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Source: *Journal of Vertebrate Paleontology*, Vol. 9, No. 2 (Jun. 30, 1989), pp. 125-136

Published by: The Society of Vertebrate Paleontology

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A NEW SPECIES OF THE THEROPOD DINOSAUR *SYNTARSUS* FROM THE EARLY JURASSIC KAYENTA FORMATION OF ARIZONA

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ABSTRACT—Until now, *Syntarsus* was based on a single species, *S. rhodesiensis*, known only from southern Africa. The discovery of *Syntarsus* in North America adds significantly to the increasingly detailed resemblance of African and North American Early Jurassic terrestrial vertebrate faunas. The new species, *Syntarsus kayentakatae*, is based on a complete skull and partial skeleton, and more fragmentary remains of at least 16 additional individuals, all from a narrow stratigraphic interval in the Kayenta Formation. *Syntarsus kayentakatae* is diagnosed by parasagittal cranial crests and fusion of the fibula to the calcaneum in adults. *Syntarsus* is the most derived member of the newly diagnosed theropod taxon Ceratosauria, possessing 22 apomorphies that arose subsequent to the divergence of ceratosaurs from other theropods. *Syntarsus* shares 20 of these with *Coelophysis bauri*, one of the earliest well-known theropods. By their first appearance, probably late Carnian, ceratosaurs already possessed a history involving considerable morphological transformation. A number of these characters arose convergently much later in time in ornithurine birds.

INTRODUCTION

During the summers of 1977 to 1979, Dr. Farish A. Jenkins, Jr. directed field crews from the Museum of Comparative Zoology, Harvard University (MCZ), and from the Museum of Northern Arizona (MNA) in a survey of the vertebrate fauna of the Early Jurassic Kayenta Formation. This work was carried out in cooperation with the Navajo Tribal Council, on lands of the Navajo Nation in northeastern Arizona. Among the nearly 100 specimens collected during those seasons are the remains of at least 14 individuals referable to a new species of the theropod dinosaur *Syntarsus*. Parts of one additional individual were collected in 1982 for the Museum of Paleontology, University of California, Berkeley (UCMP), by Clark and Fastovsky (1986), and it is now possible to refer fragments of two individuals in older collections at the Museum of Northern Arizona to this taxon.

Until now, *Syntarsus* was based on a single species, *S. rhodesiensis* Raath (1969), known only from Zimbabwe (Raath, 1969, 1977) and South Africa (Gow and Raath, 1977; Raath, 1980, 1985; Kitching and Raath, 1984). The presence of *Syntarsus* in North America adds significantly, if not surprisingly, to the increasingly detailed resemblance between North American and southern African terrestrial vertebrate faunas of the Early Jurassic (Olsen, 1980; Jenkins et al., 1983; Kitching and Raath, 1984; Olsen and Galton, 1984; Attridge et al., 1985; Clark and Fastovsky, 1986; Olsen and Sues, 1986; Sues, 1986). The Kayenta specimens also support observations by Raath (1977) and Colbert (in press) of a marked dimorphism in *Syntarsus* and its closest relatives, in which robust individuals are distinguished by hypertrophied muscle attachments and relatively massive limbs from gracile in-

dividuals that lack these features but achieve comparable adult sizes.

Assignment of the kayenta specimens to a new species of *Syntarsus* was based on a phylogenetic analysis of other theropods. Of special interest were the Triassic and Jurassic taxa *Syntarsus rhodesiensis*, *Coelophysis bauri*, *Liliensternus liliensterni*, *Dilophosaurus wetherilli*, *Ceratopsus nasicornis*, *Sarcosaurus woodi*, and *Segisaurus halli*. These were all found to share novel similarities with the Kayenta specimens. In order to judge whether the Kayenta material represented a diagnosable new taxon or was referable to an existing name, an analysis of the distributions of shared derived characters among all of those taxa was undertaken. Details of that study are presented elsewhere (Rowe and Gauthier, in press; MS), but data pertinent to the diagnosis and relationships of the new taxon are summarized below.

MATERIAL

Type Specimen

The type specimen (MNA V2623; MCZ field number 18/78a) came from a quarry that yielded one associated partial skeleton and more fragmentary remains of at least two other individuals. The most complete skeleton was chosen as the type specimen. It consists of a complete but slightly crushed skull, the first eleven vertebrae, cervical and dorsal ribs, gastralia, the right scapulocoracoid, a partial right(?) manus, the proximal portion of the left scapulocoracoid with the articulated proximal end of the left humerus, distal parts of both pubic shafts, weathered fragments of the distal ends of both ischia, right and left antitrochanteric portions of the acetabular border, a complete

right femur, a right tibia, right fibula, partial right pes, a partial left femur, the distal two-thirds of an articulated left tibia and fibula, and an articulated left pes. Fragments of fused sacral centra, portions of approximately 34 caudal centra, and numerous bone fragments were also recovered as surface float. Some of these may belong to the type, but it is impossible to ascertain to which of the three individuals they belong.

The quality of preservation varies considerably. The surface float is very hard and well preserved, but it consists of only the most resilient parts of bones, mostly the broken ends. Material quarried from bedrock was very badly weathered near the surface, but preservation was much better at depth. However, even some of the buried bone showed variable preservation, with some parts of a bone being solidly mineralized while other parts of it were soft and "chalky." Most of the skull and cervical vertebrae were encrusted in a dense hematite cement that enhanced preservation but rendered preparation exceedingly difficult and slow.

The type specimen is a fully mature, robust adult. Evidence that skeletal growth was virtually complete can be seen in the complete fusion between the atlantal centrum, axial intercentrum and centrum, as well as fusions of the mid-cervical ribs to centra, neural arches to centra, scapula to coracoid, and fusion between the proximal ends of metatarsals II and III (see Gauthier, 1984, 1986; Brinkman, 1988, and references therein for discussions of evaluating ontogenetic stages in fossils).

Referred Material

Other Type Quarry Specimens—Portions of two right femora, in addition to that of the type specimen, indicate that at least two other individuals were preserved in the type quarry. Most of these remains were recovered as surface float and it is not possible to definitely associate the disconnected elements with one or the other individual. The material includes a crushed, weathered snout with mandibles, a maxillary fragment with the 9th–11th teeth, isolated separate right and left frontals, a partial occipital condyle, two fragmentary right femora, isolated proximal ends of one right and two left tibiae, distal ends of right and left fibulae, isolated distal ends of right and left tibiae with fused astragalocalcaneum, and eight isolated ends of metatarsals. These individuals are roughly the same size as the type specimen and are probably also adults. The two femoral heads, which are the only elements that can be identified with respect to dimorphism, are of robust individuals. No other taxa have been identified in material recovered from this locality. The final disposition of this material has yet to be determined; some parts of it will be housed at the MCZ, and some may be housed at MNA.

Willow Springs Material—Two localities in the Willow Springs area produced remains referable to the new taxon, the "Shake-N-Bake" locality and a Berkeley (UCMP) locality. These sites lie roughly 10 km from

the type locality and, like the type locality, are within the stratigraphic middle third of the Kayenta Formation (Clark and Fastovsky, 1986).

Shake-N-Bake Specimens (MCZ locality 40/78a; specimens currently catalogued collectively as MCZ 8817)—This locality lies at the top of the middle third of the Kayenta Formation and is the highest locality yet discovered in the Silty Facies. It was discovered in July 1978 and produced numerous fragments of surface float that were recovered by dry screening. The material had washed down from a higher level and, although it could not have been transported far, persistent efforts over several seasons failed to locate the bedrock horizon from which it eroded. Many of the collected pieces consist of numerous small bones cemented together in a dense, black matrix. Before eroding, the specimens were probably semiarticulated and intertwined in a mat of bones that was completely encrusted by this matrix. Limestone, which occurs locally in the Silty Facies of the Kayenta Formation, adheres to several of the fragments. At least 11 individuals are present, as indicated by the proximal ends of 11 left femora. Nearly all of the identifiable fragments are from the pelvis, hindlimb, and tail. All determinable material is from robust individuals. The specimens cover a wide size range, but all are much smaller than the type specimen. I presume they are of younger ontogenetic stage, but at present the black coating obscures most sutures and prevents observation of size-independent age criteria.

Berkeley Specimen (Specimen No. UCMP 128659; Locality UCMP V82309)—A single individual was collected by a Berkeley party in 1982 (Clark and Fastovsky, 1986). It is a subadult gracile individual represented by several proximal caudal centra, a fragmentary left ilium, proximal ends of both pubes, the proximal ends of both femora, and the proximal end of a left fibula.

Rock Head Specimens (Specimen nos. MNA V100, V140, Locality MNA 219-0, "Rock Head")—Two fragmentary specimens were collected from the immediate vicinity of Rock Head. They consist of a partial left ilium with the supra-acetabular crest (MNA V100), and weathered fragments of a femur and humerus of a presumed juvenile (MNA V140).

METHODS

Identification of the new taxon described in this report was part of a more general analysis of Ceratosauria (Rowe and Gauthier, in press, MS), following methods described at length elsewhere (Gauthier, 1986; Gauthier et al., 1988a; Gauthier et al., 1988b; Rowe, 1988). In short, the analysis explored distributions of 25 polarized characters that vary among two or more of the following eight taxa: *Syntarsus rhodesiensis*, *Syntarsus kayentakatae* (sp. nov.), *Coelophysis bauri*, *Lilienster-nus lilienster-ni*, *Dilophosaurus wetherilli*, *Ceratosaurus nasicornis*, *Sarcosaurus woodi*, and *Segisaurus halli*. Autapomorphies were stripped from the analysis. Con-

secutively more distant outgroups used to determine polarity of character transformation were Tetanurae, Sauropodomorpha, Ornithischia, and Herrerasauridae (of doubtful monophyly), based on the more inclusive analysis of Saurischia by Gauthier (1986). All characters were entered on a taxon/character matrix and run through the personal computer version of Swoford's (1985) systematics program, Phylogenetic Analysis Using Parsimony (PAUP512). Results of the analysis are summarized below.

None of the referred material is sufficiently complete to preserve the diagnostic characters of *Syntarsus kayentakatae*, and its referral to the new taxon is based entirely on circumstantial evidence. All referred specimens were collected from within a few kilometers of each other and from within a stratigraphic interval of about 40 m in the Kayenta Formation. The Kayenta Formation remains roughly 120 m thick over the lateral distance between these localities (Clark and Fastovsky, 1986). In addition, all of the referred material does preserve at least some characters that are found only in ceratosaurs, such as the trochanteric shelf and fibular sulcus (Rowe and Gauthier, in press). Nevertheless, at this time the possibility cannot be refuted that some of the referred material is in fact *Segisaurus halli* or some other ceratosaur. Unless otherwise noted, discussion of the diagnosis and relationship of *Syntarsus kayentakatae* is based exclusively on data observed in the type specimen.

SYSTEMATIC PALEONTOLOGY

Systematic Hierarchy:

- DINOSAURIA Owen, 1842
- SAURISCHIA Seeley, 1887
- THEROPODA Marsh, 1881
- CERATOSAURIA Marsh, 1884

SYNTARSUS Raath, 1969

SYNTARSUS KAYENTAKATAE, sp. nov.

Etymology—Named in honor of Dr. Kathleen ("Kayenta Kay") Smith, who discovered the type specimen and many other important fossils during the Kayenta expeditions.

Holotype—MNA V2623, skull and partial postcranial skeleton of a robust, adult individual, discovered in July 1977 and collected in June 1978 by a field party including W. Amaral, F. A. Jenkins, Jr., T. Rowe, C. R. Schaff, K. K. Smith, and H.-D. Sues.

Type Locality and Horizon—MNA locality No. 555-3, "Rock Head North" (MCZ field No. 18/78/A; also recorded in field notes as "Foxtrot Mesa"); Latitude 35°41'39"N, Longitude 111°00'51"W. The specimen was extracted from a small quarry, now silted-in, on the southwestern side of Sand Mesa, near the southern end of the Adeii Eechii Cliffs, on Ward Terrace of the Little Colorado River Valley. The quarry is located in the middle third of the Silty Facies (Harshbarger et al.,

1957) of the Kayenta Formation, at an elevation of approximately 5,220 feet. This is the same stratigraphic level as the type localities of *Scutellosaurus lawleri* Colbert (1981) and *Rhamphinion jenkinsi* Padian (1984), which were found nearby. Remains of at least three individuals were semiarticulated and intertwined near the top of a meter-thick cross-bedded sandstone. The bed is a light greenish-white color, mottled with patches and bands of a dark red hematitic stain. The sandstone is composed of heterogeneous, poorly sorted, angular sand grains in a matrix of silt and clay, with a calcium carbonate cement. A few reddish-brown clayballs and pebbles were found in the matrix around the specimen. There was a dark red hematite stain in the sediments around most of the bones, and a dense hematite layer encrusted portions of the skeleton.

Diagnosis—Paired crest on skull roof, formed by lacrimal and possibly nasal, positioned parasagittally along outer "edges" of skull roof between nares and orbit; fibula fused to calcaneum in adults. (See Relationships of *Syntarsus kayentakatae*.)

Description of the Type Specimen

Skull (Fig. 1A–D)—The skull is 23 cm long from the front of the premaxilla to the back of the quadrate. The premaxillae have no bony symphysis and are held to the skull by nasal and palatal processes. The premaxilla and maxilla are separated by a deep incisure, the "subnarial gap" of Welles (1984), which interrupts the otherwise continuous alveolar margin. The maxilla curves upwards into the top of the incisure to such a degree that the mesial-most maxillary tooth is directed forward. Behind the incisure, the maxilla is strengthened by a longitudinal alveolar ridge that lies just above the tooth row and extends from the front border of the antorbital fossa to the caudal end of the antorbital fenestra. The antorbital fenestra is very long, extending for 26% of the total skull length. There are several semicircular depressions in the maxilla rostral to the antorbital fenestra, but whether any of these perforates the maxilla, producing a maxillary fenestra, remains open to some question because the bone in this region is badly fractured. There certainly was not a large circular maxillary fenestra as in tetanurine theropods. The caudal end of the maxilla abuts the base of the lacrimal, separating the lacrimal from the alveolar margin and excluding the jugal from the antorbital fenestra.

The lacrimal encloses the antorbital fenestra caudally and dorsally. Over the fenestra, the lacrimal is expanded above the skull roof to form a longitudinal crest (Fig. 1C, D), very much as in *Dilophosaurus wetherilli* (Welles, 1984). The nasals may also contribute to the crest, but no sutures are visible in this region. The crest is only 1–2 mm thick and is very fragile. Both right and left crests were preserved when the specimen was collected, but the right crest was lost during preparation. The dorsal and caudal edges of the left crest appear to be the natural borders, but poor preservation

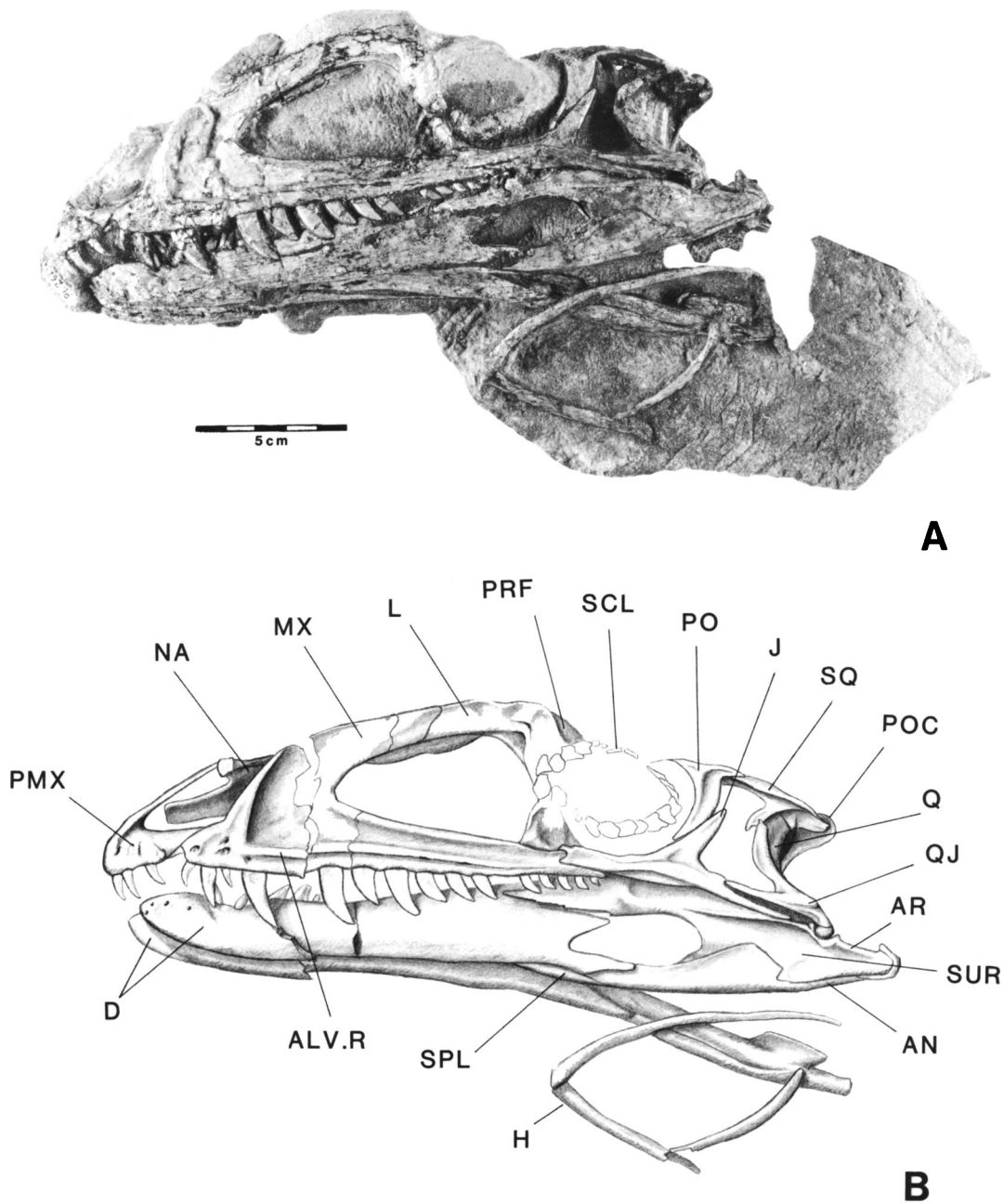


FIGURE 1. *Syntarsus kayentakatae*, MNA V2623 (type specimen). **A**, Photograph and **B**, camera lucida drawing of skull in left lateral view; **C**, photograph and **D**, camera lucida drawing of skull in right lateral view. Abbreviations: ALV.R, alveolar ridge; AN, angular; AR, articular; CR, crest; D, dentary; F.NA, nasal fenestra; F.PO, post-temporal fenestra; FR, frontal; H, →

toward the front of the snout leaves the preserved shape of the rostral edge questionable in this regard.

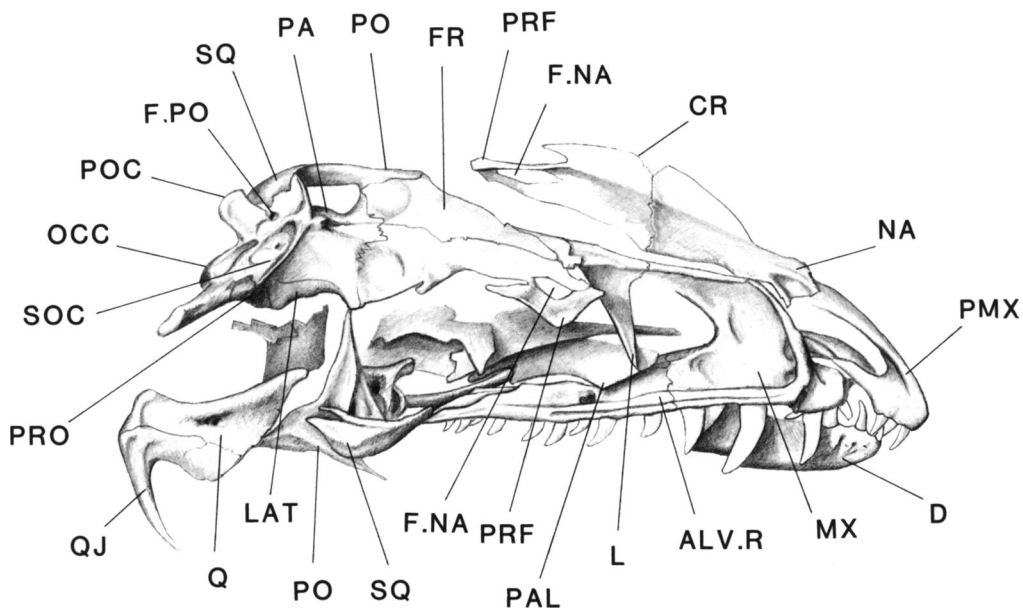
The nasals are broken and displaced into the nares. The bone surface over the nasals, frontals, and prefrontals is poorly preserved and over most of this area sutures are difficult to discern. At the junction between the nasal, prefrontal and frontal is a diamond-shaped opening, termed the nasal fenestra by Raath (1977), that lies just above and rostral to the orbit. This structure is known only in the two species of *Syntarsus* and

may have been involved with the external nasal gland or lacrimal gland. The frontals abut each other on the midline and are tightly sutured to the parietals behind the orbit. The parietals are fused along their entire length. They are widely flared caudally, where they contribute substantially to the occipital plate, meeting on the midline above the supraoccipital. The parietals abut the laterosphenoid without interdigitation; their other contacts are not visible.

The bones of the palate are crushed and telescoped



C



D

hyoid; J, jugal; L, lacrimal; LAT, laterosphenoid; MX, maxilla; NA, nasal; OCC, occipital condyle; PA, parietal; PAL, palatine; PMX, premaxilla; PO, postorbital; POC, paroccipital process; PRF, prefrontal; PRO, prootic; Q, quadrate; QJ, quadratojugal; SCL, sclerotic ring; SOC, supraoccipital; SPL, splenial; SQ, squamosal; SUR, surangular.

over each other. Their dorsal surfaces can be seen through the orbit and antorbital fenestra, but little useful detail is visible.

The orbit is 4 cm long, and on the left side the intact sclerotic ring entirely fills the orbit. The large size of the eyeball is striking, and crowding within the orbit may have played some role in development of the nasal fenestra near the upper, anterior orbital border. Behind the orbit, the postorbital, jugal, squamosal, quadrate, and quadratojugal abut one another to form the sus-

pensorium. Sutures between these elements are virtually nonexistent. On the right side of the skull they are disarticulated but still associated.

Behind the suspensorium is a long paroccipital process formed largely by the opisthotic, with a small contribution by the prootic. The opisthotic in the distal part of the process is formed of rather spongy bone enclosed by a thin, dense cortex. The right prootic and laterosphenoid are visible where they contribute to the medial and caudal borders of the supratemporal fe-

nestra, but the rest of the braincase is largely obscured by the bones of the suspensorium, displaced palatal elements, and matrix. Little can be added to Raath's (1985) description of the braincase in *Syntarsus rhodesiensis*.

The occipital plate is formed by the supraoccipital, parietals, and squamosals above the occipital condyle, and by the paroccipital processes lateral to it. Exoccipitals are not visible as separate elements, evidently being fused with the paroccipital processes laterally and with the supraoccipital dorsally. The post-temporal fenestra is reduced to a tiny foramen at the junction between the paroccipital process, supraoccipital, and parietal. The occipital condyle is a slightly depressed sphere that protrudes well behind the occipital plate.

The dentaries have no bony symphysis and only a very short overlap with the postdentary bones. A swelling near the front of the dentary marks the persistence of an enlarged dentary tooth which is currently obscured by the premaxillary teeth and by matrix. A single pair of hyoid rods, which are one-third the length of the mandible, are present.

Dentition—The premaxilla has four teeth that are only slightly recurved, subcircular in cross section, and have few or no serrations. The mesial-most dentary teeth are similar. The maxillary teeth are strongly recurved, laterally flattened, and strongly serrated distally, with varying degrees of serrations visible mesially. The largest maxillary tooth lies in the fifth alveolus on the right side (this socket is empty on the left), and the teeth gradually diminish in size on either side of it. The maxillary tooth row contains 18 teeth and extends distally to underlie the orbit. Most of the dentary teeth are obscured beneath the upper dentition.

Vertebral Column and Ribs—Only the first 11 vertebrae are present, but they are nearly complete and well preserved. There is no proatlas arch. The atlantal neural arches and intercentrum are disarticulated and the axis is dislocated but still in contact with the third vertebra. The succeeding vertebrae are in articulation. The atlantal centrum is fused to the axial centrum, forming a robust odontoid process, and the axial intercentrum is fused to these structures beneath the odontoid. The axis centrum is strongly keeled ventrally and lacks pleurocoels. The axial transverse process is absent and the diapophysis is reduced to a small swelling. The axial neural spine lacks a spine table. Post-axial cervical vertebrae have low, elongate neural arches. The third cervical retains a strong ventral keel, but whether keels persist in succeeding cervicals is not known. Pleurocoels are visible in the caudal ends of the five immediately post-axial vertebrae. Presumably, there was a second set of pleurocoels located rostrally, as is the case in other ceratosaurs (Rowe and Gauthier, in press), but they are buried in matrix beneath the heads of the cervical ribs. The pleurocoels are deep, blind pockets that do not open into a centrocoel or communicate with each other.

Ribs are present on all cervical vertebrae. The atlas

and axis ribs entirely lack the tuberculum and articulate with very poorly developed parapophyses. The weakness of the axial parapophysis led Raath (1977) to speculate that the axial rib might be absent in *Syntarsus rhodesiensis*, but it is preserved in articulation in *S. kayentakatae*. The third cervical rib has a small capitulum and tuberculum, and it retained a potentially mobile articulation throughout life. The remaining cervical ribs have well-developed capitula and tubercula, and are fused to their centra. The degree of elongation of the cervical ribs is striking. Some, if not all, pass caudally for a distance up to the length of four centra to form delicate bundles of three or four that extend along the entire neck.

The base of the neck is not well exposed because the rib bundles have prevented preparation of much of the centra and arches, and few details of the dorsal centra are visible. The dorsal vertebral arches have transverse processes that are strongly backturned and triangular when viewed from above. Proximally, each transverse process extends the entire length of the centrum, while distally the process slants backwards, being widest along its caudal edge. Fragmentary dorsal ribs are preserved with a thin web of bone connecting the capitulum and tuberculum. A tight network of gastralia is also present.

Shoulder Girdle and Forelimb—A complete right and partial left scapulocoracoid are preserved, and in both of them the scapula and coracoid are fused (Fig. 2), indicating that growth had ceased before death. The scapular blade is expanded distally, while proximally, above the glenoid, it is narrowly constricted. The coracoid is rounded posteriorly, with only a blunt protuberance marking the biceps attachment. The proximal end of the left humerus is preserved in articulation with the scapulocoracoid, but the humerus is badly weathered and is morphologically uninformative. Apart from a partial right(?) manus, nothing else is known of the forelimb. The partial manus is similar in all observable details with Galton's (1971) description of *Syntarsus rhodesiensis*. It retains a small IVth metatarsal with one unquestionable phalanx, and a small, terminal nub of bone that represents either a second phalanx or a displaced fragment of the first. The claws are laterally compressed, strongly recurved, and bear large flexor tubercles. Cross sections of the humerus, metacarpals, and phalanges show them to be hollow and thin walled.

Pelvis and Hindlimb—All that remains of the ilium is its junction with the ischium, where the two bones fuse at the flat antitrochanter. The delicate puboischial plate is also missing and only the pubic shafts are preserved. The shaft is comma shaped in cross section, with a thin, curved plate forming a narrow pubic apron that must have extended proximally almost to the acetabulum. The pubis ends distally in a rounded swelling, but there is no pubic "foot" as in tetanurine theropods. The distal end of the shaft of the ischium is preserved but badly weathered. The shaft is triangular in cross section with a slightly swollen distal end.

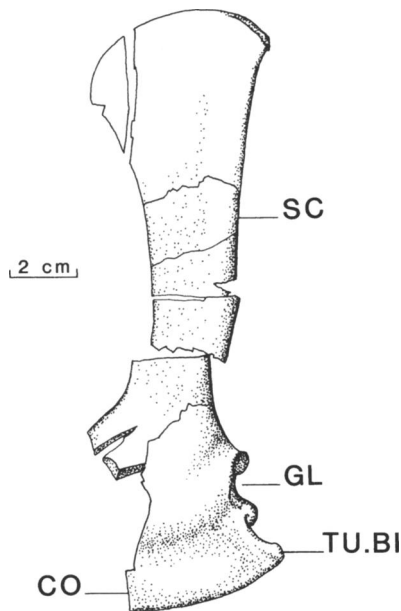


FIGURE 2. *Syntarsus kayentakatae*, MNA V2623 (type specimen). Right scapulocoracoid in medial view. Abbreviations: CO, coracoid; GL, glenoid; SC, scapula; TU.BI, biceps tubercle.

The femur, tibia, metatarsals II–IV, and phalanges are hollow and thin walled. The anterior (lesser) trochanter of the femur (Figs. 3, 4) develops at the insertion of *M. puboischiofemoralis internus pars dorsalis* on the dorsal surface of the femur (Rowe, 1986). The trochanter lies just distal to the femoral head, and there is a pronounced trochanteric shelf that wraps from the base of the lesser trochanter laterally around the femur and continues as a distinct insertion scar onto the ventral aspect of the shaft. The trochanteric shelf is absent in the gracile UCMP individual, as is the case in other gracile individuals of *Syntarsus* (Raath, 1977). The fourth trochanter is located entirely on the proximal half of the femur, along the medial edge of the shaft. The distal end of the femur bears a crista tibiofibularis that is developed into a distinctive, well-formed, kidney-shaped condyle. Along the lateral side of the base of the crista is a deep groove that lies adjacent to the articular facet for the fibula, but its shape would not have permitted the fibula to articulate within it. The femoral condyles are connected by a sharp crest in the popliteal fossa.

The fibula is expanded proximally and bears a deep sulcus on its medial surface that probably was the site of origin of part of the pedal flexor musculature (Fig. 5). The sulcus opens caudally and extends down the fibular shaft to near the top of the crista fibularis of the tibia. The tibia has a swollen proximal end and there is a simple cnemial crest. The tibial shaft is twisted as in other dinosaurs. The tibia, astragalus, and calcaneum are fused to form a tibiotarsus (Fig. 6), much like the tibiotarsus in ornithurine theropods. However, unlike ornithurines, the ascending process is very small

and is largely covered by the flared distal end of the fibula. In addition, the fibula extends to the ankle and is fused with the calcaneum, whereas it fails to reach the tarsus in ornithurine birds (Gauthier, 1986).

Distal tarsals II and III are fused to the proximal ends of their respective metatarsals (Fig. 7) forming a tibiotarsus as in ornithurines. However, distal tarsal IV remained separate throughout ontogeny, and there is no fifth distal tarsal. Like *Syntarsus rhodesiensis*, the proximal ends of metatarsals II and III are fused, and metatarsals I, IV and V are separate. The first metatarsal has lost its articulation with the ankle joint and lies along the medial side of metatarsal II in the articulated left pes. The fifth metatarsal is splint-like and, although it lies close to the ankle, it fails to contact the tarsus.

RELATIONSHIPS OF *SYNTARSUS KAYENTAKATAE*

Initial comparisons of the Kayenta material with other theropods disclosed novel similarities shared with *Syntarsus rhodesiensis* (Raath, 1969, 1977, 1980, 1985), *Coelophysis bauri* (Colbert, 1964, in press), *Liliensterius liliensterni* (Welles, 1984), *Dilophosaurus wetherilli* (Welles, 1984), *Ceratosaurus nasicornis* (Gilmore, 1920), *Sarcosaurus woodi* (Andrews, 1921), and *Segisaurus halli* (Camp, 1936). To determine which similarities bear on the identity of the new material and

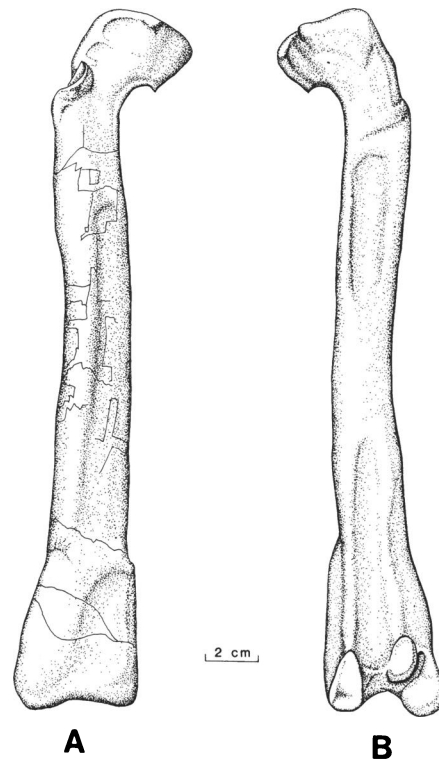


FIGURE 3. *Syntarsus kayentakatae*, MNA V2623 (type specimen). Right femur in A, dorsal (anterior) view, and B, ventral (posterior) view.

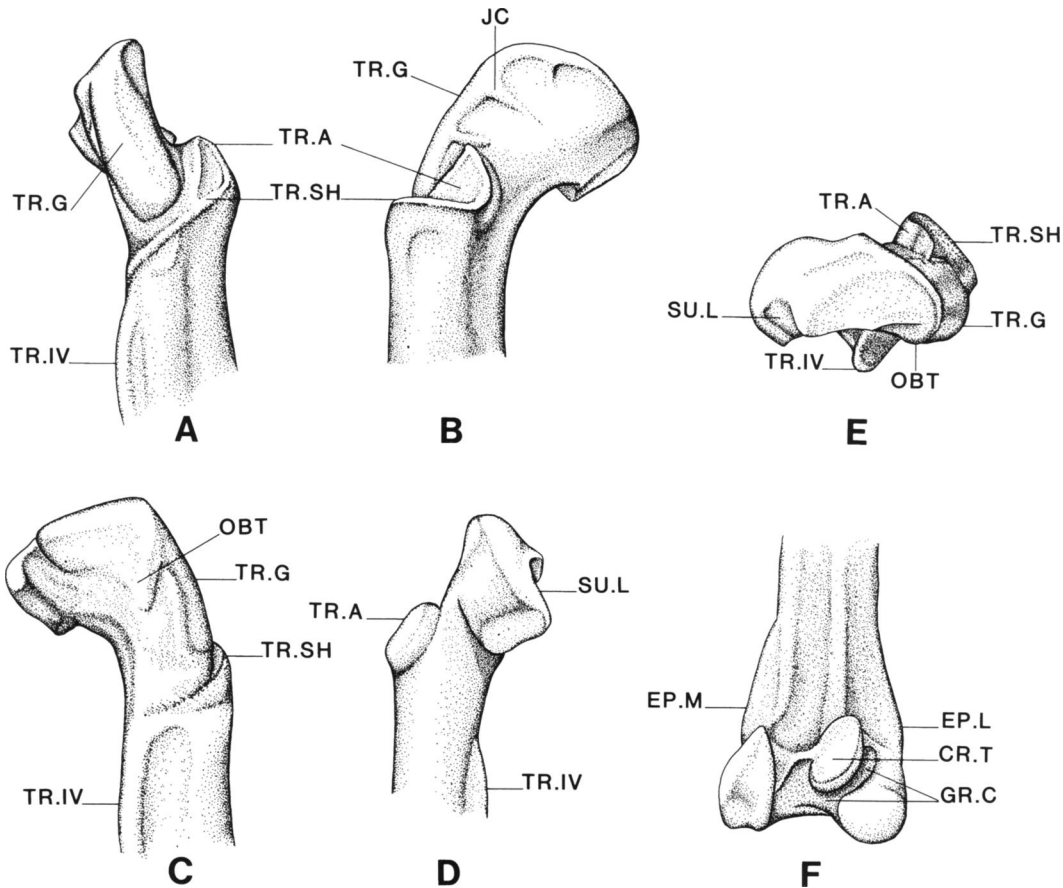


FIGURE 4. *Syntarsus kayentakatae*, MNA V2623 (type specimen). Detail of ends of femur. Proximal end in **A**, lateral view, **B**, oblique dorsal (anterior) view, **C**, ventral (posterior) view, **D**, medial view, and **E**, proximal view; and **F**, distal end in ventral (posterior) view. Abbreviations: **CR.T**, crista tibiofibularis; **EP.L**, lateral epicondyle; **EP.M**, medial epicondyle; **GR.C**, groove at base of crista tibiofibularis; **JC**, insertion scar of joint capsule; **OBT**, obturator ridge; **SU.L**, sulcus for ligamentum capitis femoris; **TR.A**, anterior ("lesser") trochanter; **TR.G**, greater trochanter; **TR.SH**, trochanteric shelf; **TR.IV**, fourth trochanter.

which indicate its placement in more inclusive groupings, a phylogenetic analysis of those taxa was undertaken (Rowe and Gauthier, in press, MS).

The framework for this study was provided by a

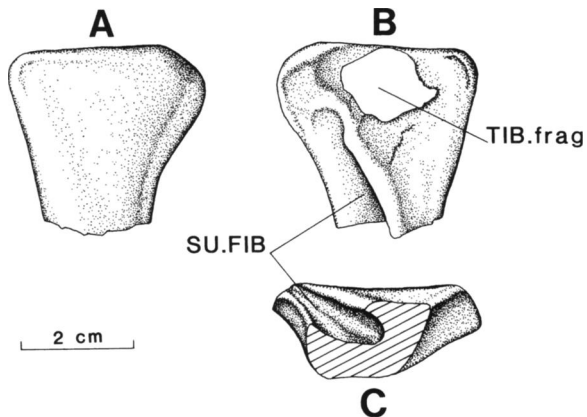


FIGURE 5. *Syntarsus kayentakatae* (referred specimen from type quarry). Proximal end of left fibula in **A**, lateral view, **B**, medial view, and **C**, cross section. Abbreviations: **SU.FIB**, fibular sulcus; **TIB.frag**, fragment of tibia.

more general analysis of theropods by Gauthier (1984, 1986; Gauthier and Padian, 1985), who concluded that Theropoda is monophyletic and that within it are two major monophyletic divisions, Tetanurae and Ceratosauria (Fig. 8). Tetanurae includes those theropods more closely related to birds (and includes birds), whereas Ceratosauria includes taxa more closely related to *Ceratosaurus nasicornis*. Analyses by Gauthier (1986) and Rowe and Gauthier (in press, MS) led to assignment of *Syntarsus kayentakatae*, *Syntarsus rhodesiensis*, *Coelophysis bauri*, *Liliensternus liliensterni*, *Dilophosaurus wetherilli*, *Ceratosaurus nasicornis*, *Sarcosaurus woodi*, and *Segisaurus halli* to Ceratosauria.

Ceratosauria is diagnosed by (1) two pairs of cervical pleurocoels, (2) dorsal transverse processes that are strongly backturned and triangular when viewed from above, (3) the pubic plate perforated by a large pubic fenestra lying just below the obturator foramen, (4) the pubic shaft bowed forwards, (5) fusion in adults between the sacral centra, neural arches, spines, transverse processes, and sacral ribs, (6) fusion between the ilium, ischium, and pubis in adults, (7) the trochanteric

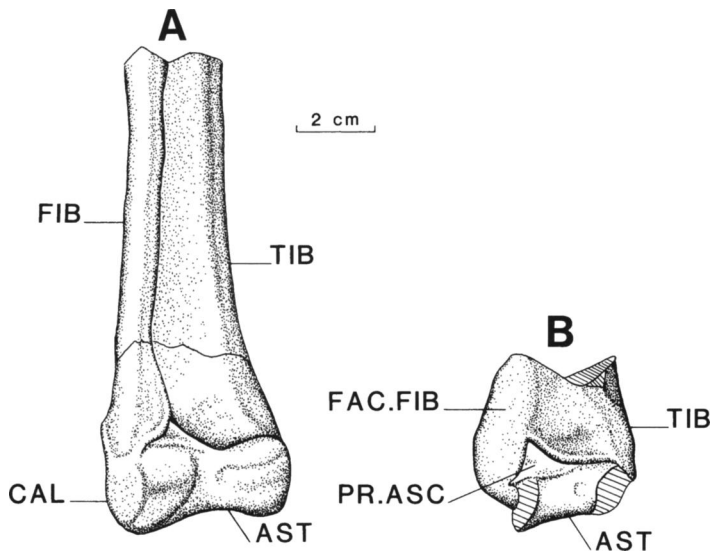


FIGURE 6. A, *Syntarsus kayentakatae*, MNA V2623 (type specimen), distal end of right tibiotarsus and fibula in anterior view. B, Referred specimen from type quarry, distal end of right tibiotarsus lacking fibula, calcaneum, and medial-most part of the astragalus (broken areas hatched). Abbreviations: AST, astragalar portion of tibiotarsus; CAL, calcaneal portion of tibiotarsus; FAC.FIB, facet on tibia for fibula; FIB, fibula; PR.ASC, ascending process; TIB, tibia.

shelf present in robust individuals on the anterior trochanter of the femur, (8) a deep sulcus along the lateral side of the base of the crista tibiofibularis, (9) a deep sulcus on the medial surface of the proximal end of the fibula, (10) fusion between the astragalus, calcaneum, and tibia in adults, (11) the distal end of the fibula flared into a sheet of bone that overlaps the ascending process of the astragalus, and (12) fusion of distal tarsals II and III to their respective metatarsals in adults (Rowe and Gauthier, in press, MS). Characters 1, 2, 4, 7, 8, 9, 10, 11, and 12 are observable in the type specimen of *Syntarsus kayentakatae*. Characters 5 and 6 (as well as some of the others) can also be observed in referred specimens.

Sarcosaurus woodi and *Segisaurus halli* are based on deficient specimens that preserve sufficient information to permit their assignment to Ceratosauria, but are not complete enough to permit their positions within the group to be determined. The other ceratosaurians can be placed in resolved positions within Ceratosauria. *Ceratosaurus nasicornis* is the sister taxon of all other ceratosaurians (Fig. 8), except possibly *Segisaurus* and *Sarcosaurus*.

Dilophosaurus, *Liliensternus*, *Coelophysis*, and *Syntarsus* are more closely related to each other than to *Ceratosaurus nasicornis* (Fig. 8, Node 2). They share (13) the subnarial "gap" between the premaxilla and maxilla, (14) complete loss of the axial diapophysis, (15) reduction of the axial parapophysis, and (16) loss of axial pleurocoels. All of these characters can be observed in the type specimen of *Syntarsus kayentakatae*.

Liliensternus, *Coelophysis*, and *Syntarsus* are more

closely related to each other than to *Dilophosaurus* (Fig. 8, Node 3) based on (17) the alveolar ridge of the maxilla. This character is present in the type specimen of *Syntarsus kayentakatae* (Fig. 1). *Liliensternus* is based on two deficient specimens that do not share any apparent apomorphies. This means that although *Liliensternus* might be a valid monophyletic taxon, without diagnostic characters of its own it might also prove synonymous with either *Coelophysis* or *Syntarsus*.

Coelophysis bauri and *Syntarsus* are more closely related to each other than to any other theropod (Fig. 8, Node 4) based on (18) an antorbital fossa that is greater than 25% of the length of the skull (indeterminate in *Liliensternus*), (19) elongated cervical ribs (indeterminate in other ceratosaurians), and (20) a sharp caudal rim on the iliac fossa for the origin of M. iliofemoralis. Characters 18 and 19 can be observed in the type of *Syntarsus kayentakatae*.

The resemblance between *Coelophysis* and *Syntarsus* is so detailed and striking that Raath (1969, 1977) faced an admittedly difficult decision when he rejected synonymizing them. His decision is justified, however, in that there are at least two characters that distinguish *Syntarsus* from *Coelophysis*: (21) the nasal fenestra, and (22) fusion of the proximal ends of metatarsals II and III. Both characters are observable in the type specimen of *Syntarsus kayentakatae* (Figs. 1, 7).

Syntarsus rhodesiensis was diagnosed by characters that now appear to obtain at a more general level than was evident twenty years ago, when Raath's (1969) original description was published. Nevertheless, Raath (1977) subsequently listed two characters that may prove diagnostic for this taxon. These are (23) antorbital fenestra more than 40% of total skull length, and (24) lacrimal overlapping jugal laterally and reaching

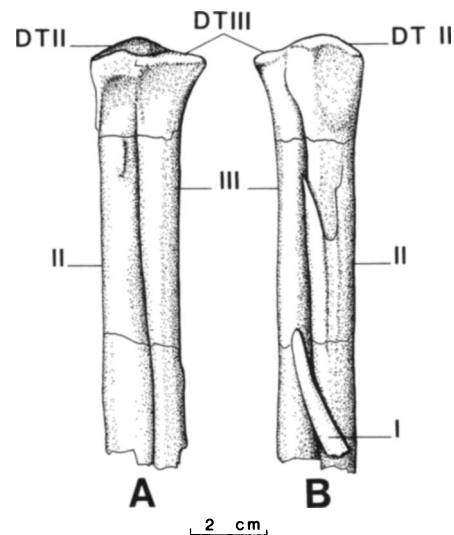


FIGURE 7. *Syntarsus kayentakatae*, MNA V2623 (type specimen). Right partial tarsometatarsus in A, anterior, and B, posterior views. Abbreviations: DT II, distal tarsal II; DT III, distal tarsal III; I, metatarsal I; II, metatarsal II; III, metatarsal III.

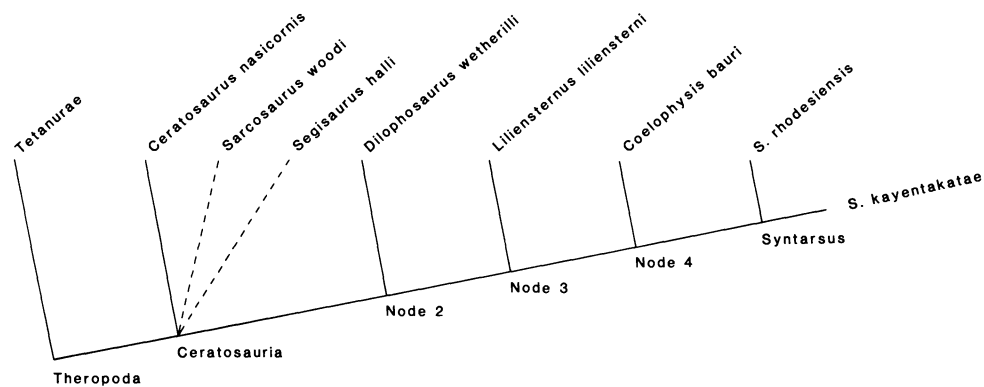


FIGURE 8. Phylogeny of Ceratosauria (from Rowe and Gauthier, in press). See text for summary of data at each node.

alveolar border. Both characters are based on reconstruction of disarticulated cranial elements. They are related in that the unusual articulation of the lacrimal largely determines the length of the antorbital fenestra. If these characters are not sustained by articulated material, a reconsideration of the monophyly and diagnosis of *Syntarsus rhodesiensis* may be necessary.

Syntarsus kayentakatae is diagnosed by (25) parasagittal cranial crest formed by the lacrimal and possibly nasal, and (26) fusion of the fibula and calcaneum in late ontogeny. A very similar crest is also known in *Dilophosaurus wetherilli* (Welles, 1984). This unique resemblance between these taxa and their co-occurrence in the Kayenta Formation have raised the question of whether *Syntarsus kayentakatae* might simply be a juvenile *Dilophosaurus*. However, fusions between skeletal elements indicate that the type specimen of *Syntarsus kayentakatae* is an adult, whereas absence of the same fusions in the type of *Dilophosaurus* attests that it is subadult. Although not fully grown at the time of its death, the type specimen of *Dilophosaurus wetherilli* is twice the size of the type specimen of *Syntarsus kayentakatae*. Moreover, as detailed above, the latter has a number of characters derived within Ceratosauria that are absent in the former (Rowe and Gauthier, in press). It is simplest to conclude that cranial crests evolved convergently within ceratosaurs, and that two different crested theropods coexisted in what is now Arizona during the Kayenta depositional interval.

DISCUSSION

The discovery of *Syntarsus kayentakatae* provides important support to the growing body of biostratigraphic evidence indicating an Early Jurassic age for the Kayenta Formation. One should bear in mind, however, that the taxonomic assignment of the Kayenta specimens rests on the two synapomorphies distinguishing *Syntarsus* from the late Carnian to Norian age *Coelophysis bauri*. Were these characters not evident, the Kayenta specimens would be equally consistent with a Late Triassic assignment.

Syntarsus is one of the most derived ceratosaurs, possessing 22 apomorphic character states that evolved

subsequent to the divergence of Ceratosauria and Tetanurae from their last common ancestor. *Syntarsus* shares 20 of these with *Coelophysis bauri*, an indication that even the earliest known theropods already possessed a history involving considerable morphological transformation. This contradicts the common view that *Coelophysis* is a uniformly primitive theropod, possibly the plesion or true ancestor of Theropoda (e.g., Padian, 1986).

A number of characters distinguishing ceratosaurs generally, and *Coelophysis* and *Syntarsus* in particular, also occur in ornithurine theropods. All involve ontogenetic fusions between bones that are presumed to have been separate throughout life in Theropoda ancestrally. These include (5) fusion between the sacral centra, neural arches, spines, transverse processes, and ribs in adults, (6) fusion between the ilium, ischium, and pubis in adults, (10) fusion between the astragalus, calcaneum, and tibia in adults, (12) fusion of distal tarsals II and III to their respective metatarsals, and (22) fusion of the proximal ends of metatarsals II and III. These would be considered evidence of close relationship between birds and ceratosaurs if it were not for the overwhelming phylogenetic evidence that birds are deeply internested within Coelurosauria (Gauthier, 1984, 1986), and that birds lack other ceratosaur apomorphies. Nevertheless, if these convergent resemblances are taken together with the many homologous "avian" features that birds and ceratosaurs both inherited from the ancestral theropod (Gauthier, 1984, 1986; Padian, 1986), the resemblance is such that one could conceivably mistake a fragmentary small ceratosaur like *Syntarsus* or *Coelophysis* for an Early Jurassic or Triassic bird.

ACKNOWLEDGMENTS

I thank Farish Jenkins for the opportunity to work in the Kayenta and for generously making this specimen available to me for study. I thank Mike Raath for data on *Syntarsus rhodesiensis*, Edwin Colbert and Kevin Padian for data on *Coelophysis bauri*, and Sam Welles for information on *Dilophosaurus wetherilli*. I am indebted to each of these individuals for substan-

tive criticism and input on this manuscript. I am also grateful to Jacques Gauthier for many great discussions about this material and for so freely sharing his wealth of knowledge on dinosaurs. I thank Chuck Schaff for arranging access to Museum of Comparative Zoology material, and Mike Morales and Ray Hodge of the Museum of Northern Arizona for access to MNA specimens and curatorial assistance. I am grateful to Elizabeth Gordon for assisting with preparation and illustrations, and to David Stephens for the photographs. I thank the Navajo Tribal Council for its cooperation in this research. This work was supported by National Science Foundation grants DEB-75-23112 and DEB-78-01327 to Farish A. Jenkins, Jr., and NSF Dissertation Improvement Grant BSR-84-13847 to the author. Funds were also provided by the Owen Coates Fund and Bill R. Payne Fellowship of the Geology Foundation, University of Texas.

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Received 26 May 1987; accepted 10 September 1988.