Raath, 1969) from southern Africa and North America is the closest known relative of the earlier dinosaur (Raath, 1977; Paul, 1984, 1988; Gauthier, 1986; Rowe, 1989; Colbert, 1989; Rowe & Gauthier, 1990). The close similarity of the skeletons of *Syntarsus* and the Whitaker theropod has not been fully appreciated. Morphological differences are too few and minor to justify generic separation, and the name *Syntarsus* is applied to the Whitaker theropod.

Abbreviations: AMNH (American Museum of Natural History, New York), CM (Carnegie Museum of Natural History, Pittsburgh), HMN (Humboldt Museum für Naturkunde, Berlin), MCZ (Museum of Comparative Zoology, Cambridge), MNA (Museum of Northern Arizona, Flagstaff), NM (National Museum, Harare); UCMP (University of California, Berkeley); USNM (United States National Museum, Washington DC).

SKELETAL COMPARISON

The author became aware of how similar the Whitaker theropod was to *Syntarsus rhodesiensis* while preparing and updating new skeletal restorations during the 1980's (Fig. 1). Numerous specimens, including complete skulls and skeletons, were examined on a number of blocks excavated at Ghost Ranch in 1947-48 and 1981-82. The most important of these was a CM block prepared at the USNM from 1987 to 92. Careful work exposed many morphological details. The new species *Syntarsus kayentakatae* (Rowe, 1989) provides additional material for comparison.

Examination of Whitaker specimens reveals that, bone for bone, they are nearly identical to those of *Syntarsus*, especially *S. rhodesiensis* (Figs. 1, 2, Table 1). Most of the differences used to justify a generic separation of the three taxa do not exist, are questionable, or are minor and at the species level.

The skulls show few differences (Fig. 2). *S. rhodesiensis* and *S. kayentakatae* are reported to share a small nasal fenestra on the skull roof (Raath, 1977; Rowe, 1989). This unusual opening is not visible in Whitaker specimens, although crushing and fracturing often obscure this region. An isolated nasal of a juvenile from the CM(USNM) block shows an indentation on the postero-lateral corner that exactly matches those observed in *Syntarsus*. This suggests that the fenestra is either present or incipient in Whitaker individuals, or is due to missarticulation of bones in *Syntarsus* specimens. The placement of the ventral end of the lacrimal lateral to the maxilla and jugal in *S. rhodesiensis* by Raath (1977) is based on disarticulated remains, is unknown in theropods, and probably incorrect. Difficult to detect interdental plates are present in some of the Whitaker specimens. Crushing makes it difficult to tell if the post-temporal fenestra is open in the Whitaker theropod.

Complete skulls from the CM(USNM) Whitaker block and in Figs. 32,33 and 35-37 in Colbert (1989) show that the palate has a normal, highly vaulted theropod design in which a tetradial palatine helps form a subsidiary palatal fenestra bordered medially by the pterygoid. This differs greatly from the unvaulted restoration in Colbert (1989), which does not match that of any other theropod. The palate of *S. rhodesiensis* restored by Raath (1977) is based upon disarticulated and often incomplete elements, is missing the vomers, does not match any other theropod, and also is in error.

Articulated vertebrae on the CM(USNM) block show that the mid-cervicals are keeled and that hyposphene-hypantrum articulations are present on the dorsals, as in *Syntarsus*. The ilial plates have a typical theropodan lateral flare in both the least crushed Whitaker specimens, and in *Syntarsus*. Two pubic foramina are present in CM(USNM) block specimens, and the pelvic elements of large examples show substantial fusion (see Figure 5.7D in Rowe and Gauthier, 1990). Fusion of bones around the ankle does not show a difference between the Whitaker and *Syntarsus* specimens, instead the proximal fusion of metatarsals II and III is a distinctive shared similarity.

The differing status of such characters as pubic foramina in Whitaker specimens appears to be due to incomplete preparation and/or differing degrees of ossification, as well as ontogenetic changes, and the population appears to represent one species.

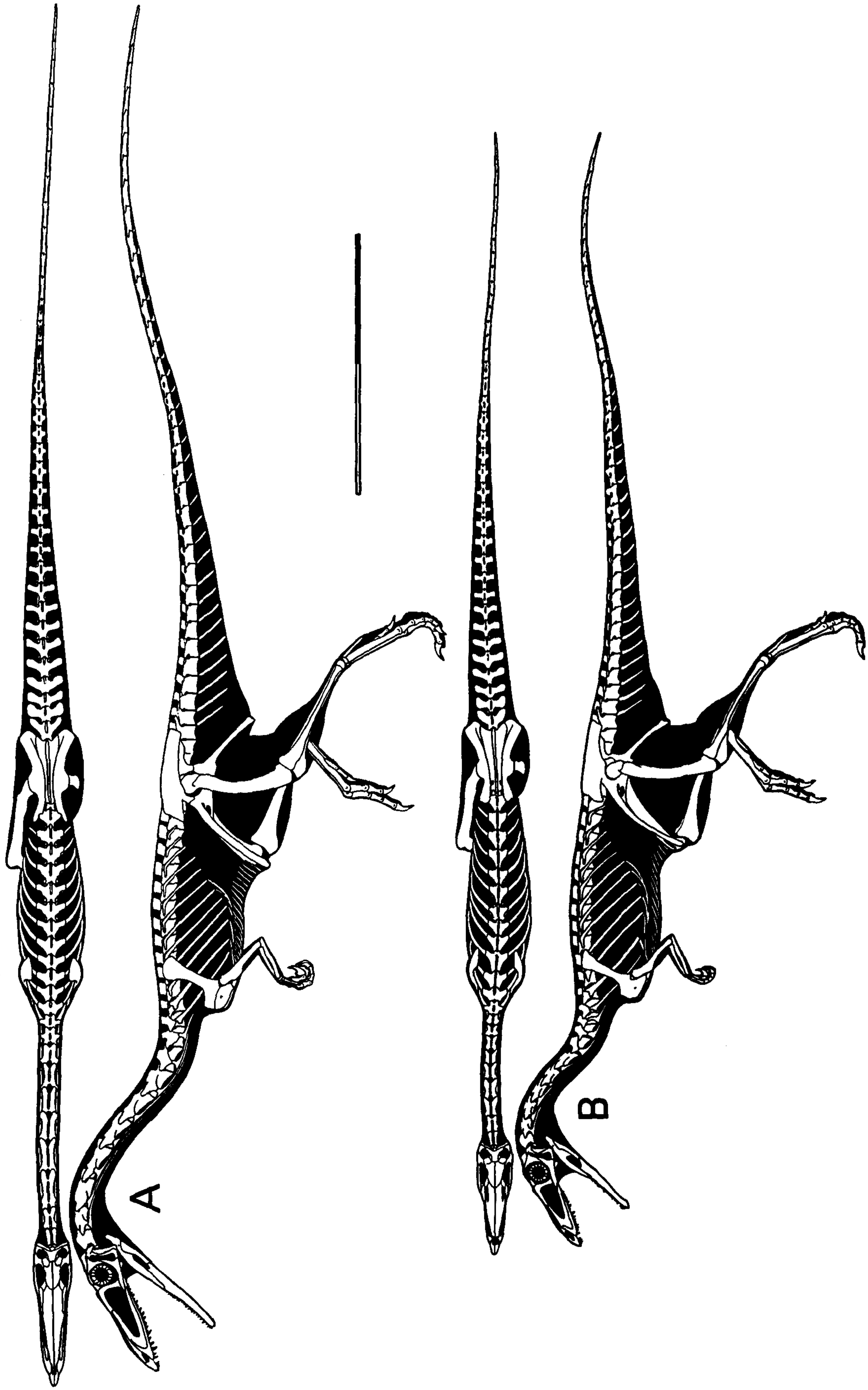


FIGURE 1. Skeletons in lateral and dorsal views of A) *Syntarsus colberti* AMNH 7223 and B) *S. rhodesiensis* holotype NM 1 with composite skull. To same scale, bar = 500 mm.

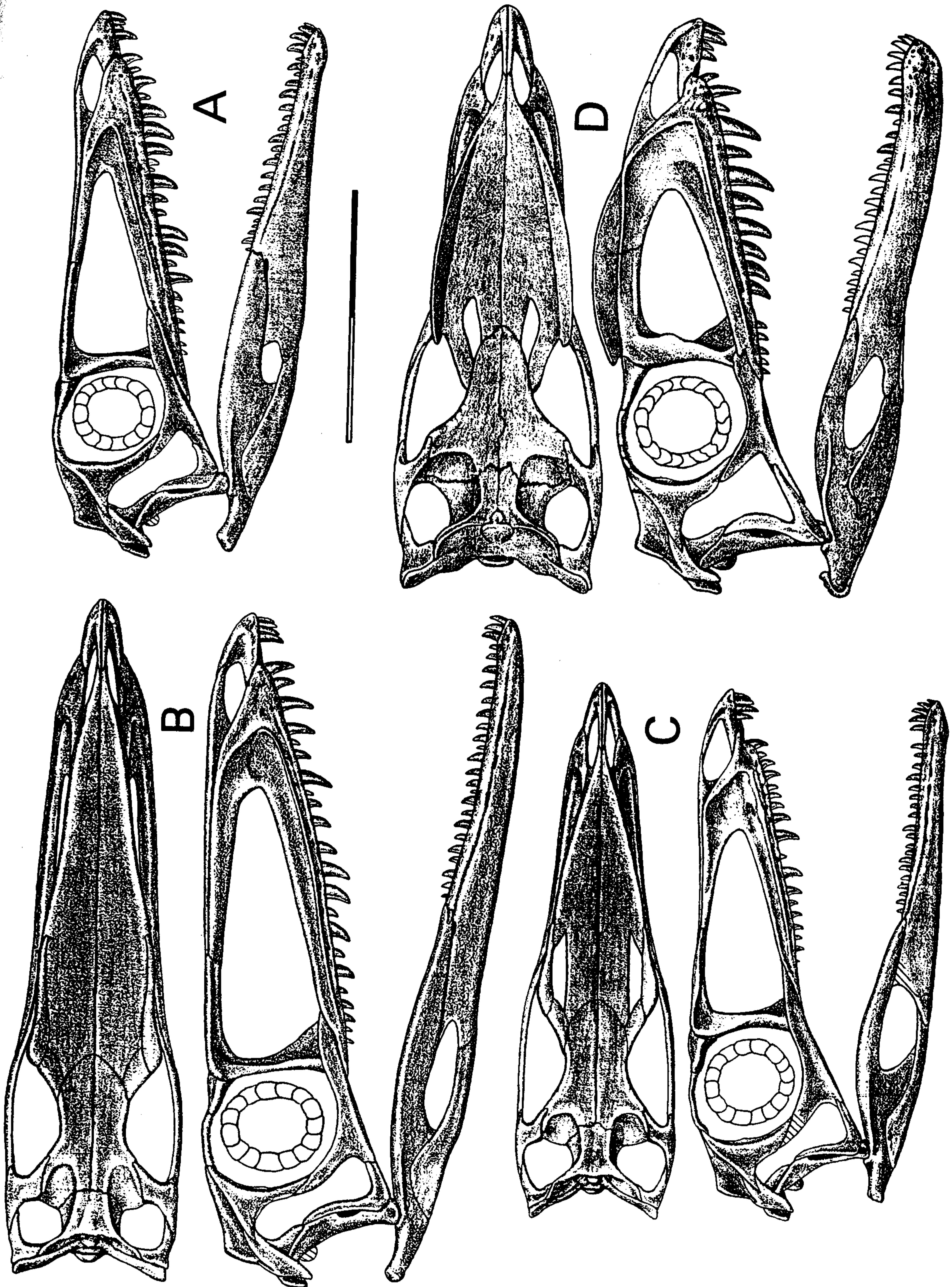


FIGURE 2. Skulls in lateral and dorsal views of A) robust *Syntarsus colberti* holotype AMNH 7224 and B) gracile MCZ 4327 / AMNH 7223, C) *S. rhodesiensis* holotype MNA V2623, and D) robust *S. kayentakatae* holotype MNA V2623. To same scale, bar = 100 mm.

TAXONOMY

If disarticulated skull and skeletal bones of the three theropods were tossed into a box and mixed together one would be hard pressed to sort them apart. If articulated specimens of *S. rhodesiensis* were in the Whitaker quarry it would be difficult to show that there were two taxa. Important characters used to separate the taxa are actually found in all of them. These includes normal vaulted theropod palate, hyposphene-hypantrum articulations on the vertebrae, and two foramina on the pubic apron. The degree of fusion of certain elements is also closer than believed in these theropods. The status of other features is uncertain, such as the nasal and post-temporal fenestrae, and the carnosaur pocket. The features that do differ in the taxa are the minor kind expected in species within a genus. Specific characters include the number and size of teeth, skull and skeletal proportions and robustness, and the delicate skull crests found on *S. kayentakatae*. The last character is a classic display feature used for species identification and interaction.

The close similarity makes it difficult to determine how the three taxa are related to one another. If the Whitaker theropod lacks a nasal fenestra and (especially) the closed post-temporal fenestra that *S. rhodesiensis* and *S. kayentakatae* have, then the first is a sister taxon to the latter two species (as per Rowe, 1989). On the other hand, the Whitaker theropod and *S. kayentakatae* share a few features not found in *S. rhodesiensis* (Table 1). In terms of gradistic differences, the lightly built, small toothed, and crestless Whitaker theropod and *S. rhodesiensis* are more like each other than either is to crested *S. kayentakatae*, which has a much more strongly built skull and larger teeth. Functionally, *S. kayentakatae* appears to be adapted to attack larger prey items than its more gracile but similar sized relatives.

Some modern and recent predatory reptile (*Varanus*) and mammal (*Canis*) genera show as much skeletal variation as is observed in the three theropods. Within genera there can large differences in size and proportions (ora and dwarf monitor, wolf and jackal), and even in skull sutural patterns (*Varanus*). Within some bovid genera there is substantial variation in such display structures as horns. Also note that multispecies genera include multiple phylogenetic nodes.

Because the Whitaker theropod, *S. rhodesiensis* and *S. kayentakatae* are very similar in all aspects of their detailed morphology, a separation above the species level cannot be justified, and they are best placed within a single genus. Temporal differences alone cannot be used to keep the Triassic and Jurassic taxa distinct. That these dinosaurs lived on a single supercontinent is compatible with generic unification. The next question is, what name should be applied to them?

Referring the Whitaker specimens to *Coelophysis bauri* (Cope 1889) has the advantage of retaining a popular name (and the name of the state fossil of New Mexico). Padian (1986) showed that the type material of *Coelophysis bauri* is indeterminate, but did not state that the name is a nomen dubium. Paul (1988) made *Syntarsus* a junior synonym of *Coelophysis*. Hunt and Lucas (1991) correctly stated that the lectotype of *C. bauri* (four coossified sacra and a fragment

of an ilium) is not diagnostic beyond the basal theropod condition, that *Coelophysis* is a nomen dubium, and named the Whitaker theropod *Rioarribasaurus colberti* (Hunt and Lucas, 1991). Whether the lectotype is from the same horizon as the Whitaker quarry (Colbert, 1989; Colbert et al., 1992) or not (Hunt and Lucas, 1991) is not of pressing relevance because the specimen is not diagnostic. The attempt by Colbert et al. (1992) to designate a diagnostic neotype for *C. bauri* (the type of *R. colberti*) effectively accepts the indeterminate nature of the lectotype, and appears to be contrary to Art.75(a) of the ICZN, which states that a neotype can be designated only in exceptional circumstances when "no holotype, lectotype, syntype or prior neotype is believed to exist".

Other small, gracile theropods of the Late Triassic and Early Jurassic cannot be shown to be con-generic with *Syntarsus* and the Whitaker theropod. *Liliensternus* (Welles, 1984) has characters that suggest it is intermediate to *Syntarsus* and *Dilophosaurus*. *Sarcosaurus* (Andrews, 1921), *Halticosaurus* (Huene, 1908), *Podokesaurus* (Talbot, 1911), *Procompsognathus* (Fraas, 1913) and *Segisaurus* (Camp, 1936) are based on fragmentary material that differs from *Syntarsus* (Welles, 1984; Paul, 1988; Norman, 1990).

It is here suggested that *Rioarribasaurus* be made a junior synonym of *Syntarsus*. The latter name has priority, and is based on diagnostic type material (most of a well preserved skeleton). In this case, *Syntarsus* would include the species *S. colberti*, *S. rhodesiensis* and *S. kayentakatae*. Alternately, if the validity of *Coelophysis* is accepted then it includes *C. bauri*, *C. rhodesiensis* and *C. kayentakatae*.

There is another taxonomic problem concerning *Syntarsus* and its relatives. This genus is placed in the family Podokesauridae (Huene, 1914) by Raath (1977), Colbert (1989) and Hunt and Lucas (1991), and *Dilophosaurus* was placed in the Halticosauridae (Huene, 1948) by Welles (1984). However, the type genera of these two families differ too much from the taxa assigned to them. Gauthier (1986) and Rowe and Gauthier (1990) place *Syntarsus*, *Liliensternus*, *Dilophosaurus*, *Sarcosaurus*, *Segisaurus* and *Ceratosaurus* in the Ceratosauria (Marsh, 1884). Whether *Ceratosaurus* is such a close relative of the other taxa is questionable. Fusion of elements diagnostic for the Ceratosauria are not convincing phylogenetic evidence. Other cited characters in the vertebrae and pelvis may be primitive for the Theropoda. In other regards *Ceratosaurus* is very distinctive from the *Syntarsus*-like theropods. In particular the former lacks a subnarial gap. The ilium and femur of *Sarcosaurus* show similarities to both *Dilophosaurus* and *Ceratosaurus* and cannot be placed with any certainty. Paul (1988) notes that poorly known *Segisaurus* has characters that suggest it is not in this group. The bent snouted theropods form a distinctive clade and require a family of their own. The author coined the family Coelophysidae (Paul, 1988), and Art. 23(c) of the ICZN (1985) require retention of a family title as long as the type material cannot be demonstrated to not belong to the higher taxon.

SYSTEMATIC PALEONTOLOGY

Order THEROPODA Marsh, 1881

Diagnosis: Obligatory bipedal predaceous dinosaurs with tridactyl foot in which metatarsal I does not contact the

	Whitaker	<u>S. r.</u>	<u>S. k.</u>
Ventral lacrimal sited medially	yes	probably	yes
Nasal fenestra	incipient?	present?	present?
Post-temporal fenestra	present?	absent	absent
Basisphenoid relatively	short?	long	
Interdental plates	present	present	
Vomers	present	not preserved	
Pterygoid carnosaur pocket	?	present	
Ectopterygoid hook	present	present	
Palate	vaulted	vaulted	
Upper tooth row ends beneath	orbit	aofe	orbit
Maxillary teeth	22-26	19-20	18
Dentary teeth	27	25	
Cervical keels	present	present	present
Two paired cervical pleurocoels	present	present	present
Hyposphene-hypantrum articul.	present	present	
Pelvic bone fusion	present	present	present
Ilium tilted dorso-laterally	yes	yes	
Posterior ilium flares laterally	yes	yes	
Two pubic foramina	present	present	
Pubic & ischial distal expansion	present	absent	present
Crus and proximal tarsals	fused	fused	fused
Metatarsals II & III proximally	fused	fused	fused
Ascending process astragalus	short	short	short
Skull/antorbital fenestra length	variable	>1/3	<1/3
Neck relatively	long	short	
Forelimbs relatively	large	small	
Pubis/femur ratio	>1.0	<1.0	

Condition of characters cited by Raath (1977), Padian (1986), Colbert (1989), Rowe (1989) or Hunt & Lucas (1991) as differing in the three taxa. Antorbital fenestra (aofe).

TABLE 1.

ankle. Antorbital fenestra and fossa large. Manus digits I-III only are complete, with II the longest. Ilium elongated, acetabulum completely open.

Family COELOPHYSIDAE Paul, 1988

Synonyms: Podokesauridae [in part], Halticosauridae [in part]

Diagnosis: Basal theropods with slender body proportions. Skull long and fairly low, subnarial gap between premaxilla and maxilla, antorbital fenestra large, dentary slender, anterior tip slightly expanded and supports radiating tooth arrangement, teeth heterodont because those of premaxilla are more conical and less serrated than maxillary examples, 4 premaxillary teeth. Tail very long. Ilium fairly short.

Genus *Syntarsus* Raath, 1969

Synonyms: *Rioarribasaurus*, *Coelophysis*, *Coelurus*

Diagnosis: Total length 2.5-4 m, skeleton gracile. Skull length ~210-270+ mm, premaxilla small, external nares small, premaxilla and nasal do no contact beneath external nares, nasal fenestra incipient or present, maxilla long, antorbital fenestra and fossa very large, area anterior and ventral to antorbital fossa very limited, ventral edge of

antorbital fossa has a raised rim, jugal triradiate, orbit large and subcircular, quadrate processes of squamosal and quadratojugal slender and contact each other, quadrate vertical, mandible slender, mandibular fenestra large, retroarticular process long. Cervicals slender, transverse process of first caudal more swept back than others, anterior caudal spines very short and transverse processes long so tail base is flat topped. Scapular blade fairly short and broad, forelimbs short. Ilium height/length ratio low, cleft between anterior blade and pubic peduncle broad, posterior ilia flare strongly laterally, brevis fossa well exposed in lateral view, pubic shaft curved, ascending process of astragalus short, metatarsals II & III fuse proximally.

Syntarsus colberti (Hunt and Lucas, 1991)

Synonyms: *Rioarribasaurus colberti*, *Coelophysis bauri*, *Coelurus bauri*

Holotype: AMNH 7224

Type locality, horizon, age: New Mexico, Chinle Formation, late Carnian-Norian.

Diagnosis: Moderately gracile skull and skeleton. Post temporal fenestra may be present, teeth small, row of 22-26 maxillary teeth ends beneath orbit, 27 dentary teeth. Neck relatively long. Pubis as long as or longer than femur, distal

pubic and ischial expansions relatively large, hindlimbs relatively short.

Syntarsus rhodesiensis Raath, 1969

Holotype: NM 1

Type locality, horizon, age: Zimbabwe, Forest Sandstone, Hettangian.

Diagnosis: Gracile skull and skeleton. Post temporal fenestra absent, teeth small, row of 19-20 maxillary teeth ends beneath antorbital fenestra, 25 dentary teeth. Neck relatively short. Pubis shorter than femur, no distal pubic expansions, distal ischial expansion relatively small, hindlimbs relatively long.

Syntarsus kayentakatae Rowe, 1989

Holotype: MNA V2623

Type locality, horizon, age: Arizona, Kayenta Formation, Sinemurian-Pliensbachian.

Diagnosis: Robust skull, small paired crests, lacrimal bar thick, post temporal fenestra absent, retroarticular process moderately long, teeth fairly large, row of 18 maxillary teeth ends beneath orbit. Distal pubic and ischial expansions relatively large.

Genus *Liliensternus* Welles, 1984

Synonym: *Halticosaurus* [in part]

Type locality, horizon, age: Germany, upper Keuper Formation, late Norian.

Diagnosis: Total length ~5 m, skeleton gracile. Skull length ~400 mm, ventral edge of antorbital fossa has a raised rim. Cervicals moderately slender. Ilium short and deep, cleft between anterior blade and pubic peduncle narrow, pubis straight and very long, brevis fossa not well exposed in lateral view, ascending process of astragalus short.

Liliensternus liliensterni (Huene, 1934)

Synonym: *Halticosaurus liliensterni*

Lectotype: HMN dd

Genus *Dilophosaurus* Welles, 1970

Synonym: *Megalosaurus* [in part]

Type locality, horizon, age: Arizona, Kayenta Formation, late Sinemurian-Pliensbachian.

Diagnosis: Total length ~6 m, skeleton fairly robust. Skull length ~500 mm, skull robust, premaxilla large, external nares large, premaxilla and nasal contact beneath external nares, large paired crests, maxilla fairly short and deep, antorbital fenestra and fossa modest in size, area anterior and ventral to fossa extensive, ventral edge of antorbital fossa smooth, jugal tetraradiate, orbit modest in size and elongated vertically, quadrate processes of squamosal and quadratojugal robust and do not contact each other, quadrate slopes ventro-posteriorly, post-temporal fenestra closed, mandible fairly deep, mandibular fenestra small, retroarticular process short, teeth large, 12 maxillary teeth, 17 dentary teeth. Cervicals robust, anterior

caudal spines moderately short so tail base is curved on top. Scapular blade fairly short and very broad and subrectangular dorsally, forelimbs fairly long. Ilium short and deep, cleft between anterior blade and pubic peduncle very narrow, small postero-dorsal process on ilium, brevis fossa not well exposed in lateral view, pubic shaft straight, ascending process of astragalus fairly tall.

Dilophosaurus wetherilli Welles 1954

Synonym: *Megalosaurus wetherilli*

Holotype: UCMP 37302

CONCLUDING COMMENTS

Syntarsus is the only dinosaur genus known to have species based on complete skeletons found on both above and below the boundary between major geological periods, the Triassic and Jurassic. The taxon may have survived the formation of the giant Manicouagan impact crater (Paul, 1989). The genus was long lived, up to ~25 Myr from the Carnian-Norian to the Sinemurian-Pliensbachian. The close similarity of North American *S. colberti* and southern African *S. rhodesiensis* is an exceptional example of the uniformity of the early Mesozoic supercontinental fauna.

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REFERENCES

- Colbert, E. H. 1947. *Nat. Hist.*, v. 56, p. 392-399.
 Colbert, E. H. 1989. *Mus. North. Az. Bull.*, v. 57, p. 1-160.
 Colbert, E. H., Charig, A. J., Dodson, P., Gillette, D. D., Ostrom, J. H. and Weishampel, D. 1992. *Bull. Zool. Nomen.*, v. 49, p. 276-279.
 Gauthier, J. 1986. *Mem. Calif. Acad. Sci.*, v. 8, p. 1-55.
 Hunt, A. P. and Lucas, S. G. 1991. *Palaont. Z.*, v. 65, p. 191-198.
 International Commission on Zoological Nomenclature 1985. *International Code of Zoological Nomenclature*: London, International Trust for Zoological Nomenclature.
 Norman, D. B. 1990. in Weishampel, D. B., Dodson, P. and Osmolska, H., eds., *The Dinosauria*: Berkeley, University of California Press, p. 280-305.
 Padian, K. 1986. in Padian, K., ed., *The Beginning of the Age of Dinosaurs*: Cambridge, Cambridge University Press, p. 45-60.
 Paul, G. S. 1984. in Reif, W.-E. and Westphal, F., eds., *Third Symposium on Mesozoic Terrestrial Ecosystems*: Tubingen, ATTEMPTO Verlag, p. 175-180.
 Paul, G. S. 1988. *Predatory Dinosaurs of the World*: New York, Simon & Schuster.
 Paul, G. S. 1989. *Bioscience*, v. 39, p. 162-172.
 Raath, M. A. 1977. *The Anatomy of the Triassic Theropod Syntarsus rhodesiensis* (Saurischia: Podokesauridae), Ph.D. dissertation: Salisbury, Rhodes University.
 Rowe, T. 1989. *J. Vert. Paleont.*, v. 9, p. 125-136.
 Rowe, T. and Gauthier, J. A. 1990. in Weishampel, D. B., Dodson, P. and Osmolska, H., eds., *The Dinosauria*: Berkeley, University of California Press, p. 151-168.
 Welles, S. P. 1984. *Palaeontographica (A)*, v. 185, p. 85-180.