A STAURIKOSAURID DINOSAUR FROM THE UPPER TRIASSIC ISCHIGUALASTO FORMATION OF ARGENTINA AND THE RELATIONSHIPS OF THE STAURIKOSAURIDAE

by D. B. BRINKMAN *and* H.-D. SUES

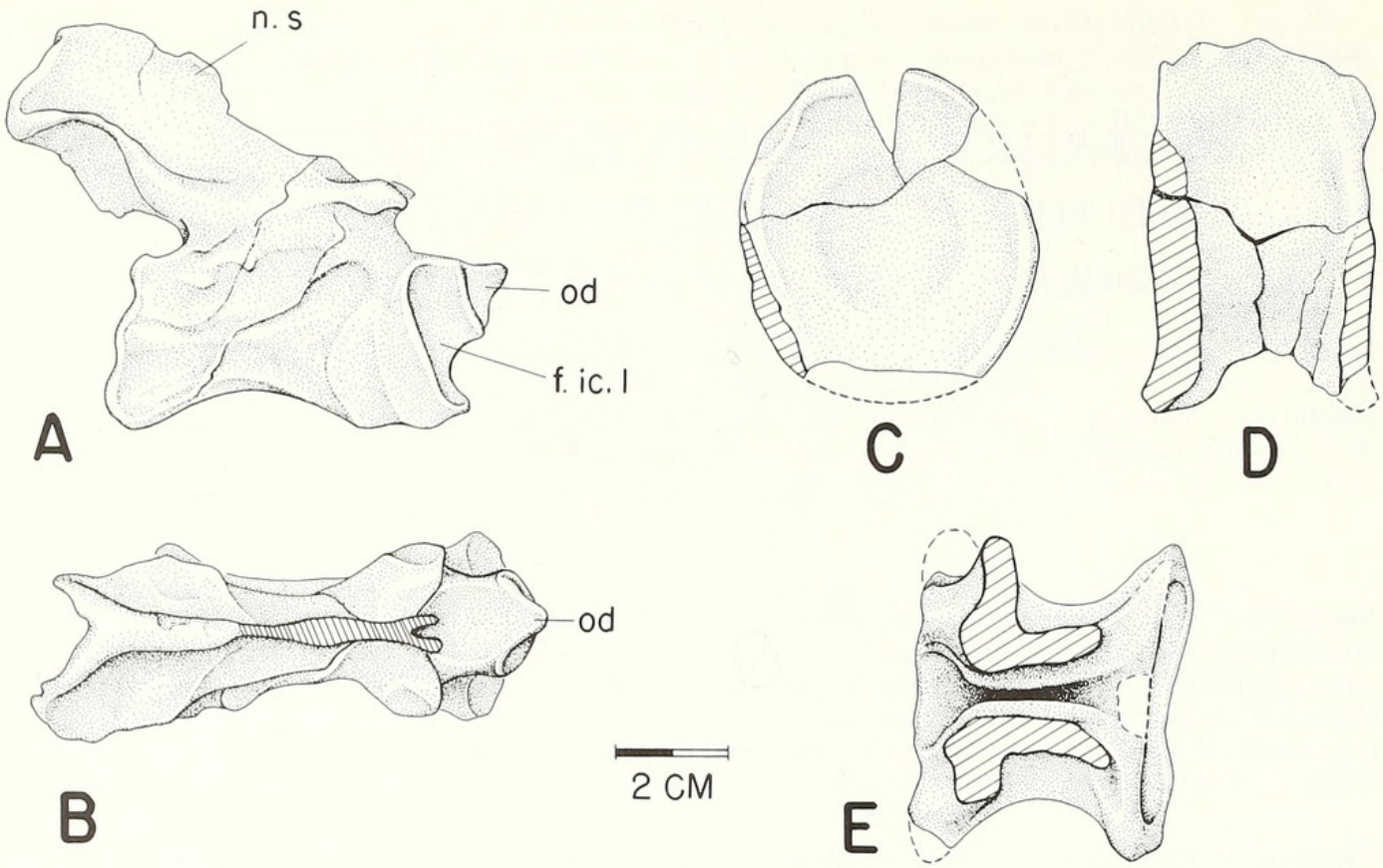
ABSTRACT. A partial skeleton of a staurikosaurid, cf. *Staurikosaurus* sp. is described from the Ischigualasto Formation of Argentina. This specimen provides additional anatomical data for an evaluation of the phylogenetic affinities of the Staurikosauridae. Colbert's (1970) assignment of *Staurikosaurus* to the Dinosauria is supported. No synapomorphies exist to support close relationships between *Herrerasaurus* and *Staurikosaurus*. It is concluded that *Staurikosaurus* and *Herrerasaurus* form successive sister taxa to an assemblage composed of Ornithischia and Saurischia, with the latter only including Sauropodomorpha and Theropoda.

THE early diversification of the Dinosauria is documented virtually exclusively by skeletal remains from a sequence of Late Triassic continental strata in South America (Bonaparte 1978). The oldest known dinosaurs occur in the Santa Maria Formation of Rio Grande do Sul, Brazil, which is most likely Carnian in age (Colbert 1970). *Staurikosaurus* Colbert, 1970 is the best known of these forms (Colbert 1970; Galton 1977) and is documented by lower jaws and a fairly complete postcranial skeleton (MCZ 1669). *Spondylosoma* Huene, 1942 from the same formation is very poorly known but has also been classified as dinosaurian (Huene 1942; Bonaparte 1978). The holotype material consists of vertebrae, parts of both scapulae, the proximal end of a left humerus, the proximal end of a right femur, and a partial right pubis and is currently being redescribed by Galton (pers. comm.). The Ischigualasto Formation of north-western Argentina, which is probably slightly younger than the Santa Maria Formation, has yielded material referable to three genera of dinosaurs (Bonaparte 1978). Of these, *Herrerasaurus* and *Ischisaurus*, first described by Reig (1963), are generally classified as primitive saurischians, and *Pisanosaurus* Casamiquela, 1967 is referred to the Ornithischia. Reig (1963) also described '*Triassolestes*' (*Trialestes* Bonaparte, 1982) as a podokesaurid theropod but Bonaparte (1978, 1982) has reinterpreted this taxon as a crocodylomorph archosaur. The material referable to *Herrerasaurus* and *Ischisaurus* has only been described in a most preliminary fashion. *Pisanosaurus* is based on an extremely poorly preserved specimen, and Bonaparte's (1976) assignment of this genus to the Heterodontosauridae (which are otherwise only definitely known from the Lower Jurassic of southern Africa) is indeed questionable.

In this paper we describe a single fragmentary skeleton of a primitive dinosaur, which we interpret as the first record of a staurikosaurid from the Ischigualasto Formation. This specimen provides much additional information on the structure of these dinosaurs, and, based on these new data, the phylogenetic position of *Staurikosaurus* and related forms will be reconsidered.

The occurrence of a staurikosaurid in the Ischigualasto Formation is documented by a single specimen in the collections of the Museum of Comparative Zoology at Harvard University, MCZ 7064. It consists of a partial postcranial skeleton including the atlas-axis complex, parts of at least five dorsal vertebrae, fragments of both scapulocoracoids, proximal and distal ends of both humeri, a partial left ilium, the proximal ends of both ischia, the distal end of a right femur, the proximal and distal ends of a right tibia, the proximal end of a right fibula, and some pedal phalanges. The

[Palaeontology, Vol. 30, Part 3, 1987, pp. 493–503.]



TEXT-FIG. 1. Cf. *Staurikosaurus* sp., MCZ 7064. A, B, atlas centrum, atlas intercentrum, and axis, in A, right lateral and B, dorsal view. C–E, centrum of a posterior dorsal vertebra, in C, anterior, D, lateral, and E, dorsal view. Abbreviations: f.ic.l—facet for atlas intercentrum, n.s—neural spine of axis, od—odontoid process.

material was collected by A. S. Romer in 1958 from a site 1 km north-west of Arroyo de Agua, San Juan province, Argentina. In the field-notes, the specimen (field-number 295-58M) is recorded as much of an indeterminate skeleton. Some of the preserved pieces still show evidence of articular context: the tibia and fibula are preserved in articulation and the left humerus is in contact with the left scapulocoracoid. Thus the material probably represents the remains of a single skeleton. A nearly complete skull of a large archosaur, MCZ 7063, was possibly originally part of the same specimen but regrettably all direct information bearing on this appears to have been lost. The skull is definitely not referable to the rauisuchid *Saurosuchus* from the same formation (Bonaparte 1978), but determination of its affinities must await further preparation. Many of the bones were covered by hematite, the removal of which is extremely laborious.

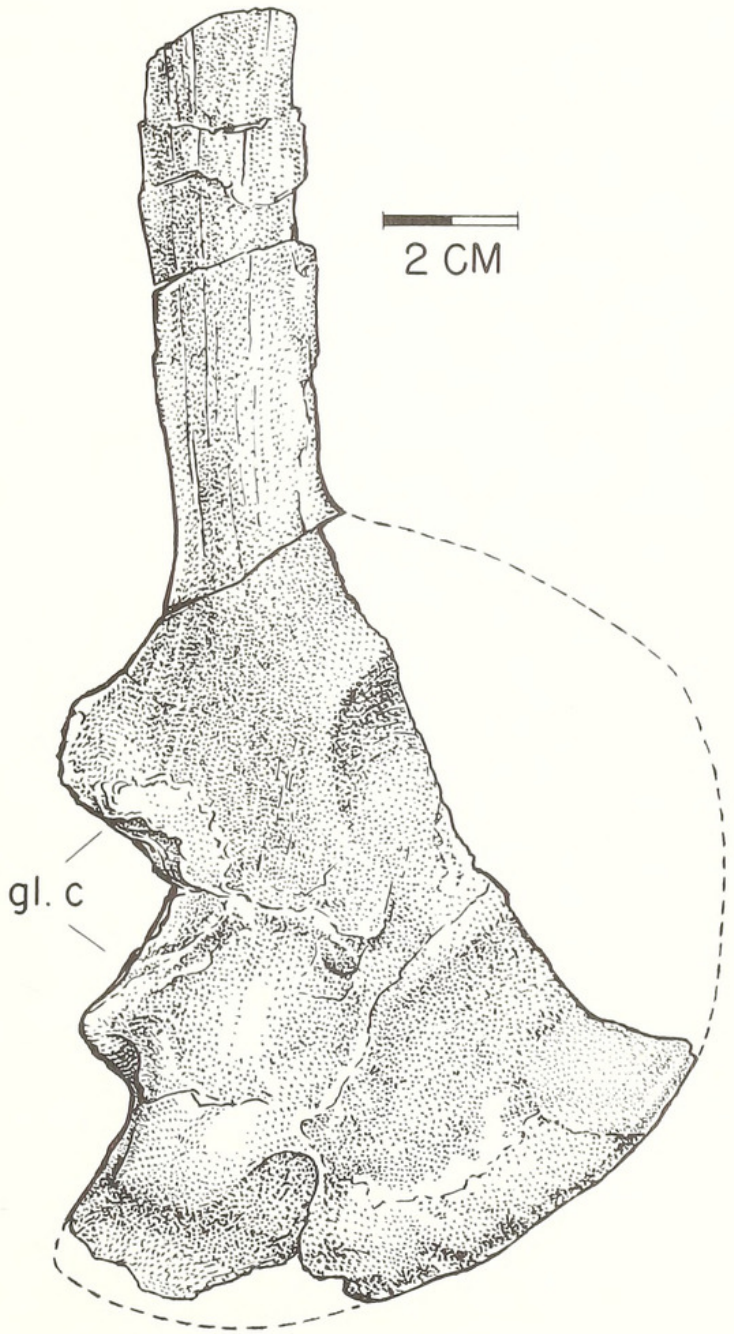
DESCRIPTION

Subdivision ARCHOSAURIA
DINOSAURIA
Family STAURIKOSAURIDAE
cf. *Staurikosaurus* sp.

Postcranial axial skeleton. The postcranial axial skeleton is documented by the atlas-axis complex and parts of at least five dorsal vertebrae. The atlas centrum, axis intercentrum, and axis are preserved in association (text-fig. 1) but it is uncertain whether they are fused or whether their contacts are merely obscured by adhering hematite.

The atlas centrum bears a prominent odontoid process (od, text-fig. 1A, B). Its height is about half that of the axis centrum. Below the atlas centrum, the anterior face of the axis intercentrum forms a crescent-shaped surface for the atlas intercentrum (f.ic.1). The axis is elongate, the length of its centrum being about twice its height. The neural arch bears a large posteriorly directed spine (n.s). The neural spine is bifurcated at its apex, with each branch extending to the posterior extremity of a postzygapophysis. Transverse processes are absent. The sides of the axis centrum are pinched in at a point just about mid-height; the ventral edge of the centrum is rounded. The posterior articular face of the centrum is concave.

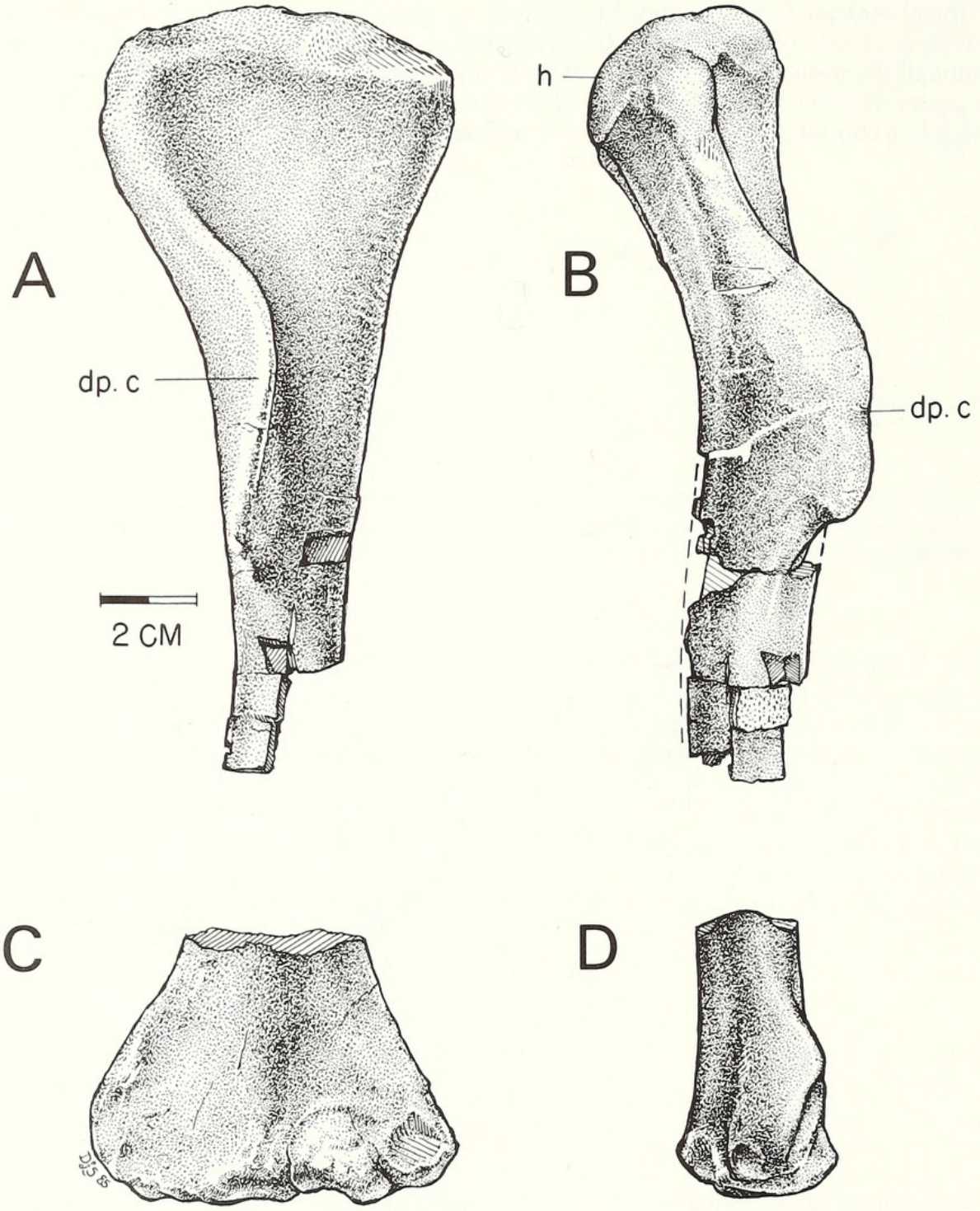
One dorsal centrum is nearly complete (text-fig. 1C–E). It is short, slightly more than half as long as it is high (text.-fig. 1D), and probably represents a posterior dorsal. Its articular ends are nearly flat, although the posterior face shows a slight central depression. The floor of the neural canal on broken centra narrows toward the centre where it sinks deeply into the centrum (text-fig. 1E), rather than extending continuously on level with the pedicles of the neural arch. A similar inward extension



TEXT-FIG. 2. Cf. *Staurikosaurus* sp., MCZ 7064. Conjoined right scapula and coracoid in lateral view. Abbreviation: gl.c—glenoid cavity.

of the floor has elsewhere only been reported in dorsal vertebrae of the theropod *Dilophosaurus* (Welles 1984); the distribution of this peculiar feature among other archosaurian groups remains to be determined.

Appendicular skeleton. The scapula and coracoid form a single element but the line of fusion between the two bones remains apparent. The scapulocoracoids are documented by the left scapula and



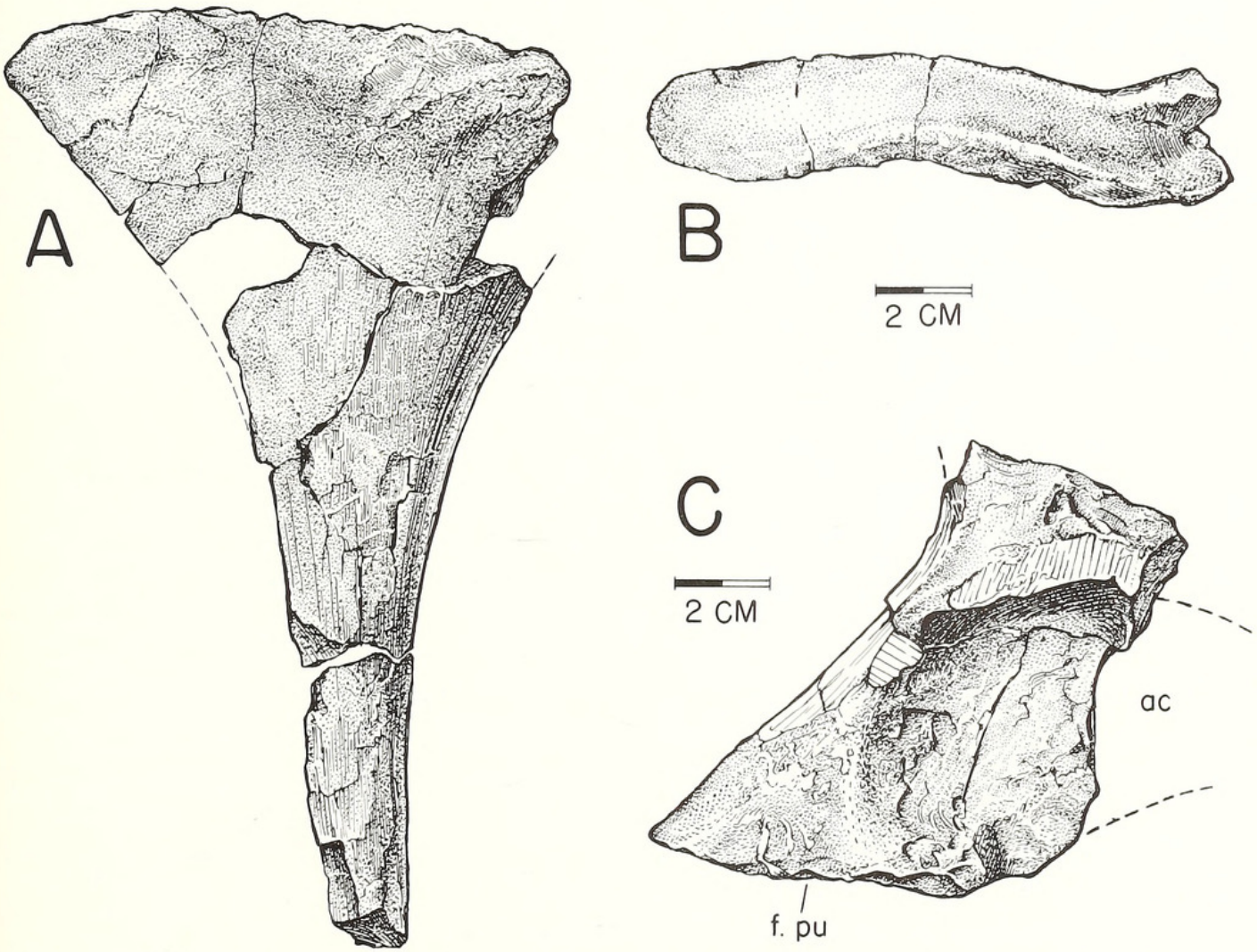
TEXT-FIG. 3. Cf. *Staurikosaurus* sp., MCZ 7064. A, B, proximal end of right humerus in A, medial and B, anterior views; C, D, distal end of left humerus in C, medial and D, anterior views. Abbreviations: dp.c—delto-pectoral crest, h—proximal articular head.

anterior half of the conjoined coracoid and a nearly complete right coracoid, and the base of the attached scapula.

The scapulocoracoid is characterized by a very slender scapular blade and a large, plate-like coracoid (text-fig. 2). The basal portion of the scapulocoracoid is rectangular in outline and bears the glenoid posteriorly. The scapular blade is narrow anteroposteriorly and is oval in transverse section. Although its dorsal margin is not preserved there are no indications for an expansion of the dorsal (vertebral) end.

The humerus (text-fig. 3) is represented by the proximal and distal ends of both elements. Its overall length cannot be determined. The articular ends are two-and-a-half times as wide as the humeral shaft. The humeral head (h, text-fig. 3A) is hemispherical and is restricted to the centre of the proximal end of the bone. The deltopectoral crest (dp.c) is prominent and arises slightly distal to the proximal articular end. It extends more or less perpendicular to the long axis of the proximal portion of the humerus (text-fig. 3B). The humeral shaft is circular in transverse section distal to the deltopectoral crest. The distal articular end of the humerus bears distinct radial and ulnar condyles. The radial condyle faces distinctly ventrally. The ulnar condyle is situated distal to it and faces primarily distally. The ectepicondyle has a notch of uncertain significance in its lateral margin.

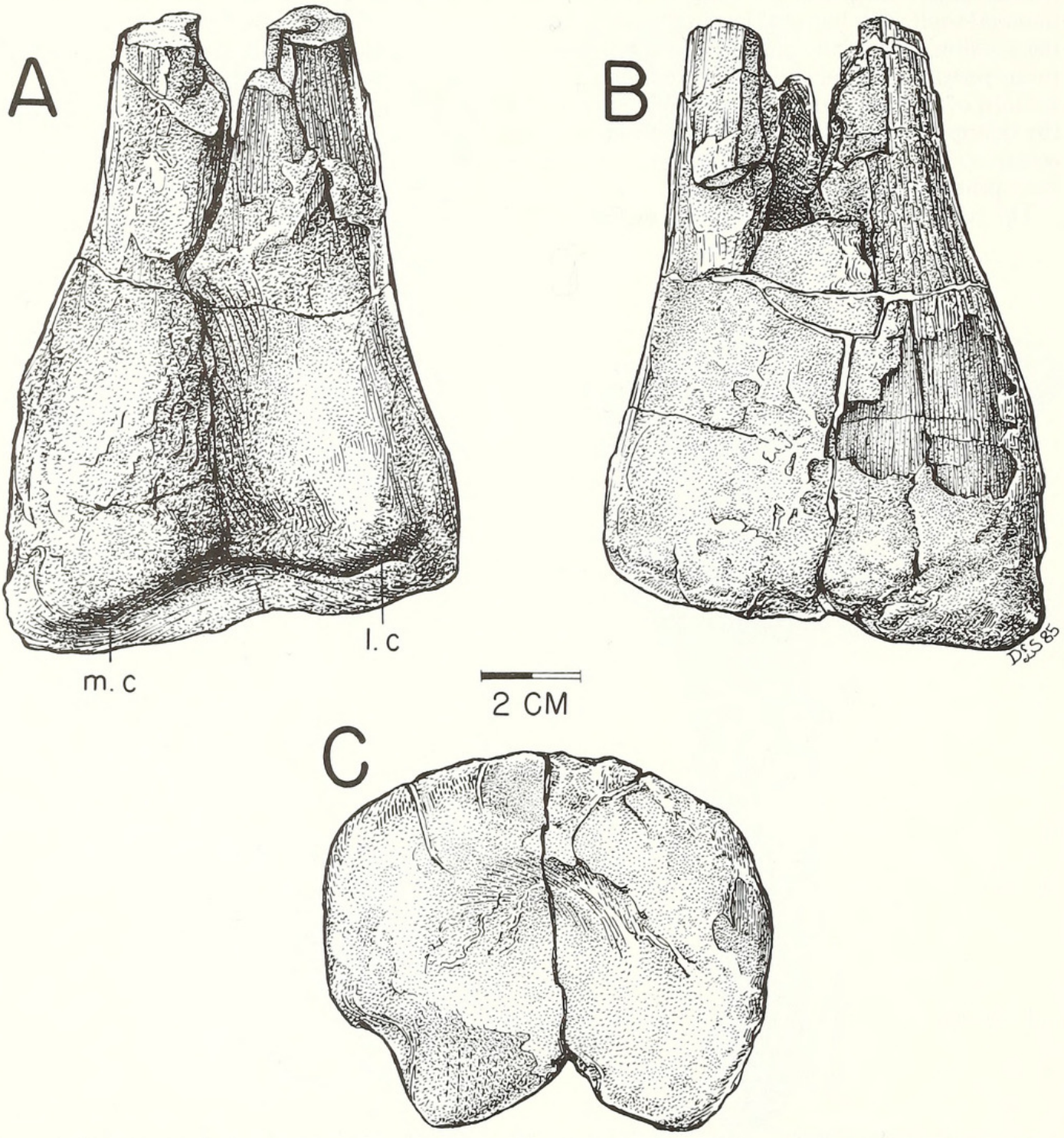
The partial left ilium (text-fig. 4C) includes the supra-acetabular rim and the pubic ramus. The



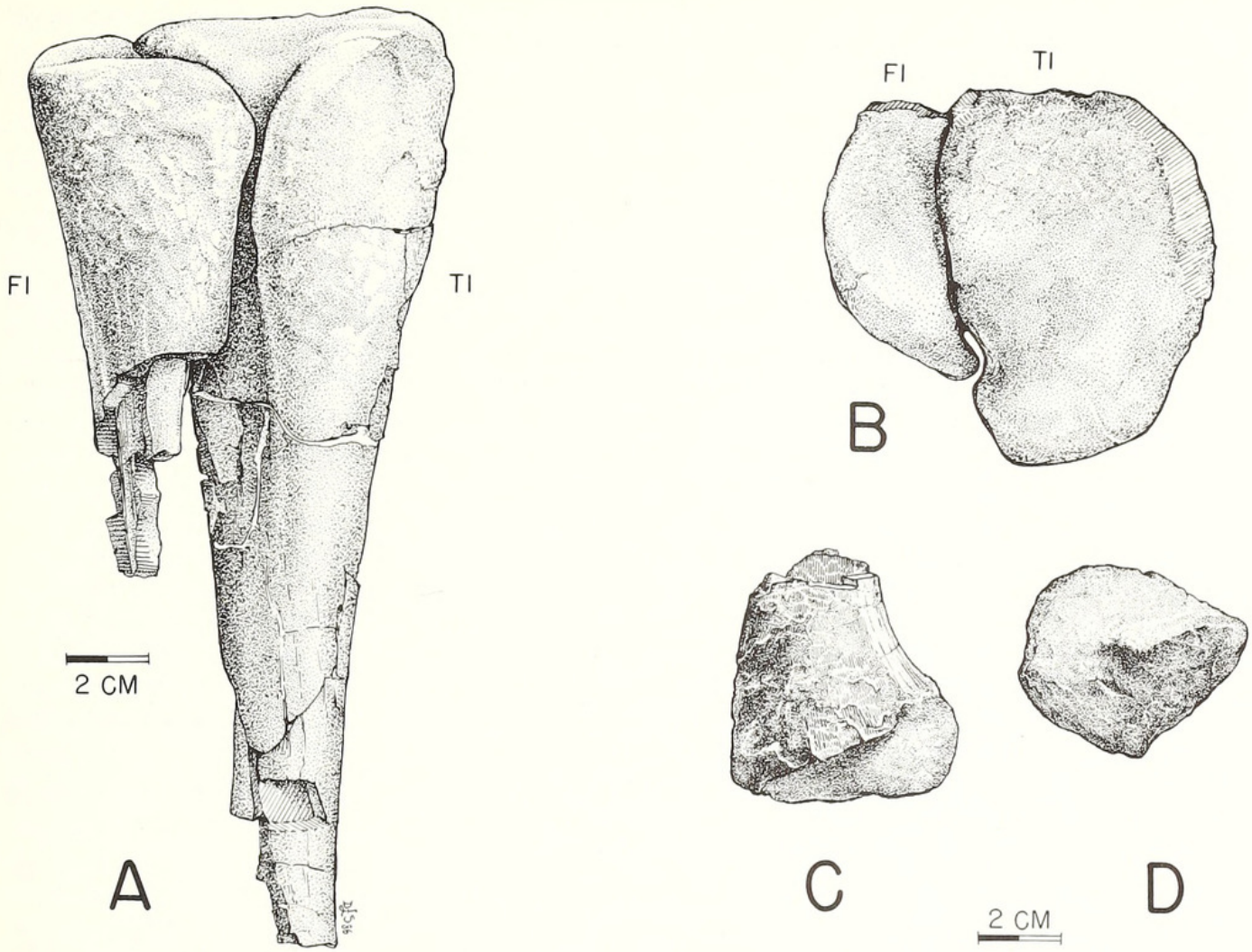
TEXT-FIG. 4. Cf. *Staurikosaurus* sp., MCZ 7064. A, B, partial right ischium in A, lateral and B, proximal end view. C, partial left ilium in lateral view. Abbreviations: ac—acetabular wall, f.pu—articular facet for pubis.

supra-acetabular rim is prominent. It is concave ventrally, forming a socket for the reception of the proximal head of the femur. The lateral aspect of the iliac blade lacks the strong vertical buttress extending dorsally from the supraacetabular rim present in certain rauisuchians (Chatterjee 1985). The well-developed medial wall of the acetabulum (ac) extends far ventrally and forms a knife-like edge at about the level of the articular contact for the pubis (f.pu). While the acetabulum probably was perforated, the opening was quite small. The pubic peduncle of the ilium is robust and large.

The proximal ends of both ischia are preserved. The ischium has a broad, triangular proximal



TEXT-FIG. 5. Cf. *Staurikosaurus* sp., MCZ 7064. Distal end of right femur in A, posterior, B, anterior, and C, distal end view. Abbreviations: l.c—lateral condyle, m.c—medial condyle.



TEXT-FIG. 6. Cf. *Staurikosaurus* sp., MCZ 7064. Partial right tibia and fibula. A, B, articulated proximal portions of tibia and fibula in A, anterior and B, proximal end view. C, D, distal end of tibia in C, anteromedial and D, distal end view.

portion and a rod-like distal region (text-fig. 4A, B). The articular surfaces for the ilium and pubis are separated only by a slight narrowing of the bone, with that for the former being larger and situated at a low angle relative to the latter.

The femur is documented by the distal end of the right bone (text-fig. 5). The diameter of the femoral shaft increases toward the distal articular end. At the proximal end of the preserved fragment, the diameter of the shaft is slightly more than half the width across the distal end. This increase in width is developed asymmetrically so that the medial portion of the distal end is more prominent than the lateral one (text-fig. 5A, B). The distal end of the femur is rounded in outline. It bears a central depression, which is surrounded in front and on either side by a low, broad ridge (text-fig. 5C). A smaller depression is developed anterior to the central one. The distal condyles (l.c, m.c, text-fig. 5A) occupy subterminal positions on the posterior (ventral) aspect of the femur.

Both the proximal and distal ends of the right tibia are preserved. It has an expanded proximal portion that rapidly becomes narrow distally (text-fig. 6A). A distinct cnemial crest, laterally bordered by a groove, is developed. The proximal portion of the right fibula (text-fig. 6A, B) is preserved in its original articular context. It has a broad semilunate proximal end, which fits tightly against the lateral aspect of the tibia. Together the two bones form a rounded articular surface. The distal end of the tibia (text-fig. 6C, D) is rounded in articular view and is much smaller in diameter than the proximal end. Its articular surface has a helical shape with the two ends of the spiral joined by

a flat surface. The difference in the relative position of the two ends of the spiral produces a notch for the reception of the ascending process of the astragalus.

No tarsal bones are preserved. The pedal digits are only documented by a few non-diagnostic articular ends of phalanges.

TAXONOMIC AFFINITIES OF MCZ 7064

MCZ 7064 is identified as a staurikosaurid, rather than as a herrerasaurid, based on the structure of the ischium and of the distal end of the tibia. The triangular proximal end of the ischium matches that of *Staurikosaurus pricei* (MCZ 1669) closely and differs from that of *Herrerasaurus*, which shows a distinct angulation between the posterior margin of the ischiadic shaft and the posterior edge of the acetabular portion (Reig 1963, fig. 2). The outline of the distal end of the tibia is again closely similar to that of *S. pricei* (Galton 1977, fig. 2M) and different from that in *Herrerasaurus* where the distal end is more expanded (Reig 1963, fig. 3B, C). The distal ends of both tibiae in the holotype of *S. pricei* have a deep groove extending proximally from the notch formed by the helical articular surface but this feature has been exaggerated by overpreparation; the distal end of the right tibia in MCZ 7064 has no comparable distal groove.

Direct comparison of MCZ 7064 with the type specimens of *Spondylosoma absconditum* and *I. cattoi* was not possible. The former differs from *Staurikosaurus pricei* in the development of the pubic apron (Galton, pers. comm.) as well as in the structure of the vertebrae (Colbert 1970). *Staurikosaurus* differs from *I. cattoi*, currently being restudied by F. Novas, in the presence of a low lesser trochanter on the proximolateral aspect of the femur (Galton 1977). In both *Ischisaurus* and *Herrerasaurus* the lesser trochanter forms a small but very prominent ridge in a more distal position on the proximolateral aspect of the femur (Novas, pers. comm.).

Considering its slightly later occurrence in time and the possible structural differences to the holotype of *S. pricei*, specimen MCZ 7064 is tentatively identified as cf. *Staurikosaurus* sp.

DISCUSSION

The new data on skeletal structure provided by MCZ 7064 invite examination of the phylogenetic position of the Staurikosauridae relative to dinosaurs and other archosaurs. Outgroups used in determining the polarity of character states displayed by *Staurikosaurus* were Lagosuchidae (Bonaparte 1975*a*), Ornithosuchidae (Walker 1964; Bonaparte 1975*b*), and Rauisuchia (= Rauisuchidae + Poposauridae; Chatterjee 1985). These extensive comparisons with non-dinosaurian archosaurs were undertaken because of the current debate about which group of archosaurs is most closely related to the Dinosauria. We regard Dinosauria as a monophyletic assemblage, following the recent discussions by Benton (1984) and Gauthier and Padian (1985), rather than as an artificial grouping comprising two distinct orders Ornithischia and Saurischia, which supposedly have independent, possibly multiple origins among 'thecodontian' archosaurs (Charig 1982).

The first problem to be considered is the placement of *Staurikosaurus* in the taxon Dinosauria. Colbert (1970) listed seven characters in support of his assignment of this genus to the Dinosauria:

(1) transverse processes supported by a pair of strong ventral buttresses;
(2) acetabulum perforated;
(3) ischium rod-like;
(4) ilium as deep as long and truncated posteriorly;
(5) femur shorter than tibia;
(6) proximal head of femur set off from shaft;
(7) fourth trochanter on femur strongly developed.

Since the publication of Colbert's original description of *Staurikosaurus* much new material of early Mesozoic non-dinosaurian archosaurs has been described, including forms that share some of the character-states enumerated by Colbert. Characters (1) and (3) are also developed in the poposaurid rauisuchian *Postosuchus* (Chatterjee 1985). *Lagosuchus* shares characters (5) and (7) with dinosaurs

(Bonaparte 1975*a*). Characters (5) and (6) are present in pterosaurs (Wellnhofer 1978; Padian 1983). The size of the acetabular opening is uncertain in MCZ 7064, and the opening (2) may not have been much larger than that in certain Ornithosuchidae (Walker 1964; Bonaparte 1975*b*) and in *Postosuchus* (Chatterjee 1985). Character (4) is possibly autapomorphous for *Staurikosaurus*, particularly the marked posterior truncation of the iliac blade. None of the above characters are unique to dinosaurs.

In the asymmetrical development of the distal articular end of the femur, *Staurikosaurus* resembles both other dinosaurs and *Lagosuchus*. In most more primitive archosaurs the distal end is also asymmetrical but the *lateral* portion is more prominent. This structural difference can be related to a difference in the function of the femur; the femur extends laterally during femoral retraction in primitive archosaurs (Brinkman 1980).

Gauthier and Padian (1985, p. 189) hypothesized the following set of synapomorphies in a common ancestor of Dinosauria (= Sauropodomorpha + Theropoda and Ornithischia):

(1) Manus with phalangeal formula 2-3-4-3-2 (reduction in outer digits);
(2) semiperforate acetabulum;
(3) prominent supraacetabular buttress {supraacetabular rim in our usage};
(4) fossa on ventral margin of postacetabular portion of ilium (for origin of M. caudifemoralis brevis);
(5) prominent anterior (or lesser) trochanter of femur;
(6) prominent cnemial crest on tibia, projecting beyond femoral condyles and curving anterolaterally;
(7) tibia in which proximal end is expanded anteroposteriorly and in which distal end is broadened transversely ('twisted' tibia), with notch in distal end for reception of ascending process.

In addition, Gauthier and Padian note the existence of 'several other synapomorphies' but these were not specified in their paper and cannot be critically evaluated. Of these features, *Staurikosaurus* shares (2) to (4) and (6). The presence of character (1) cannot be determined. Character (5) is found in *Herrerasaurus* but the feature is apparently developed in a rather different fashion in *Staurikosaurus*. *Staurikosaurus* lacks tibial twisting, representing the plesiomorphous condition, but has a notch in the distal end of the tibia for the reception of the ascending process of the astragalus. Thus character (7) actually consists of two independently acquired features and should be modified accordingly.

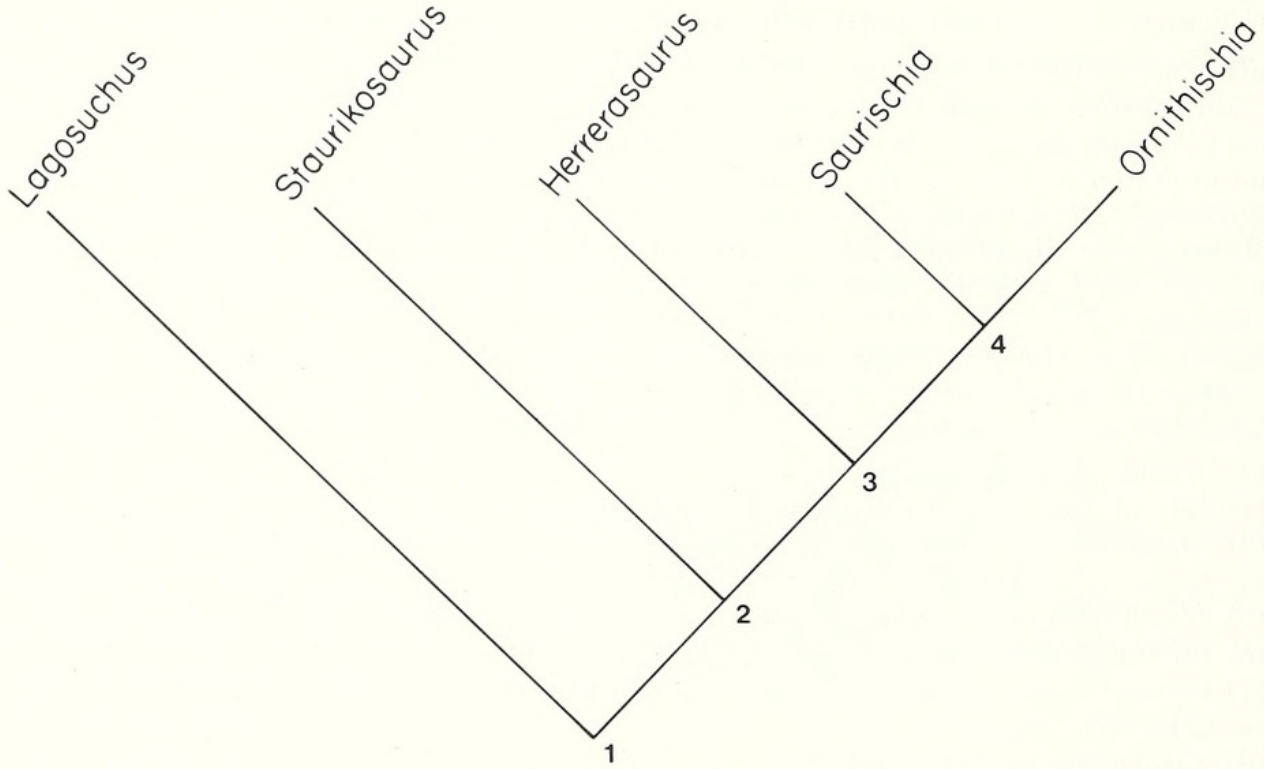
Benton (1984, pp. 13-14) has presented a list of possible synapomorphies for a monophyletic assemblage Dinosauria, which, in addition to characters (5) and (7) listed by Gauthier and Padian, includes the following features:

(1) Absence of postfrontal;
(2) deltopectoral crest extending far down along humeral shaft;
(3) forelimb about half as long as hindlimb;
(4) reduced contact between pubis and ischium;
(5) fourth trochanter prominent and positioned low on femur;
(6) proximal head of femur set off from shaft;
(7) reduced, roller-like astragalus with ascending process;
(8) calcaneum reduced or absent;
(9) advanced mesotarsal ankle joint;
(10) pedal digits II to IV bundled, elongate, and subequal in length;
(11) pedal digits I and V reduced and divergent;
(12) foot with digitigrade pose.

Characters (8), (10), and (11) of this list are also found in *Lagosuchus* (Bonaparte 1975*a*); metatarsal II in *Lagosuchus* is but slightly shorter than are metatarsals III and IV. characters (1), (3), (6), part of (7), (8), (9), part of (10) and (12) are shared by pterosaurs (Wellnhofer 1978; Padian 1983). Characters (1), (3), and (7) to (12) cannot be determined in the presently available staurikosaurid material but characters (2), (4), (5), and (6) are developed in *Staurikosaurus*.

We support Colbert's assignment of *Staurikosaurus* to the Dinosauria. Like *Herrerasaurus*, *Staurikosaurus* occupies a basal position within this group as defined by recent authors and is more primitive than other dinosaurs in the outline of the distal end of the tibia. *Herrerasaurus* also has a semiperforate acetabulum with a strongly developed medial wall but is more derived in the transverse expansion of the distal end of the tibia (Reig 1963; Benedetto 1973). The markedly anteroposteriorly expanded distal end of the pubis is probably an autapomorphy for this genus. This feature is also developed, to a lesser extent, in *S. pricei*; in the podokesaurid theropod *Coelophysis* the pubis terminates distally in a knob-like thickening (Colbert 1970).

Staurikosaurus and *Herrerasaurus* were placed in a single family Herrerasauridae by Benedetto (1973) who noted numerous similarities between them. Galton (1977), emphasizing certain differences between these two genera, proposed a separate family Staurikosauridae for the reception of *Staurikosaurus* but left the question of their interrelationships unresolved. With the possible exception of the anteroposterior expansion of the distal end of the pubis, we find no synapomorphies in support of a sister-group relationship between *Herrerasaurus* and *Staurikosaurus* and regard the similarities between the two taxa as plesiomorphous. Only one feature of *Staurikosaurus*, the presence of a narrow scapular blade, is an apparent autapomorphy for this genus. Judging from outgroup comparisons (particularly with *Lagosuchus*; Bonaparte 1975*a*) and the condition in most early dinosaurs including prosauropods and *Coelophysis*, a wide scapular blade is primitive for Dinosauria. According to Reig's (1963, pp. 6–8) list of skeletal material for *Herrerasaurus*, the scapula in this form is unknown. We hypothesize *Staurikosaurus* and *Herrerasaurus* as successive



TEXT-FIG. 7. Hypothesis of interrelationships for *Staurikosaurus*, *Herrerasaurus*, and other Dinosauria (Saurischia only including Theropoda and Sauropodomorpha). *Lagosuchus* is included in the cladogram as an outgroup, following Bonaparte (1975*a*) and Gauthier and Padian (1985). Selected synapomorphies are: (1) neck sigmoidally curved, 'three-regionalized' vertebral column, femur with moderately developed lateral condyle, astragalus with ascending process, mesotarsal joint (Gauthier and Padian 1985); (2) semiperforate acetabulum with prominent supraacetabular rim, distinct lesser (anterior) trochanter on femur, distal end of tibia with fossa for reception of ascending process of astragalus (see text); (3) distal end of tibia transversely expanded ('twisted' tibia); (4) medial wall to acetabulum less well developed, pedal digit V small.

sister taxa to a clade Saurischia + Ornithischia as defined by Gauthier and Padian (1985) (text-fig. 7). *Staurikosaurus* is clearly the most primitive known representative of the Dinosauria. Galton (1977) classified both *Herrerasaurus* and *Staurikosaurus* as Saurischia *incertae sedis*. We accept Gauthier and Padian's more restrictive use of the term 'Saurischia' to include only Theropoda and Sauropodomorpha (which, in fact, agrees with the traditional usage of that name) and suggest placement of the two primitive South American dinosaurs in separate and distinct higher taxa to reflect their respective phylogenetic positions.

Acknowledgements. We thank P. M. Galton, University of Bridgeport, and F. Novas, Museo Argentino de Ciencias Naturales, for sharing unpublished information with us. K. Padian, University of California, and Greg Paul provided an insightful review of the manuscript. D. Sloan, Tyrrell Museum of Palaeontology, prepared text-figs. 2–6.

REFERENCES

BENEDETTO, J. L. 1973. Herrerasauridae, nueva familia de saurisquios Triásicos. *Ameghiniana*, **10,** 89–102.

BENTON, M. J. 1984. Fossil reptiles from the German Late Triassic and the origin of dinosaurs. *In* REIF, W.-E. and WESTPHAL, F. (eds.). *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*, 13–18. Attempto Verlag, Tübingen.

BONAPARTE, J. F. 1975*a*. Nuevos materiales de *Lagosuchus talampayensis* Romer (Thecodontia—Pseudosuchia) y su significado en el origen de los Saurischia. Chañares inferior, Triásico medio de Argentina. *Acta geol. lilloana*, **13,** 5–90.

—— 1975*b*. The family Ornithosuchidae (Archosauria: Thecodontia). *Coll. Internatn. C.N.R.S.* **218,** 485–502.

—— 1976. *Pisanosaurus mertii* Casamiquela and the origin of the Ornithischia. *J. Paleont.* **50,** 808–820.

—— 1978. El Mesozoico de América del Sur y sus tetrápodos. *Op. lilloana*, **26,** 5–596.

—— 1982. Faunal replacement in the Triassic of South America. *J. vert. Paleont.* **2,** 362–371.

BRINKMAN, D. 1980. The hind limb step cycle of *Caiman sclerops* and the mechanics of the crocodile tarsus and metatarsus. *Can. J. Zool.* **58,** 2187–2200.

CHARIG, A. J. 1982. Problems in dinosaur phylogeny: a reasoned approach to their attempted resolution. *Géobios, Mém. Spéc.* **6,** 113–126.

CHATTERJEE, S. 1985. *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. *Phil. Trans. R. Soc.* **B309,** 395–460.

COLBERT, E. H. 1970. A saurischian dinosaur from the Triassic of Brazil. *Am. Mus. Novit.* **2405,** 1–39.

GALTON, P. M. 1977. On *Staurikosaurus pricei*, an early saurischian dinosaur from the Triassic of Brazil, with notes on the Herrerasauridae and Poposauridae. *Paläont. Z.* **51,** 234–245.

GAUTHIER, J. and PADIAN, K. 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. *In* HECHT, M. K., OSTROM, J. H., VIOHL, G. and WELLNHOFER, P. (eds.). *The beginnings of birds*, 185–197. Freunde des Jura-Museums Eichstätt, Eichstätt.

HUENE, F. v. 1935–1942. *Die fossilen Reptilien des südamerikanischen Gondwanalandes. Ergebnisse der Saurier-grabungen in Südbrasilien 1928/29*, viii + 332 pp. C. H. Beck, Munich. (Archosauria are described in Lieferung 3, which was published in 1942.)

PADIAN, K. 1983. Description and reconstruction of new material of *Dimorphodon macronyx* (Buckland) (Pterosauria, Rhamphorhynchoidea) in the Yale Peabody Museum. *Postilla*, **189,** 1–44.

REIG, O. A. 1963. La presencia de dinosaurios saurisquios en los 'Estratos de Ischigualasto' (Mesotriásico Superior) de las provincias de San Juan y La Rioja (Republica Argentina). *Ameghiniana*, **3,** 3–20.

WALKER, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Phil. Trans. R. Soc.* **B248,** 53–134.

WELLES, S. P. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. *Palaeontographica*, **A185,** 85–180.

WELLNHOFER, P. 1978. Pterosauria. *In* P. WELLNHOFER (ed.). *Handbuch der Paläoherpetologie*, **Teil 19,** x + 82 pp. Gustav Fischer Verlag, Stuttgart.

DONALD B. BRINKMAN

Tyrrell Museum of Palaeontology, Box 7500
Drumheller, Alberta T0J 0Y0, Canada

HANS-DIETER SUES

Museum of Comparative Zoology, Harvard University
Cambridge, MA 02138, USA

Typescript received 10 June 1986
Revised typescript received 13 October 1986