

A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan & Lucas, 1999 from the Upper Triassic of New Mexico, USA

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ABSTRACT

Eucoelophysis baldwini Sullivan & Lucas, 1999 is represented by several post-cranial elements from the Petrified Forest Formation (Norian), New Mexico, USA. *Eucoelophysis* Sullivan & Lucas, 1999 was widely considered as a coelophysoid dinosaur by several authors, but the hindlimb anatomy of this genus clearly indicates that it belongs to neither of these groups. The following features exclude *Eucoelophysis* from Neotheropoda: absence of oblique ligament groove on caudal surface of femoral head, femoral medial epicondyle small and smoothly rounded, absence of caudal cleft between medial part of the proximal end of the tibia and fibular condyles, cnemial crest low, and fibular crest absent. Moreover, *Eucoelophysis* lacks dinosaurian synapomorphic characters, but has a plesiomorphic slightly inturned femoral head that prevents its assignment to Dinosauria. Interestingly, the morphology of the femur of *Eucoelophysis* is extremely similar to that of the basal dinosauriform *Silesaurus opolensis* Dzik, 2003 from the Late Triassic of Poland. In order to determine the phylogenetic position of *Eucoelophysis*, a cladistic analysis was carried out, which depicts *Eucoelophysis* as a non-dinosaurian dinosauriform. Thus reinterpreted, *Eucoelophysis* constitutes the youngest record of a non-dinosaurian dinosauriform, indicating their survival into the Norian, being co-eval with early dinosaurs.

KEY WORDS

Dinosauriformes,
Coelophysoidea,
Eucoelophysis,
Chinle Group,
Upper Triassic,
New Mexico.

RÉSUMÉ

Une révision de la position systématique de l'archosaure dinosauriforme Eucoelophysis baldwini Sullivan & Lucas, 1999 du Trias supérieur du Nouveau Mexique, États-Unis.

Eucoelophysis baldwini Sullivan & Lucas, 1999 est connu d'après plusieurs éléments postcraniaux qui proviennent de la Formation Petrified Forest (Norien) au Nouveau Mexique (États-Unis). *Eucoelophysis* Sullivan & Lucas, 1999 fut généralement considéré comme un théropode coelophyside. Cependant, l'anatomie du membre postérieur de ce genre indique clairement que ce n'est ni un neothéropode, ni un coelophyside. Les caractéristiques suivantes excluent ce taxon des Neotheropoda : absence de rainure du ligament oblique sur la surface caudale de la tête fémorale, épicondyle fémoral intermédiaire petit et régulièrement arrondi, absence de fissure caudale sur la partie intermédiaire entre l'extrémité proximale fibulaire du tibia et le condyle fibulaire, la crête cnémiale est réduite, et la crête fibulaire absente. De plus, aucune des synapomorphies des dinosaures n'existe chez *Eucoelophysis*, et le partage d'un caractère primitif (tête fémorale légèrement tournée vers l'intérieur) ne permet pas de rapporter ce taxon aux dinosaures. Par ailleurs, la morphologie du fémur d'*Eucoelophysis* est très semblable à celle du dinosauriforme basal *Silesaurus opolensis* Dzik, 2003 du Trias supérieur de Pologne. Afin de déterminer la position phylogénétique d'*Eucoelophysis*, une analyse cladistique a été réalisée, qui positionne *Eucoelophysis* comme un Dinosauriformes non-dinosaurien. Ainsi ré-interprété, *Eucoelophysis* représente le plus jeune Dinosauriformes non-dinosaurien connu, indiquant leur survivance dans le Norien et leur co-existence avec les premiers dinosaures.

MOTS CLÉS

Dinosauriformes,
Coelophysoidea,
Eucoelophysis,
groupe Chinle,
Trias supérieur,
Nouveau Mexique.

INTRODUCTION

Sullivan & Lucas (1999) described *Eucoelophysis baldwini* on the basis of an incomplete articulated leg, pelvic girdle, and other incomplete postcranial elements (Figs 1B; 2B, G, H; 4B, H; 5B, C, F; 6D). Its type material was found in the Petrified Forest Formation (Norien; Lucas & Hunt 1992; Lucas 1998) directly associated with phytosaur bones and some unidentified elements within a square meter area (Sullivan & Lucas 1999). Sullivan & Lucas (1999) originally assigned *Eucoelophysis* to a monophyletic Ceratosauria Marsh, 1884 (*sensu* Rowe & Gauthier 1990) on the basis of triangular and caudally directed transverse processes of its dorsal vertebrae and a prominent trochanteric shelf on the lesser trochanter of the femur. They also interpreted the postcranial elements as belonging to a coelophysoid theropod. Sullivan & Lucas (1999) also pointed out that *Eucoelophysis* differs from

Coelophysis bauri Cope, 1887 and *C. rhodesiensis* Raath, 1969 in lacking a well developed posterior femoral notch below the femoral head (Fig. 4B, H), and also from *C. bauri* in having a tibia that has a distinct appressed surface along the distal two-thirds of the bone and lacks a fibular crest (Fig. 2G, H). *Eucoelophysis* was diagnosed by the presence of an ischio-acetabular groove and a sulcus on the proximal articular surface of the femur (Fig. 1B) (Sullivan & Lucas 1999). However, several features mentioned above are plesiomorphic traits of Dinosauria Owen, 1842 and Neotheropoda Bakker, 1986 (Novas 1996; Sereno 1999; Holtz 2000; Rauhut 2003). Additionally, no dinosaurian synapomorphic traits are present in *Eucoelophysis*, preventing its assignment to the Dinosauria. On the other hand, the anatomy of *Eucoelophysis* is more congruent with the dinosaurian close relative *Silesaurus opolensis* Dzik, 2003. Moreover, several autapomorphic traits support the validity of the genus *Eucoelophysis*,

distinguishing it from *Silesaurus* and other basal Dinosauriformes Novas, 1992.

The type material of *Eucoelophysis* has already been described in detail and excellently documented with photographs by Sullivan & Lucas (1999), and a new description is not necessary. The main purpose of this paper is to discuss the systematic position of this interesting taxon testing its status as a coelophysoid theropod, and determining its phylogenetic relationships.

METHODS

The re-evaluation of the systematic position of *Eucoelophysis baldwini* was carried out on basis of unpublished photographs of its type material and the published data. Throughout the text, materials indicated by their respective collection numbers correspond to studied materials, casts, or unpublished photographs of dinosaurian materials.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York;
HMN BM	Humboldt Museum für Naturkunde, Berlin;
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts;
MLP	Museo de La Plata;
NMMNH	New Mexico Museum of Natural History and Science, Albuquerque;
PULR	Paleontología, Universidad Nacional de La Rioja;
PVL	Fundación “Miguel Lillo”, Universidad Nacional de Tucumán, San Miguel de Tucumán;
PVSJ	Museo de Ciencias Naturales, Universidad Nacional de San Juan;
UCMP	University of California Museum of Paleontology, Berkeley;
YPM	Yale Peabody Museum, New Haven, Connecticut.

SYSTEMATIC NOMENCLATURE

This paper follows the phylogenetic hypothesis and systematic nomenclature employed by Novas (1996) for basal Dinosauriformes relationships. Regarding saurischian nomenclature, the term Eusaurischia is applied following the definition

stated by Padian *et al.* (1999) (see Langer 2004), Herrerasauridae is considered to lie outside Theropoda, being the sister-taxon of Eusaurischia, and Averostris is used for the Ceratosauria + Tetanurae clade (see Paul 2002). The coelophysoid species “*S.*” *rhodesiensis* is here considered to belong to the genus *Coelophysis* Cope, 1889, i.e. *Coelophysis rhodesiensis*, following Tykoski (2005) and Ezcurra & Novas (2006).

SYSTEMATICS

ORNITHODIRA Sereno, 1991
DINOSAURIFORMES Benton, 1975
DINOSAURIFORMES Novas, 1992

Genus *Eucoelophysis* Sullivan & Lucas, 1999

TYPE SPECIES. — *Eucoelophysis baldwini* Sullivan & Lucas, 1999.

STRATIGRAPHIC DISTRIBUTION. — Petrified Forest Formation, Chinle Group, Upper Triassic (Norian; Lucas & Hunt 1992; Lucas 1998; Sullivan & Lucas 1999).

GEOGRAPHIC DISTRIBUTION. — Ghost Ranch Quadrangle, Rio Arriba County, New Mexico, USA (Sullivan & Lucas 1999).

Eucoelophysis baldwini Sullivan & Lucas, 1999
(Figs 1B; 2B, G, H; 4B, H; 5B, C, F; 6D)

HOLOTYPE. — NMMNH P-22298, incomplete postcranial material consisting of two dorsal and four incomplete caudal vertebrae, nearly complete right pubis, partial right ischium, ilium fragment?, fragmentary femora, proximal half of the left tibia, incomplete right metatarsal II and IV, and complete metatarsal III, phalanges, unidentified bone fragments, and probably an incomplete left scapulocoracoid (Sullivan & Lucas 1999).

EMENDED DIAGNOSIS. — Dinosauriform diagnosable by the following autapomorphies (see Discussion): non-invasive pleurocoels in the dorsal vertebrae; strongly marked U-shaped ischio-acetabular groove (Sullivan & Lucas 1999); absence of femoral trochanteric shelf; cnemial crest distinctively offset from the tibial shaft, cranially straight, and without lateral notch; and probably femoral fourth trochanter reduced (see below).

DISCUSSION

THE TYPE MATERIAL OF *EUCOELOPHYSIS BALDWINI* Before discussing the phylogenetic relationships of *Eucoelophysis*, I state some comments on its type material. Sullivan & Lucas (1999: 83) mentioned that the scapulocoracoid was referred “with a query to this taxon owing to its incomplete nature”. In fact, the scapulocoracoid of coelophysoid theropods closely resembles those of basal dinosauriforms such as *Silesaurus*; so the assignment of the pectoral girdle is far from conclusive. Sullivan & Lucas (1999) also stated that the dorsal vertebrae present triangular and caudally directed transverse processes, and a large, distinct, non-invasive pleurocoel on each side of the centra. In this regard, the pleurocoel present in *Eucoelophysis* differs from that of coelophysoids, because, in the latter, pleurocoels are only restricted to the cervical vertebrae, where two pairs are present. Interestingly, the pleurocoels of *Eucoelophysis* resemble the condition present in the putative harrerasaurid *Chindesaurus* Long & Murry, 1995 (Long & Murry 1995), but in the former the centrum is much longer and lower than in *Chindesaurus*.

The proximal end of the right pubis of NMMNH P-22298 resembles the overall morphology present in the coelophysoid theropod *Liliensternus* (HMN BM.R. 2175), but also a broken pubis of the basal dinosauriform *Marasuchus* Sereno & Arcucci, 1994 (PVL 3870). The NMMNH P-22298 pubis seems to lack the acetabular depression present in basal dinosauriforms (e.g., *Silesaurus*), which forms the enclosed acetabulum. Note that an open acetabulum has been also indicated in the basal dinosauriform *Marasuchus* (PVL 3870, MCZ 4116; Bonaparte 1975; Sereno & Arcucci 1994) because of the observed perforation of the pubis and ischium (Novas 1996). However, this interpretation was contradicted by Novas (1996). The available pubis of *Eucoelophysis baldwini* was not found in articulation to the hindlimb and the presence of an ischio-acetabular groove, straight shaft, and absence of acetabular depression, features only present in basal dinosaurs, might suggest that this bone does not belong to the holotype. Nevertheless, since in the present phylogenetic

context, the pubic morphology matches with the overall condition of the hindlimb, the pubis is here considered as belonging to the holotype of *Eucoelophysis baldwini*.

The proximal end of the left tibia of *Eucoelophysis baldwini* differs from the typical anatomy exhibited by Dinosauriformes, because its cnemial crest is distinctly tapering and does not present their typical lateral curvature. Yet the lower origin of the tibio-fibular contact surface and the fact that the cnemial crest continues well down the shaft suggest that at least the proximal end of the tibia is almost complete. In this context, the proximal end of the left tibia seems not to be as damaged as the poor preservation and unusual morphology of this element might at first suggest.

Sullivan & Lucas (1999) indicated that the fragmentary metatarsals (Fig. 6) differ from those of coelophysids (e.g., *Coelophysis*, *Syntarsus*) in lacking metatarsal fusion. This trait resembles the condition present in basal dinosauriforms, ornithischians, sauropodomorphs, and several theropods, including non-coelophysid coelophysoids (e.g., *Dilophosaurus* Welles, 1954, *Liliensternus* Welles, 1984). The metatarsus of *Eucoelophysis* exhibit a basal articulation of metatarsal II overlapping metatarsal III and the latter metatarsal IV. This trait was considered as synapomorphic of Saurischia Seeley, 1888 (Sereno *et al.* 1993), but its presence in non-dinosaurian dinosauriforms (Novas 1993), crurotarsans, and also basal diapsids indicate a lesser inclusive distribution of the feature.

THE PHYLOGENETIC RELATIONSHIPS OF *EUCOELOPHYSIS*

As noted above, Sullivan & Lucas (1999) assigned *Eucoelophysis baldwini* to a monophyletic Ceratosauria (= Coelophysoidea Nopcsa, 1928 + Neoceratosauria Novas, 1992; *sensu* Rowe & Gauthier 1990), on the basis of the following characters: triangular and caudally directed transverse processes of dorsal vertebrae and a prominent trochanteric shelf on the lesser trochanter of the femur. However, these features deserve the following comments:

1) As Rauhut (2003) mentioned, the transverse processes of dorsal vertebrae are nearly subtriangular in dorsal view in most saurischians. Furthermore, the

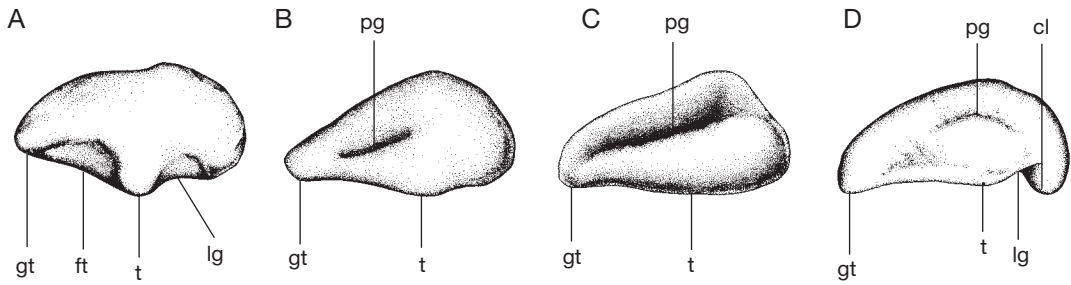


FIG. 1. — Femur of several dinosauriforms in proximal view; **A**, *Marasuchus*; **B**, *Eucoelophysis*; **C**, *Silesaurus*; **D**, *Coelophysis*. Abbreviations: **cl**, caudal lip; **ft**, fossa trochanterica; **gt**, greater trochanter; **lg**, oblique ligament groove; **pg**, proximal groove; **t**, tuberosity. Not to scale. A, after Novas 1996; B, after Sullivan & Lucas 1999; C, after Dzik 2003; D, after Padian 1986.

presence of distinct triangular and strongly caudally directed transverse processes seems to represent an apomorphic character restricted to Coelophysidae (*Coelophysis* + *Syntarsus*) (Sereno 1999), rather than a diagnostic feature of a monophyletic Ceratosauria, as originally proposed by Rowe & Gauthier (1990). Thus, this feature seems to be shared by *Eucoelophysis* and coelophysids.

2) *Eucoelophysis* does not have a trochanteric shelf (Irmis pers. comm.). On the other hand, the presence of a prominent trochanteric shelf, which Gauthier (1986) had indicated originally as diagnostic of “Ceratosauria”, was also reported in basal dinosauriforms (e.g., *Pseudolagosuchus*, *Marasuchus*, *Silesaurus*; Arcucci 1987; Sereno & Arcucci 1994; Dzik 2003), *Saturnalia* Langer, Abdala, Richter & Benton, 1999 (Langer 2003), and herrerasaurids (Novas 1993) (Figs 4; 5), being reconsidered as a synapomorphic trait of Dinosauriformes (Novas 1992a). Supporting this line of evidence, a trochanteric shelf is absent in *Lagerpeton* (Sereno & Arcucci 1993), *Scleromochlus* Woodward, 1907 (Benton 1999), and pterosaurs (e.g., *Rhamphorhynchus* Meyer, 1847; Wellnhofer 1975). Furthermore, as Novas (1996) pointed out, the presence of the trochanteric shelf in coelophysoids and ceratosaurids seems to be a retention of a plesiomorphic feature.

Additionally, Sullivan & Lucas (1999) indicated that the femoral morphology of *Eucoelophysis* resembles the gracile morph of *Coelophysis rhodesiensis* (Raath 1969, 1990), because of its narrow and crest-like cranial trochanter (Figs 4B; 5B, C, F). Several basal dinosauriforms, including the non-dinosaurian

Marasuchus and *Pseudolagosuchus* (Novas 1996) and the basal saurischians *Herrerasaurus* (Fig. 4D) (Novas 1993, 1996), *Saturnalia* (Langer 2003), and *Eoraptor* Sereno, Forster, Rogers & Monetta, 1993 (PVSJ 512), exhibit a small cranial trochanter. Nevertheless, *Silesaurus* presents a well developed and crest-like cranial trochanter (Figs 4C; 5D) (Dzik 2003), resembling in this aspect the condition of *Eucoelophysis* and neotheropods.

Because Sullivan & Lucas (1999) interpreted the type material of *Eucoelophysis* as a coelophysoid theropod, this taxon was widely considered to belong to this clade by several authors (Heckert *et al.* 2000; Tykoski & Rowe 2004; Carrano & Sampson 2004), and as one of its oldest members (see Carrano & Sampson 2004). However, Sullivan & Lucas (1999) did not indicate any coelophysoid synapomorphies in the type material of *Eucoelophysis baldwini*.

In contrast, the available elements of *Eucoelophysis baldwini* clearly indicate that this taxon is not a member of the Neotheropoda (= Coelophysoidea + (Neoceratosauria + Tetanurae Gauthier, 1986); *sensu* Sereno 1997). The following plesiomorphic features present in *Eucoelophysis* distinguish it from neotheropods:

1) Absence of an oblique ligament groove on caudal surface of femoral head (Rauhut 2003). As Rauhut (2003) indicated, the path of the *ligamentum capitis femoris* on the caudal side of the femoral head is not marked or absent in *Lagerpeton* Romer, 1971 (Novas 1996: fig. 3A), basal dinosauriforms (Fig. 1A, C) (e.g., *Marasuchus*, *Silesaurus*; Novas

1996), ornithischians (e.g., *Lesothosaurus* Galton, 1978, *Scutellostaurus* Colbert, 1981; Sereno 1991; Colbert 1981), basal sauropodomorphs (e.g., *Plateosaurus* Meyer, 1837, *Riojasaurus* Bonaparte, 1969, *Efraasia* Galton, 1973; Huene 1926, Bonaparte 1972, Galton 1973), and *Herrerasaurus* (Novas 1993). In *Eucoelophysis* the sulcus for the *ligamentum capitis femoris* is also poorly developed (Fig. 1B) (Sullivan & Lucas 1999: fig. 7D). On the other hand, all neotheropods (e.g., *Liliensternus*, *Allosaurus* Marsh, 1877, *Coelophysis*, *Syntarsus*, *Sinraptor* Currie & Zhao, 1993, *Ceratosaurus* Marsh, 1884; HMN BM.R. 2175, Madsen 1976; Padian 1986; Rowe 1989; Currie & Zhao 1993; Madsen & Welles 2000), excluding *Avimimus* Kurzanov, 1981 and Abelisauridae Bonaparte & Novas, 1985 (e.g., *Carnotaurus* Bonaparte, 1985; Bonaparte *et al.* 1990) (Rauhut 2003), show a strongly developed sulcus for the *ligamentum capitis femoris* that runs obliquely from proximomedially to laterodistally on the caudal side of the femoral head, bounded medially by a well developed caudal lip (Figs 1D; 4K, L; 5G) (Rauhut 2003).

2) Femoral medial epicondyle small and smoothly rounded (Forster 1999). The femur of neotheropod dinosaurs exhibits a well developed medial epicondyle or craniomedial crest. In this clade the craniomedial crest presents two distinct morphologies: it is either extended and crest-like in several basal Neotheropoda, such as *Coelophysis*, *Syntarsus*, *Dilophosaurus*, *Sinraptor*, *Ceratosaurus*, and *Allosaurus*, or hypertrophied and flange-like in abelisauroids (e.g., *Masiakasaurus* Sampson, Carrano & Forster, 2001, *Carnotaurus*) (Tykoski & Rowe 2004). In contrast, in *Herrerasaurus* (Novas 1993), basal Sauropodomorpha Huene, 1932 (e.g., *Riojasaurus*; Bonaparte 1972), Ornithischia Seeley, 1887, and basal Dinosauriformes (e.g., *Silesaurus*; Dzik 2003), there is a small and smoothly rounded craniomedial crest. In the same way, the distal portion of the femur of *Eucoelophysis* does not exhibit a well developed medial epicondyle resembling the condition present in non-neotheropod dinosauriforms.

3) Absence of caudal cleft between medial and lateral condyle on the proximal end of the tibia (Rauhut 2003). In *Eucoelophysis* the caudal margin of the

tibia is represented by a continuous convex surface in proximal view. In fact, although the proximal articular surface of the tibia could be partially broken, no cleft is present in *Eucoelophysis* (Fig. 2B). In basal dinosauriforms (Fig. 2A, C) (e.g., *Marasuchus*, *Silesaurus*; Sereno & Arcucci 1994; Dzik 2003), ornithischians (e.g., *Lesothosaurus*; Sereno 1991), basal sauropodomorphs (e.g., *Anchisaurus* Marsh, 1885, *Mussaurus* Bonaparte & Vince, 1979; Galton 1976; MLP 61-III-20-25, following the statement of Pol & Powell [2005] that the *Plateosaurus* sp. from the same locality are referred to *Mussaurus*), and herrerasaurids (Fig. 2D) (e.g., *Staurikosaurus* Colbert, 1970; *Herrerasaurus*; Galton 1977; Novas 1993) the medial condyle is separated from the lateral one by a slightly developed groove, being accompanied by a shallow concavity on the caudal margin of the proximal end of the femur. On the other hand, a deep cleft clearly separates the fibular and the medial condyles in Neotheropoda (Fig. 2E, F) (e.g., *Allosaurus*, *Dilophosaurus*, *Coelophysis*, *Sinraptor*, *Masiakasaurus*; Madsen 1976; Welles 1984; Padian 1986; Currie & Zhao 1993; Carrano *et al.* 2002), which moderately continues down the tibial shaft (e.g., *Coelophysis*, *Gojirasaurus* Carpenter, 1997; Padian 1986: fig. 5.5A; Carpenter 1997: fig. 7F).

4) Cnemial crest low (Sereno 1999). In basal dinosauriforms (Fig. 2A) (e.g., *Marasuchus*, *Pseudolagosuchus*; Novas 1996), ornithischians (e.g., *Dryosaurus* Marsh, 1894, *Scutellostaurus*, *Lesothosaurus*, *Pisanosaurus* Casamiquela, 1967; Galton 1981; Colbert 1981; Santa Luca 1984; Novas 1996), basal sauropodomorphs (e.g., *Mussaurus*, *Riojasaurus*, *Anchisaurus*; MLP 61-III-20-25; Bonaparte 1972; Galton 1976), *Staurikosaurus* (Galton 1977), and *Herrerasaurus* (Fig. 2D) (Novas 1993) the cnemial crest shows a slight craniolateral projection from the shaft. In the same way, this crest seems to be also low in *Eucoelophysis* (Fig. 2B). In contrast, neotheropod dinosaurs (Fig. 2E, F) (e.g., *Liliensternus*, *Allosaurus*, *Dilophosaurus*, *Coelophysis*, *Carnotaurus*, *Sinraptor*, *Syntarsus*, *Ceratosaurus*; Huene 1934; Madsen 1976; Welles 1984; Padian 1986; Bonaparte *et al.* 1990; Currie & Zhao 1993; Tykoski 1998; Madsen & Welles 2000) exhibit a strongly developed cnemial crest,

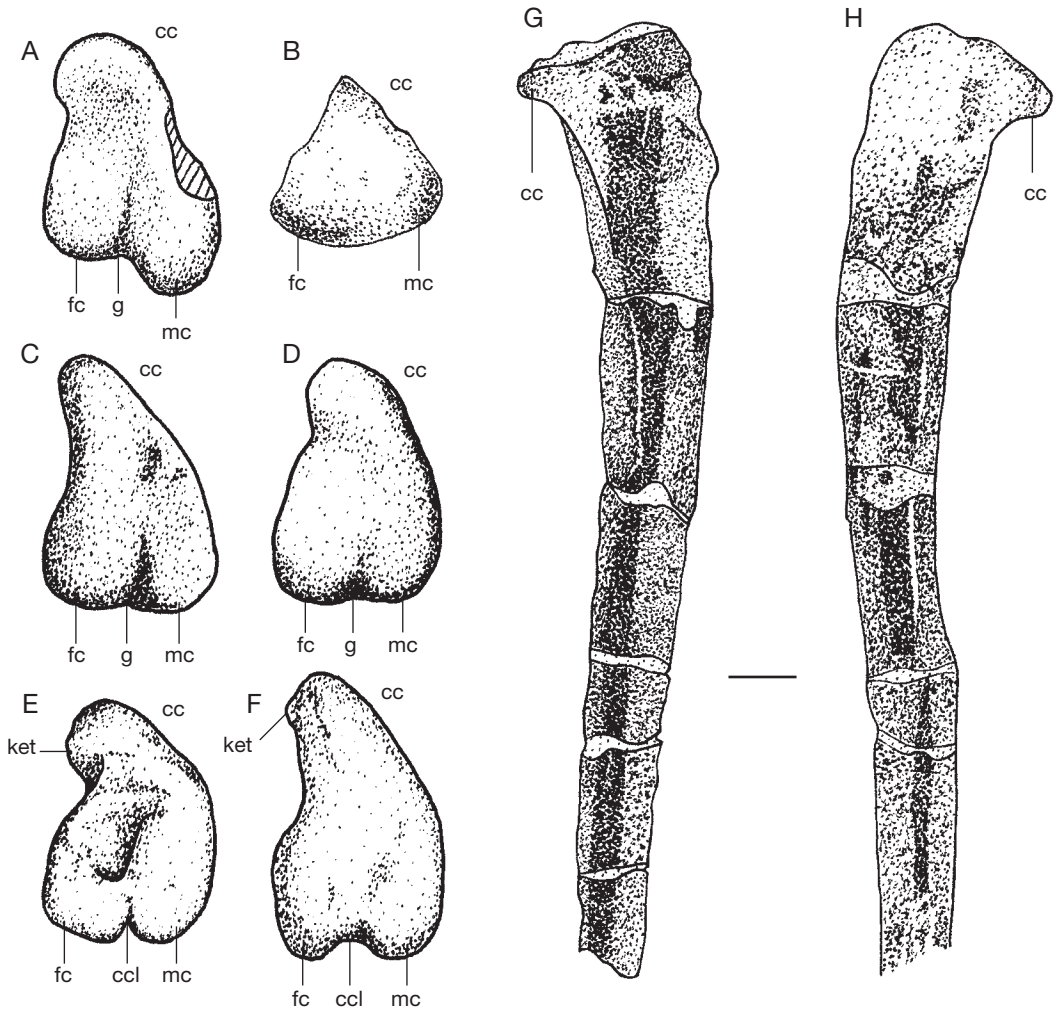


FIG. 2. — Tibiae of several dinosauriforms in proximal view and nearly complete left tibia of *Eucoelophysis baldwini* Sullivan & Lucas, 1999; **A**, *Marasuchus*, proximal view; **B**, **G**, **H**, *Eucoelophysis*; **B**, proximal view; **G**, lateral view; **H**, medial view; **C**, *Silesaurus*, proximal view; **D**, *Herrerasaurus*, proximal view; **E**, *Coelophysis*, proximal view; **F**, *Gojirasaurus*, proximal view. Abbreviations: **cc**, cnemial crest; **ccl**, caudal cleft; **fc**, fibular condyle; **g**, groove; **ket**, knee extensor tuberosity; **mc**, medial condyle. A, after Sereno & Arcucci 1994; C, after Dzik 2003; D, after Novas 1993; E, after Padian 1986; F, after Carpenter 1997. Scale bar: G, H, 1 cm.

the cranio-lateral length of which nearly reaches the sagittal extension of the proximal end of the tibial shaft. Furthermore, the hypertrophied cnemial crest of basal neotheropods is associated with a marked knee extensor tubercle. In the basal dinosauriform *Silesaurus* (Dzik 2003) a well developed cnemial crest is also present (Fig. 2C). The plesiomorphic state of this feature in *Eucoe-*

lophysis, basal dinosauriforms, herrerasaurids, ornithischians, and sauropodomorphs suggests that this trait was convergently acquired in Neotheropoda and in *Silesaurus*.

5) Absence of fibular crest (Gauthier 1986). The absence of the fibular crest was pointed out by Sullivan & Lucas (1999) as one of the characters that distinguished *Eucoelophysis* from *Coelophysis*

(Fig. 2G). However, the absence of the fibular crest not only distinguishes *Eucoelophysis* from *Coelophysis*, it contrasts with the condition presented by all neotheropods. In fact, Neotheropoda (e.g., *Liliensternus*, *Segisaurus* Camp, 1936, *Allosaurus*, *Syntarsus*, *Dilophosaurus*, *Coelophysis*, *Carnotaurus*, *Sinraptor*, *Gojirasaurus*, *Ceratosaurus*; see Huene 1934; Camp 1936; Madsen 1976; Raath 1977; Welles 1984; Padian 1986; Bonaparte *et al.* 1990; Currie & Zhao 1993; Carpenter 1997; Madsen & Welles 2000) is characterized by the presence of a fibular crest, a lateral ridge that runs proximodistally for the attachment of the fibula (Rauhut 2003). In contrast to the condition present in all neotheropods, the fibular crest is completely absent in Dinosauriformes ancestrally (Rauhut 2003), ornithischians (*Dryosaurus*; Galton 1981), Sauropodomorpha (e.g., *Mussaurus*, *Plateosaurus*, *Brachiosaurus* Riggs, 1903, *Riojasaurus*, *Anchisaurus*; MLP 61-III-20-25; Huene 1926; Janensch 1961; Bonaparte 1972; Galton 1976), *Guaibasaurus* Bonaparte, Ferigolo & Ribeiro, 1999, *Eoraptor* (Rauhut 2003, PVSJ 512), *Herrerasaurus* (Novas 1993), and *Staurikosaurus* (Galton 1977), resembling the condition of *Eucoelophysis*. On the other hand, a low fibular flange is present in the basal dinosauriform *Silesaurus* (Dzik 2003).

Based on the above comparisons, the postcranial anatomy of *Eucoelophysis* clearly indicates that this taxon is not a member of Neotheropoda, and so cannot be a coelophysoid theropod.

An apomorphic character shared by Herrerasauridae and Neotheropoda is the presence of a large cranial attachment depression on the cranial surface of the distal end of the femur (Serenó 1997). However, the state of this character could not be determined in the distal portion of the femur of *Eucoelophysis*. Unfortunately, none of the synapomorphies used by several authors to diagnose Theropoda (*sensu* Serenó 1999; Holtz 2000; Rauhut 2003) are preserved in *Eucoelophysis*.

The femoral head of *Eucoelophysis* (Fig. 4B, H) is almost identical morphologically (see below), as well as in proportion, to that of the basal dinosauriform *Silesaurus* (Fig. 4C, I). In consequence, it is important to discuss the possible phylogenetic position of *Eucoelophysis* within Dinosauriformes.

PHYLOGENETIC ANALYSIS

In order to test the phylogenetic relationships of *Eucoelophysis baldwini* a widely modified version of the dataset of Ezcurra & Novas (2006) was employed. Several characters were added, mainly gathered from previously published matrices (Novas 1996; Serenó 1999; Benton *et al.* 2000), and others deleted and modified. Neotheropodan taxa based on fragmentary remains were deleted (*Gojirasaurus*, *Zupaysaurus* Arcucci & Coria, 2003, *Procompsognathus* Fraas, 1913, *Segisaurus*, *Masiakasaurus*), whereas *Eucoelophysis*, the herrerasaurid *Staurikosaurus*, and putative primitive dinosauriforms were added (*Marasuchus*, *Pseudolagosuchus*, *Silesaurus*). Thus, the new data matrix is composed by 287 characters scored across 26 taxa (Appendices 1 and 2). The taxon sampling was focused on coelophysoids, basal saurischians, and more inclusive dinosauriforms, yet some basal ornithischians, sauropodomorphs, and basal ceratosaurian and tetanuran averostrans were also included. Character polarity was established employing the stem-dinosauromorph *Lagerpeton chanerensis* as an outgroup taxon.

The data matrix was analyzed under equally weighted parsimony using TNT version 1 (Goloboff *et al.* 2003), running a traditional search with tree bisection reconnection (TBR) swapping algorithm, consisting of 1000 replications. The result was a single most parsimonious tree of 794 steps, with CI = 0.44 and RI = 0.68 (Fig. 3). This tree depicted *Eucoelophysis baldwini* outside Coelophysoidea and even more inclusive than the Neotheropoda and Dinosauria nodes, re-positioning *Eucoelophysis* as the sister-taxon of Dinosauria. Thus, *Eucoelophysis* is here re-interpreted as a dinosauriform, and not as a coelophysoid theropod (*contra* Sullivan & Lucas 1999). *Marasuchus*, *Pseudolagosuchus*, and *Silesaurus* were depicted as successive sister-taxa of the *Eucoelophysis* + Dinosauria node. Both traditional Ornithischia and Saurischia were obtained, but within the latter, Herrerasauridae (*Herrerasaurus* + *Staurikosaurus*) was positioned as stem-saurischians (cf. Yates 2003; Langer 2004), and not as a member of the Theropoda clade (Serenó *et al.* 1993; Novas 1993; Serenó 1999; Ezcurra & Novas 2006). In this phylogenetic context, herrerasaurids are the sister-group of Eusaurischia (Sauropodomorpha +

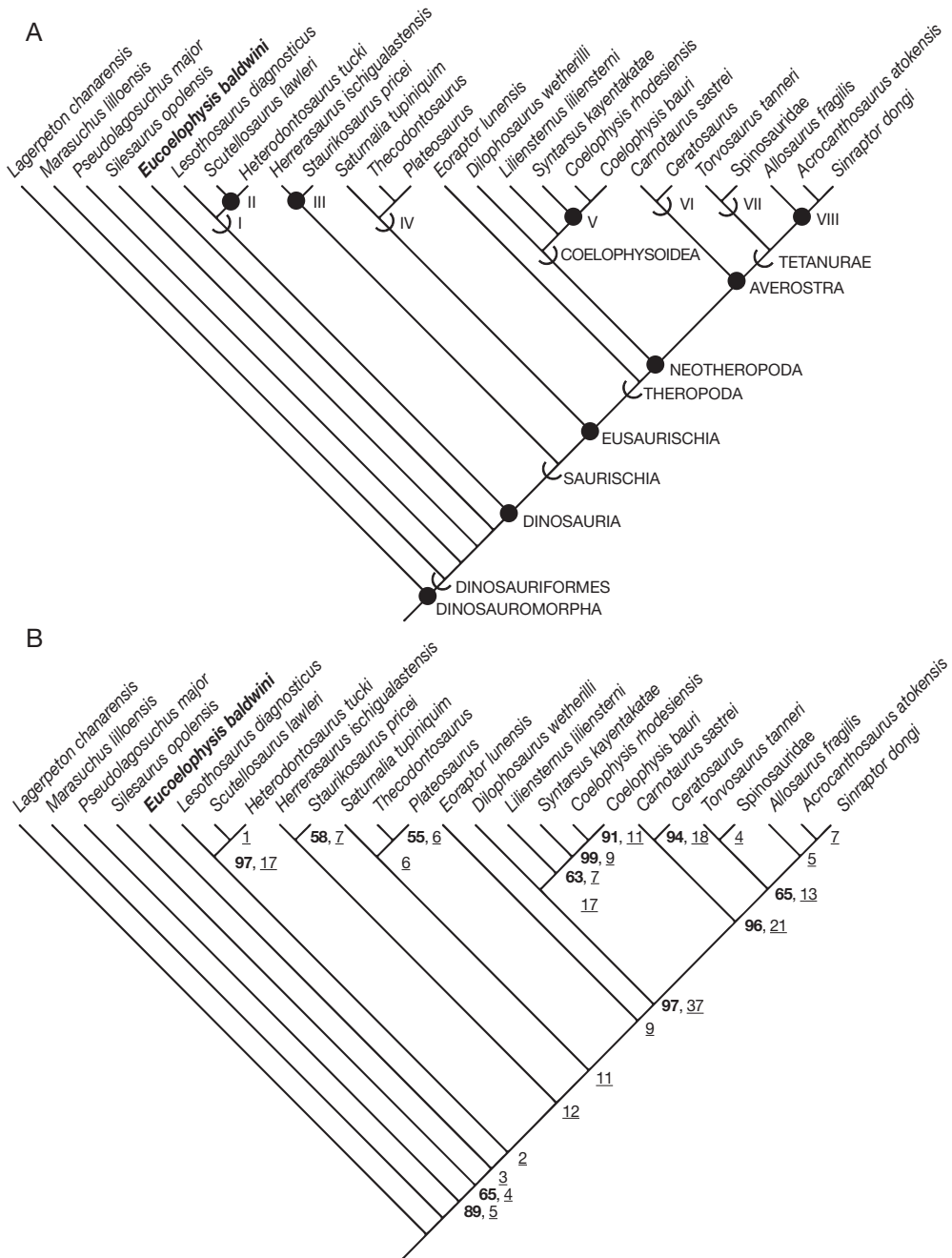


FIG. 3. — Cladograms showing the single most parsimonious tree obtained depicting the phylogenetic relationships of *Eucoelophysis baldwini* Sullivan & Lucas, 1999 within Dinosauriformes: **A**, cladogram indicating the nomenclature of more inclusive clades within Dinosauriformes, circles indicate node-based clades and arcs stem-based clades; **B**, cladogram indicating bootstrap values greater than 50% (numbers in bold) and branch lengths alongside each node (underlined numbers). The bootstrap analysis was performed under 10000 replications. Numbered nodes are as follows: **I**, Ornithischia; **II**, Genasauria; **III**, Herrerasauridae; **IV**, Sauropodomorpha; **V**, Coleophysidae; **VI**, Ceratosauria; **VII**, Spinosauroidae; **VIII**, Allosauroidae.

Theropoda, see Padian *et al.* 1999; Langer 2004). Within Theropoda, *Eoraptor* is its most basal member, being the sister-taxon of Coelophysoidea + Averostria (i.e. Ceratosauria + Tetanurae). In the following, the apomorphic characters that supported the placement of *Eucoelophysis* in the present phylogenetic hypothesis will be discussed.

The following synapomorphic characters of Dinosauriformes are present in *Eucoelophysis*, placing this taxon phylogenetically above the basal dino-sauromorph *Lagerpeton*:

1) Cranial trochanter on femur (Novas 1996). The basal dino-sauromorph *Lagerpeton* (Novas 1996) and the basal ornithodiran *Scleromochlus* (Benton 1999) lack a cranial trochanter on the femur. In contrast, in *Eucoelophysis* (Figs 4B; 5B, C, F) (Sullivan & Lucas 1999), basal dinosauriforms (Fig. 4C) (e.g., *Marasuchus*, *Pseudolagosuchus*, *Silesaurus*; Arcucci 1987; Sereno & Arcucci 1994), as well as Dinosauria (Fig. 5D-F) (e.g., *Lesothosaurus*, *Massospondylus* Owen, 1854, *Herrerasaurus*, *Syntarsus*; Cooper 1981; Rowe 1989; Sereno 1991; Novas 1993), a subvertical cranial trochanter is present.

2) Cnemial crest on proximal tibia (Novas 1996). Sullivan & Lucas (1999: 85) stated that the tibial shaft shows a "broadly triangular cross section that continues well down, because of the prominent projecting ridge formed by the cnemial crest" (Fig. 2B, G, H). This condition resembles the morphology exhibited in the most basal dinosauriforms (Fig. 2A) (e.g., *Pseudolagosuchus*, *Marasuchus*, *Silesaurus*; Arcucci 1987; Sereno & Arcucci 1994; Dzik 2003), ornithischians (e.g., *Dryosaurus*, *Lesothosaurus*; Galton 1981; Santa Luca 1984), sauropodomorphs (e.g., *Mussaurus*, *Riojasaurus*; MLP 61-III-20-25; Bonaparte 1972), herrerasaurids (Fig. 2D) (e.g., *Herrerasaurus*, *Staurikosaurus*; Novas 1989; Galton 1977), and neotheropods (Fig. 2E, F) (e.g., *Liliensternus*, *Coelophysis*, *Ceratosaurus*, *Masiakasaurus*; Huene 1934; Padian 1986; Madsen & Welles 2000; Carrano *et al.* 2002). Yet, Novas (1996: 729) has pointed out the absence of the cnemial crest in Archosauria Cope, 1869 ancestrally (e.g., Pterosauria Kaup, 1834, Crocodylomorpha Walker, 1968, *Lagerpeton*, *Scleromochlus*; Wellnhofer 1975; Walker 1990; Sereno & Arcucci 1993; Benton

1999: fig. 13C, D), in which the cranial margin of the tibia is nearly straight in lateral view, with a slightly forward projection proximally.

The above-mentioned synapomorphies of Dinosauriformes clearly indicate that *Eucoelophysis* belongs to this clade. Furthermore, *Eucoelophysis* also shares with *Pseudolagosuchus*, *Silesaurus*, and Dinosauria the following features, absent in more basal Dinosauriformes:

3) Greater trochanter of femur angular in contour in caudal view (Sereno 1999). Sereno (1999) interpreted the presence of a greater trochanter with an angular contour on the caudomedial corner of the proximal articular surface of the femur as a synapomorphic trait of Dinosauria (e.g., *Scelidosaurus* Owen, 1860, *Ceratosaurus*, *Plateosaurus*, *Riojasaurus*, *Anchisaurus*, *Scutellosaurus*, *Syntarsus*, *Herrerasaurus*; Owen 1863; Gilmore 1920; Huene 1926; Bonaparte 1972; Galton 1976; Colbert 1981; Rowe 1989; Novas 1993). However, the enlargement of the fossil record of basal dinosauriforms shows that *Silesaurus* (Fig. 4I) (Dzik 2003: fig. 13A) also exhibits this condition, as does the basal dinosauriform *Pseudolagosuchus* (Novas 1996) (Fig. 4G) and *Eucoelophysis* (Fig. 4H). In contrast, the greater trochanter exhibits a rounded contour in *Euparkeria* Broom, 1913 (Paul 2002), Crocodylomorpha (e.g., *Caiman*; Novas 1996: fig. 3L), Pterosauria (e.g., *Rhamphorynchus*; Wellnhofer 1975), *Lagerpeton* (Sereno & Arcucci 1993), and *Marasuchus* (Sereno & Arcucci 1994). Thus the presence of an angular greater trochanter is here considered a synapomorphy of *Pseudolagosuchus*, *Silesaurus*, *Eucoelophysis*, and the Dinosauria.

4) Fourth metatarsal sigmoidally curved in cranial aspect (Novas 1996). In *Eucoelophysis* the fourth metatarsal is badly crushed, being only represented by its distal end. However, the preserved portion of this metatarsal shows an incipient sigmoidal curvature of its shaft in cranial view (Fig. 6D). This condition contrasts with that present in most pterosaurians (e.g., *Rhamphorhynchus*; Wellnhofer 1975), *Scleromochlus* (Benton 1999), *Lagerpeton* (Fig. 6A) (Sereno & Arcucci 1993), and the basal dinosauriform *Marasuchus* (Fig. 6B) (Sereno & Arcucci 1994), but approaches the morphology exhibited by *Pseudolagosuchus* (Novas 1996), *Sile-*

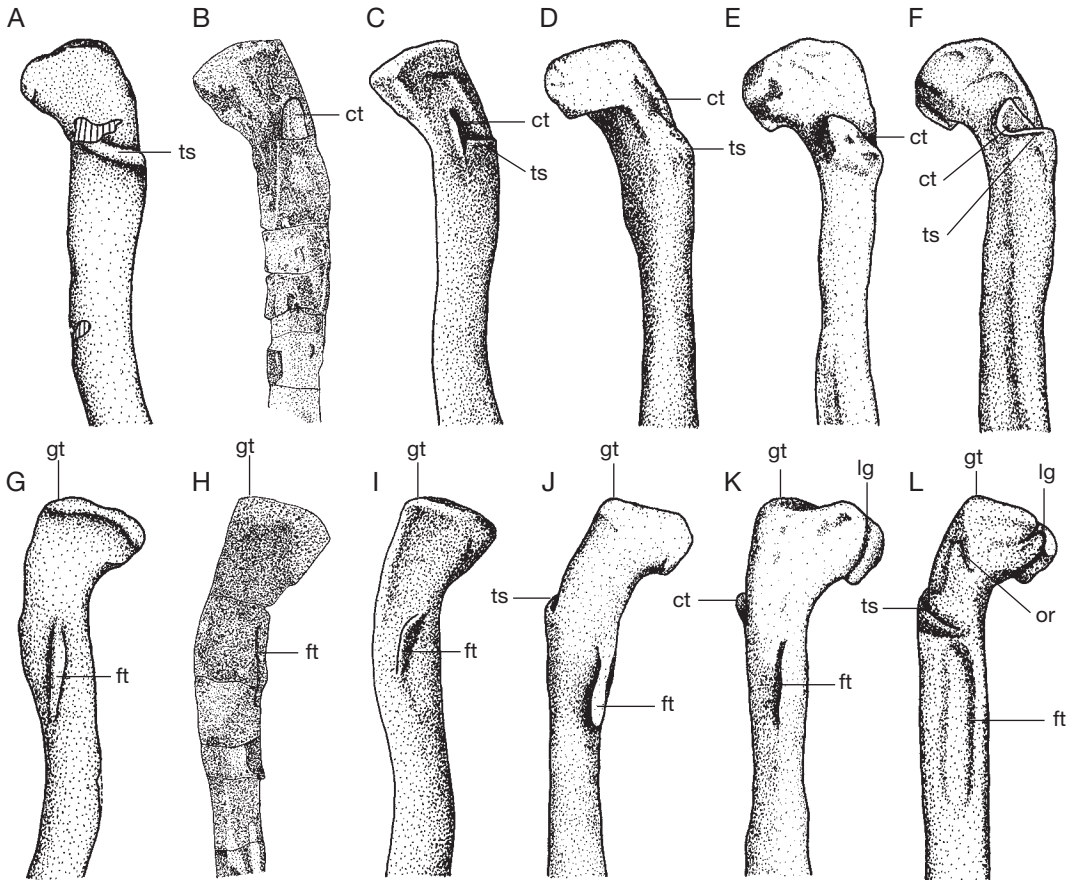


FIG. 4. — Proximal half of femur of several dinosauriforms in cranial and caudal views; **A, G**, *Pseudolagosuchus* (PULR-PV 53); **B, H**, *Eucoelophysis*; **C, I**, *Silesaurus*; **D, J**, *Herrerasaurus*; **E, K**, *Coelophysis* (gracile morph); **F, L**, *Syntarsus* (robust morph); **A-F**, cranial views; **G-L**, caudal views. Abbreviations as in Figure 1, and **ct**, cranial trochanter; **ft**, fourth trochanter; **or**, obturator ridge; **ts**, trochanteric shelf. Not to scale. B, H, after Sullivan & Lucas 1999; C, I, after Dzik 2003; D, J, after Novas 1993; E, K, after Padian 1986; F, L, after Rowe 1989.

saurus (Fig. 6C) (Dzik 2003), and the Dinosauria (Fig. 6E) (e.g., *Riojasaurus*, *Dryosaurus*, *Lesothosaurus*, *Dilophosaurus*, *Coelophysis*, *Herrerasaurus*; Bonaparte 1972; Galton 1981; Santa Luca 1984; Welles 1984; Padian 1986; Novas 1993).

Moreover, *Eucoelophysis* seems to exhibit more advanced traits in comparison with the more basal dinosauriforms, such as *Marasuchus* and *Pseudolagosuchus*. Dzik (2003) has pointed out the dinosaurian affinities of *Silesaurus* due to six characters shared by this taxon and the Dinosauria. The postcranial anatomy of *Eucoelophysis* allows to

determine two of those six characters, both of which are apomorphic condition in *Eucoelophysis*. In this phylogenetic context, *Eucoelophysis* shares the following characters with *Silesaurus* and the Dinosauria:

5) Reduction of the tuberosity that laterally bounds the ligament of the femoral head (Novas 1996). The caudal surface of the femoral head of *Eucoelophysis* shows a strongly reduced tuberosity, being represented by a slight prominence that projects caudally (Fig. 1B). In the basal dinosauriform *Silesaurus* this tuberosity is also extremely reduced (Fig. 1C)

(Dzik 2003). Furthermore, within Dinosauria, Novas (1996) indicated that the caudal tuberosity is strongly reduced in basal ornithischians (e.g., *Hypsilophodon* Huxley, 1869, *Lesothosaurus*; Galton 1974; Sereno 1991), *Herrerasaurus* (Novas 1993), early sauropodomorphs (e.g., *Efraasia*, *Anchisaurus*; Galton 1973, 1976), and theropods (Fig. 1D) (e.g., *Coelophysis*, *Syntarsus*; Padian 1986; Rowe 1989). In contrast, the tuberosity situated on the caudal surface of the femoral head is well developed in Crocodylomorpha (e.g., *Caiman*; Novas 1996; pers. obs.) and Dinosauria ancestrally (Fig. 1A) (i.e. *Lagerpeton*, *Marasuchus*, *Pseudolagosuchus*).

6) Prominent cranial trochanter on the femur (Novas 1996). Sullivan & Lucas (1999: 84) stated that “the cranial trochanter is a prominent ridge of bone that stands out laterally from the shaft”. In this way, *Eucoelophysis* (Fig. 5B, C, F) resembles the proximally projected and cranially extended cranial trochanter exhibited by *Silesaurus* (Fig. 5D) (Dzik 2003) and most Dinosauria (Fig. 5G, H) (e.g., *Riojasaurus*, *Coelophysis*, *Syntarsus*, *Lesothosaurus*; Bonaparte 1972; Padian 1986; Rowe 1989; Sereno 1991). On the other hand, the basal Dinosauriformes *Marasuchus* and *Pseudolagosuchus* show a distinctly reduced cranial trochanter (Novas 1996). The latter condition is also present in the basal saurischians *Herrerasaurus* (Novas 1993), *Eoraptor* (PVSJ 512), *Guaibasaurus* (Bonaparte et al. 1999), and *Saturnalia* (Langer 2003), which could suggest that a prominent cranial trochanter is a homoplasy acquired by *Eucoelophysis*, *Silesaurus*, ornithischians, and neotheropods, rather than be lately reduced in those basal saurischians.

7) Well delimited groove on the proximal articular surface of femur. Sullivan & Lucas (1999) pointed out that one of the diagnostic characters of the genus *Eucoelophysis* was the presence of a sulcus on the proximal surface of the femur, distinguishing this taxon from other “ceratosaurians”. Those authors (1999: 84) described this sulcus as “a narrow, slit-like depression, or groove, that is oriented nearly medio-laterally” (Figs 1B; 5F). Resembling the condition exhibited by *Eucoelophysis*, a nearly identical sulcus is also present on the femoral head of *Silesaurus* (Fig. 1C) (Dzik 2003). In contrast, the femoral head of basal dinosauromorphs (e.g.,

Lagerpeton, *Marasuchus*; Sereno & Arcucci 1993, 1994) presents a smooth and convex proximal articular surface (Fig. 1A).

Within the Dinosauria this deep and marked sulcus is also present in the basal sauropodomorph *Saturnalia* (Langer 2003), closely resembling the morphology exhibited by *Silesaurus* and *Eucoelophysis*. Additionally, a longitudinal groove is also present in the proximal articular surface of the femur of the herrerasaurid *Staurikosaurus* (Galton 1977), the basal sauropodomorph *Anchisaurus* (Galton 1976: fig. 8E), and possibly the putative basal saurischian *Alwalkeria* Chatterjee & Creisler, 1994 (Chatterjee 1987; Langer 2004). Moreover, in *Coelophysis* (Fig. 1D) (Padian 1986, UCMP 129618) and *Lesothosaurus* (Sereno 1991: fig. 8E) a shallow longitudinal groove is also present. In this context, the presence of a longitudinal sulcus on the articular proximal surface of the femur seems to be widely distributed within Dinosauria, although absent in several taxa within the group (e.g., *Herrerasaurus*, *Chindesaurus* Long & Murry, 1995; Novas 1993; Long & Murry 1995). Yet, a deep, wide, and marked longitudinal sulcus seems to be restricted to *Eucoelophysis*, *Silesaurus*, and the basal sauropodomorphs *Saturnalia* and *Anchisaurus*. As mentioned by Sullivan & Lucas (1999: 84), this condition differs from the shallow grooves of theropod dinosaurs.

Some apomorphic features may suggest a close relationship between *Eucoelophysis* and Dinosauria rather than to other Dinosauriformes:

8) Proximal end of the pubis without acetabular depression. The proximal end of the pubis of *Euparkeria* (Ewer 1965), *Ornithosuchus* (Walker 1964), *Riojasuchus* (Bonaparte 1972), *Lagerpeton* (Sereno & Arcucci 1993), *Marasuchus* (Novas 1996), and *Silesaurus* (Dzik 2003) presents a distinct depression, between the iliac and ischiadic articular surfaces, that forms part of the closed acetabulum. Otherwise, in *Eucoelophysis*, as well as dinosaurs (e.g., *Mussaurus*, *Eoraptor*, *Liliensternus*, *Scutellosaurus*, *Dilophosaurus*, *Coelophysis*, *Lesothosaurus*; MLP 61-III-20-23; PVSJ 512; Huene 1934; Colbert 1981; Welles 1984; Padian 1986; Sereno 1991), no acetabular depression is present on the proximal end of the pubis.

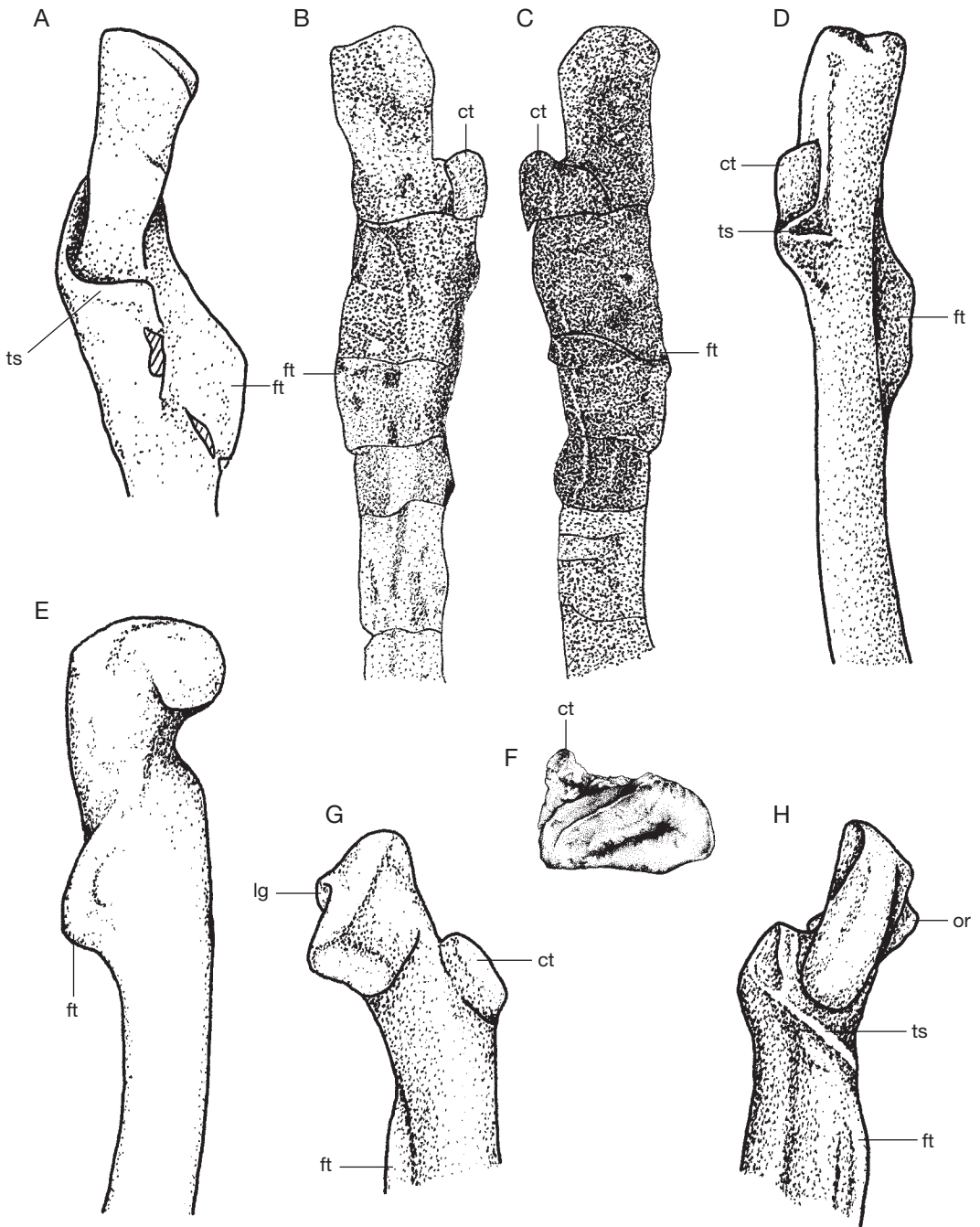


FIG. 5. — Proximal half of femur of several dinosauriforms in lateral and medial views and left femur of *Eucoelophysis baldwini* Sullivan & Lucas, 1999 in proximal view; **A**, *Marasuchus*; **B**, **C**, **F**, *Eucoelophysis*; **D**, *Silesaurus*; **E**, *Herrerasaurus*; **G**, **H**, *Syntarusus*. **A**, **C**, **D**, **H**, lateral views; **B**, **E**, **G**, medial views; **F**, proximal view. Abbreviations as in previous figures. Not to scale. **A**, after Sereno & Arcucci 1994; **D**, after Dzik 2003; **E**, after Novas 1993; **G**, **H**, after Rowe 1989.

9) Pubic shaft nearly straight (Serenó 1999). In ancestral archosauriforms, such as *Euparkeria* (Ewer 1965), Crurotarsi Sereno & Arcucci, 1990 (e.g., *Ornithosuchus*, *Riojasuchus*; Walker 1964; Bonaparte 1972), *Lagerpeton* (Serenó & Arcucci 1993), *Marasuchus* (Serenó & Arcucci 1994), *Pseudolagosuchus* (Arcucci 1987), and *Silesaurus* (Dzik 2003) the pubic shaft exhibits a caudal curvature. In contrast with the latter condition, in *Eucoelophysis* and Dinosauria, including ornithischians (e.g., *Heterodontosaurus*, *Lesothosaurus*; Santa Luca 1980; Sereno 1991), *Herrerasaurus* (Novas 1993), *Staurikosaurus* (Colbert 1970), sauropodomorphs (e.g., *Mussaurus*, *Plateosaurus*, *Riojasaurus*, *Saturnalia*; MLP 61-III-20-23; Huene 1926; Bonaparte 1972; Langer 2003), and theropods (e.g., *Liliensternus*, *Allosaurus*, *Dilophosaurus*, *Torvosaurus*, *Masiakasaurus*; Huene 1934; Madsen 1976; Welles 1984; Britt 1991; Carrano *et al.* 2002) the pubic shaft is almost straight along its extension. Thus, the presence of a caudal curvature in the pubes of coelophysids, *Guaibasaurus* (Bonaparte *et al.* 1999), and *Ceratosaurus* (Gilmore 1920) are better interpreted as apomorphic reversals.

10) Femoral trochanteric shelf absent (Gauthier 1986). As mentioned above, Sullivan & Lucas (1999) interpreted the presence of a “well developed” lesser trochanter in *Eucoelophysis* as a diagnostic feature of a monophyletic Ceratosauria (*sensu* Gauthier 1986; Rowe & Gauthier 1990). However, this character is not actually present in *Eucoelophysis* (Irmis pers. comm.). Novas (1992a, 1996) recognized this character as a synapomorphy of Dinosauriformes, because of its presence in basal dinosauriforms (e.g., *Pseudolagosuchus*, *Marasuchus*, *Silesaurus*; Arcucci 1987; Sereno & Arcucci 1994; Dzik 2003), basal-most sauropodomorphs (e.g., *Saturnalia*; Langer 2003), and *Herrerasaurus* (Novas 1992a, 1993). On the other hand, the absence of a trochanteric shelf in ornithischians (e.g., *Lesothosaurus*; Norman *et al.* 2004), allowed Novas (1996) to interpret the presence of this feature in Herrerasauridae, robust specimens of Coelophysoidea, and Ceratosauria as a retention of a plesiomorphic trait. Nevertheless, due to the absence of the trochanteric shelf in *Eucoelophysis*, the present phylogenetic analysis interpreted it as an apomorphic reversal diagnostic of the *Eucoelophysis* + Dinosauria node. Yet, the loss of a trochanteric

shelf could be also interpreted as an autapomorphy of *Eucoelophysis*, convergently acquired with the Ornithischia and some basal saurischians.

The above-mentioned characters suggest a close relationship of *Eucoelophysis* and *Silesaurus* with the Dinosauria. However, *Eucoelophysis* and *Silesaurus*, as well as other basal dinosauromorphs, exhibit a plesiomorphic character for Dinosauria: a femoral head weakly developed and only slightly inturned (Benton 1990). The femoral head of *Eucoelophysis* is slightly developed, almost proximomedially oriented at 140° with respect to the femoral main axis, and without a well developed caudal notch below the femoral head (Fig. 4B, H) (Sullivan & Lucas 1999). In the same way, a weakly developed and slightly inturned femoral head is also present in *Euparkeria* (145°), crocodylomorphs (e.g., *Malawisuchus* Gomani, 1997, *Caiman Spix*, 1825 [130°]), pterosaurs (e.g., *Rhamphorhynchus*), *Lagerpeton* (125°), and basal dinosauriforms (e.g., *Marasuchus* [140°], *Pseudolagosuchus* [120°], *Silesaurus* [135°]) (Fig. 4A, C, G, I). Additionally, the morphology and proportions of the proximal end of the femur of *Eucoelophysis* are extremely similar to those of *Silesaurus* (see below).

On the other hand, the femoral head is strongly inturned and distinctively separated from the shaft by a well developed femoral neck in ornithischian (e.g., *Scelidosaurus* [95°]) and saurischian (e.g., *Massospondylus* [100°], *Plateosaurus* [100°], *Riojasaurus* [100°], *Herrerasaurus* [95°], *Syntarsus* [60°], *Dilophosaurus* [100°]) dinosaurs (Fig. 4D-F, J-L). In the same way, several specimens of the basal neotheropod *Coelophysis bauri* clearly show a strongly inturned femoral head, being well separated from the shaft by a prominent neck, resulting in a head oriented at an angle of 55° with respect to the femur axis (Fig. 4E, K) (e.g., UCMP 129618 [Padian 1986], YPM 41197, MCZ 4779), resembling the typical dinosaurian condition (*contra* Colbert 1989: fig. 80).

As previously mentioned, the proximal end of the femora of *Eucoelophysis* and *Silesaurus* closely resemble to each other. In fact, both taxa share the following derived feature:

11) Femoral proximal articular surface subtriangular in contour. The proximal articular surface of

Eucoelophysis shows a subtriangular contour, due to the acute angles between the straight cranial and caudal surfaces, the tapering lateral corner of the proximal articular surface, and the above-mentioned orientation of the femoral head. This morphology results in a structure composed of three distinct faces, the straight cranial and caudal margins and the craniomedially oriented and also caudomedially straight femoral head (Fig. 1B). This condition closely approaches that present in the basal dinosauriform *Silesaurus* (Fig. 1C) (Dzik 2003). On the other hand, in basal dinosauromorphs (Fig. 1A) (e.g., *Lagerpeton*, *Marasuchus*; Sereno & Arcucci 1993, 1994), as well as *Herrerasaurus* (Novas 1993), sauropodomorphs (e.g., *Efraasia*, *Anchisaurus*; Galton 1973, 1976), ornithischians (e.g., *Lesothosaurus*; Sereno 1991), and basal theropods (Fig. 1D) (e.g., *Coelophysis*, *Syntarsus*, *Chindesaurus*; Padian 1986; Rowe 1989; Long & Murry 1995) the proximal articular surface of the femoral head exhibits a wedge-shaped or oval contour.

AUTAPOMORPHIC CHARACTERS OF *EUCOELOPHYSIS*
Eucoelophysis baldwini has been diagnosed by Sullivan & Lucas (1999) on the basis of an ischio-acetabular groove in the pubis and a sulcus in the proximal surface of the femur. However, the marked sulcus on the proximal articular surface of the femur, as mentioned above, is also exhibited by *Silesaurus* and several dinosaurs. Furthermore, the presence of an ischio-acetabular groove seems to be absent, as indicated by Sullivan & Lucas (1999) in theropods, and also other basal dinosauriforms, including *Silesaurus*. Thus it is here considered that the (12) presence of an ischio-acetabular groove is a valid diagnostic trait of *Eucoelophysis*.

Moreover, *Eucoelophysis baldwini* exhibits the following autapomorphies:

13) Non-invasive pleurocoels in the dorsal vertebrae. The dorsal vertebrae of *Eucoelophysis* (following Sullivan & Lucas 1999 assignment) exhibit a single blind fossa at the lateral surface of the centrum. Pleurocoels were not described in any other non-dinosaurian dinosauromorph at the moment, and they are restricted to derived sauropodomorphs, *Chindesaurus*, and neotheropods among Dinosauria.

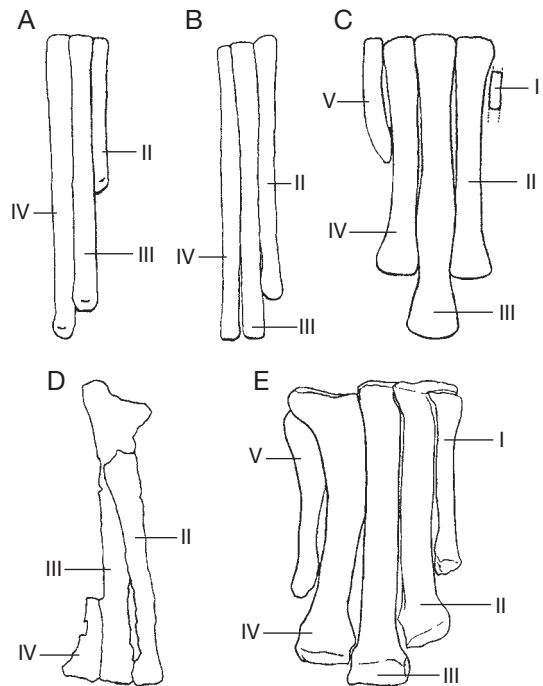


FIG. 6. — Metatarsals of several dinosauromorphs in cranial view; **A**, *Lagerpeton*; **B**, *Marasuchus*; **C**, *Silesaurus*; **D**, *Eucoelophysis*; **E**, *Herrerasaurus*. Abbreviations: I-V, first to fifth metatarsal. Not to scale. A, after Sereno & Arcucci 1993 and Novas 1996; B, after Sereno & Arcucci 1994 and Novas 1996; C, after Dzik 2003; D, after Sullivan & Lucas 1999; E, after Reig 1963.

Thus, the presence of these non-invasive pleurocoels in the dorsal vertebrae of *Eucoelophysis* seems to be an autapomorphy.

14) Cnemial crest distinctively offset from the tibial shaft, cranially straight, and without lateral notch. The cnemial crest is acquired by Dinosauriformes, being absent in Archosauria ancestrally (Novas 1996) (see above). In dinosauriforms (e.g., *Mussaurus*, *Pseudolagosuchus*, *Herrerasaurus*, *Marasuchus*, *Ceratosaurus*, *Silesaurus*; MLP 61-III-20-25; Arcucci 1987; Novas 1993; Sereno & Arcucci 1994; Madsen & Welles 2000; Dzik 2003) this crest projects from the shaft, in lateral view, forming a marked tuberosity on the cranial margin of the tibia. Distally, the cnemial crest merges smoothly onto the tibial shaft. In contrast, *Eucoelophysis* shows a distinctly cranially offset cnemial crest from the

tibial shaft. Although this crest is highly reduced, it forms distally an acute angle with the tibial shaft (Fig. 2G, H). Moreover, the cnemial crest projects cranially in a straight line and is subtriangular in proximal view. In consequence, *Eucoelophysis* also differs from other Dinosauriformes because it lacks a cranio-lateral curvature or a lateral notch on the cnemial crest (Fig. 2B).

Furthermore, the fourth trochanter of *Eucoelophysis* is highly reduced, being represented by a low vertical ridge, poorly distinguished from the caudomedial surface of the femoral shaft. Its morphology clearly contrasts with that of other basal dinosauromorphs (e.g., *Plateosaurus*, *Liliensternus*, *Riojasaurus*, *Staurikosaurus*, *Scutellosaurus*, *Dilophosaurus*, *Lesothosaurus*, *Herrerasaurus*, *Lagerpeton*, *Marasuchus*, *Guaibasaurus*, *Silesaurus*, *Saturnalia*; Huene 1926, 1934; Bonaparte 1972; Galton 1977; Colbert 1981; Welles 1984; Sereno 1991; Novas 1993; Sereno & Arcucci 1993, 1994; Bonaparte *et al.* 1999; Dzik 2003; Langer 2003), in which the fourth trochanter is a well developed structure, caudomedially extended, and dorsoventrally tall (Fig. 5A, D). However, the reduced condition of the fourth trochanter could be due to crushing (Irmis pers. comm.), thus this feature is considered as a probable autapomorphy of *Eucoelophysis*.

REFERRED MATERIALS OF *EUCOELOPHYSIS*

Sullivan & Lucas (1999) considered as referred material of *Eucoelophysis* a nearly complete right pubis (AMNH 2706). This pubis preserves the pubic plate, showing the possible presence of both an obturator foramen and a pubic fenestra (the region where the obturator foramen and pubic fenestra lie is filled with plaster; Sullivan & Lucas 1999). This condition resembles the morphology present in Coelophysidae (e.g., *Coelophysis*, *Syntarsus*, *Segisaurus*) and *Ceratopsosaurus* (Rowe & Gauthier 1990). In *Dilophosaurus*, *Liliensternus*, and *Gojirasaurus* the pubic plate is not preserved. Furthermore, AMNH 2706 differs from the pubis of the holotype of *Eucoelophysis* in some anatomical aspects, including: 1) iliac facet well developed dorsoventrally; 2) acetabular facet dorsoventrally reduced; 3) ischio-acetabular groove weakly developed; and 4) shaft caudally bowed. The ischio-

acetabular groove in the holotype of *Eucoelophysis* is a “U”-shaped sulcus in lateral view, and deeply developed between both acetabular and ischial facets. On the other hand, AMNH 2706 shows an ischio-acetabular groove hardly noticeable in lateral view. The presence of a pubic plate perforated by a large pubic fenestra below the obturator foramen differs from the condition exhibited in basal dinosauriforms, sauropodomorphs, ornithischians, and most theropods, where this fenestra is absent below the obturator foramen (Rowe & Gauthier 1990). In fact, this condition resembles the morphology present in Coelophysidae and *Ceratopsosaurus*. In sum, AMNH 2706 is here considered to belong to a coelophysid theropod, and is not referable to *Eucoelophysis*.

In addition, Heckert *et al.* (2000) described some small theropod dinosaurs represented by several cranial and postcranial elements, including a left premaxilla and maxilla, a putative left lacrimal, several cervical and dorsal vertebrae, a fused synsacrum, an incomplete left scapulocoracoid, a fragmentary right ilium, right ischium, two femora, portions of three left tibiae, two incomplete fibulae, and numerous metapodial elements and phalanges from the Snyder Quarry, Chinle Group (early-mid Norian; Heckert *et al.* 2000). Those theropods were referred by Heckert *et al.* (2000: 30) to coelophysoid theropods. Heckert *et al.* (2000: 30) indicated that this assignment was supported by the presence of “a subnarial gap, heterodont premaxilla, gracile limb bones, and numerous other features”. Heckert *et al.* (2000: 31) also pointed out that these theropods “closely resemble *Eucoelophysis*, particularly in details of the scapulocoracoid, ischium, and tibia”, referring them to *Eucoelophysis* sp. Yet the Snyder Quarry theropods exhibit differences with the holotype material of *Eucoelophysis*, mainly in the femoral morphology. These were interpreted as possibly sex-related by Heckert *et al.* (2000), who considered that the differences “may warrant erection of a new species”.

Heckert *et al.* (2000) pointed out that only one diagnostic character is shared by *Eucoelophysis* and the new material: a strongly appressed surface on the tibia that was held in contact with the fibula. However, as these authors indicated, the articulated

nature of the *Coelophysis* specimens of Ghost Ranch (Colbert 1989) and the fused tibiotarsus present in *Syntarsus* species (Raath 1977; Rowe 1989) makes this condition difficult to determine in those genera. Furthermore, Heckert *et al.* (2000: 30) also noted that the scapulocoracoid “is somewhat similar to *Eucoelophysis*”. Nevertheless, as mentioned above, the scapulocoracoid of coelophysoids resembles the morphology exhibited in basal dinosauriforms (e.g., *Silesaurus*; Dzik 2003), because of the retention of plesiomorphic features.

In contrast, Heckert *et al.* (2000) noted the following valid differences between the holotype of *Eucoelophysis baldwini* and the referred material: 1) medially offset femoral head that is slightly “hooked”; and 2) the femoral head lacks the proximal groove. The first trait shows the presence of a diagnostic dinosaurian condition in the Snyder Quarry theropods (see above), with a femoral head oriented at 60° with respect to the femoral main axis, closely resembling the angle exhibited by *Coelophysis*, *Syntarsus*, and other more derived theropods; and the second feature is widely present among Neotheropoda.

In this context, the Snyder Quarry theropods, in contrast with *Eucoelophysis*, resemble the dinosaurian condition (e.g., femoral head strongly inturned). Furthermore, the Snyder Quarry taxon exhibits several synapomorphic characters of Coelophysoidea, including: premaxillary body rostrocaudally lengthened, heterodont premaxilla (Heckert *et al.* 2000), premaxillary nasal process forms more than half of the rostradorsal narial border, subnarial gap (Heckert *et al.* 2000), rostral end of the maxillary alveolar border sharply upturned, and cervical vertebrae rostrocaudally elongated. Additionally, the theropods of the Snyder Quarry are more closely related to *Liliensternus* and Coelophysidae than to *Dilophosaurus*, due to the presence of an alveolar ridge defining the ventral margin of the antorbital fossa. Moreover, the maxilla exhibits a square rostral end of the antorbital fossa, resembling the condition of *Zupaysaurus* (Ezcurra & Novas 2005) and Coelophysidae (Rauhut 2003). In this morphological context, the Snyder Quarry theropod is here interpreted as Coelophysoidea indet., cf. Coelophysidae.

CONCLUSIONS

Eucoelophysis baldwini has been widely considered a coelophysoid theropod by several authors (Sullivan & Lucas 1999; Heckert *et al.* 2000; Tykoski & Rowe 2004; Carrano & Sampson 2004). However, the comparisons carried out above clearly indicate that *Eucoelophysis* is not a neotheropod dinosaur, and in consequence not a coelophysoid.

The reduction of the tuberosity that laterally bounds the ligament of the femoral head, the presence of a deep sulcus on the proximal articular surface of the femur, and a prominent cranial trochanter on the femur are apomorphic traits shared by *Silesaurus*, *Eucoelophysis* and the Dinosauria. On the other hand, no diagnostic feature of the Dinosauria is present in *Eucoelophysis*, suggesting that *Eucoelophysis* is not a member of that clade. Additionally, the lack of the dinosaurian apomorphic trait, strongly inturned femoral head, distinguishes *Eucoelophysis* and *Silesaurus* from dinosaurs.

Further to the phylogenetic position of *Eucoelophysis* within Dinosauriformes, the position of *Silesaurus opolensis* as the sister-taxon of the Dinosauria, as implicitly proposed by Dzik (2003) is also interesting. In this phylogenetic context, *Silesaurus* presents several features considered diagnostic of the Dinosauria (see Dzik 2003), which turn to be synapomorphic for a more inclusive clade within Dinosauriformes, composed of *Silesaurus*, *Eucoelophysis*, and the Dinosauria.

Until few years ago the biochron of basal Dinosauromorpha (e.g., *Lagerpeton*, *Marasuchus*) was considered restricted to the late Ladinian. This was recently enlarged by the discovery of *Silesaurus opolensis* in the late Carnian of Poland (Dzik 2003), and the Norian age of *Eucoelophysis baldwini* comes to constitute the youngest record for a pre-dinosaur basal Dinosauriformes. Thus, this evidence suggests that late dinosauriforms were co-eval with Carnian and early Norian dinosaurs, at least (Novas & Ezcurra 2005).

The phylogenetic analysis presented here, depicted *Eucoelophysis* as the sister-taxon of Dinosauria, and some common characters shared by *Silesaurus* and *Eucoelophysis* (e.g., prominent cranial trochanter, subtriangular femoral head in proximal view) support

the non-dinosaurian status of *Eucoelophysis*. However, the incomplete fossil record of early dinosaurs and the fragmentary nature of the type material of *Eucoelophysis*, including some bones assigned with query to this taxon, hampers a conclusive phylogenetic status of *Eucoelophysis baldwini* within basal Dinosauriformes, until new material of this taxon is described.

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APPENDIX 1

List of the characters used in the current phylogenetic analysis. Original citations and subsequent modifications are detailed.

1. Skull length (premaxilla-quadrato condyle) versus skull height (articular condyle of quadrato to dorsal most edge of parietal): less than 3 times (0); equal or more than 3 times (1). (Forster 1999; Sereno 1999; Tykoski 2005).
2. Skull: longer than two-thirds of the femoral length (0); shorter than two-thirds of the femoral length (1). (Gauthier 1986).
3. Skull height at the caudal margin of the external naris: more than 0.6 of its height at the middle of the orbit (0); less than 0.6 of its height at the middle of the orbit (1). (Langer 2004).
4. Height:length ratio of premaxilla below external naris: 0.5-1.25 (0); less than 0.5 (1); greater than 1.25 (2). (Holtz 1994, 2000; unordered).
5. Angle between rostral margin and alveolar margin of premaxilla: equal or more than 70° (0); less than 70° (1); equal or less than 40° (2). (Rauhut 2003; Ezcurra & Novas 2006; unordered).
6. Lateral surface of premaxillary body: smooth (0); pierced by a single neurovascular foramina above the second premaxillary tooth (1); pierced by several neurovascular foramina (2). (Tykoski 1998; Ezcurra & Novas 2006; ordered).
7. Narial fossa: absent or shallow in the rostroventral corner of the naris (0); expanded in the rostroventral corner of the naris (1). (Sereno 1999; Langer 2004).
8. Premaxillary nasal process: less than or equal to half of the rostradorsal narial border (0); forms more than half the rostradorsal narial border (1). (Holtz 2000).
9. Premaxilla-nasal suture: V-shaped (0); W-shaped (1). (Sereno 1999).
10. Caudal process of the premaxilla contacts: wide, plate-like, broadly contacting the nasals and excluding the maxilla from the external nares (0); strongly reduced in width, but still contacting the nasals (1); strongly reduced process does not contact the nasals, and the maxilla forms part of the caudoventral border of the external nares (2). (Gauthier 1986; Benton *et al.* 2000; Rauhut 2003; ordered).
11. Ventral process at the caudal end of premaxillary body: absent (0); present (1). (Rauhut 2003).
12. Subnarial gap (i.e. caudal part of premaxillary alveolar margin unedentulous, resulting in an interruption of the upper tooth row): absent (0); present (1). (Gauthier 1986).
13. Mesial premaxillary teeth cross-section: labiolingually flattened (0); subcircular (1); asymmetrically D-shaped (2). (Rowe 1989; unordered).
14. Serrations on mesial-most premaxillary teeth: not substantially different from other teeth (0); greatly reduced or absent (1). (Tykoski 1998).
15. Constriction between articulated premaxillae and maxillae: absent (0); present (1). (Rauhut 2003).
16. Subnarial foramen: absent (0); present (1). (Sereno & Novas 1993).
17. External nares: laterally facing (0); strongly rostrolaterally facing (1). (Rauhut 2003).
18. Alveolar margin of rostral-most maxilla: relatively straight or slightly concave (0); strongly but gradually upturned from an extension of more than three teeth along the alveolar margin and orienting the first maxillary alveolus rostroventrally (1); sharply mediadorsally upturned in the rostral-most tip of the maxilla and orienting the first maxillary alveolus rostroventrally (2). (Rowe 1989; Tykoski 1998; Ezcurra & Novas 2006; unordered).
19. Angle between the dorsoventral margin of the maxilla and the alveolar margin: equal or more than 75° (0); less than 75° (1). (Ezcurra & Novas 2006).
20. Rostral process of maxilla: between 10% and 25% of total maxilla length (0); equal or less than 10% of total maxilla length (1); equal or more than 25% of total maxilla length (2). (Tykoski 2005; unordered).
21. Ratio of dorsoventral height of proximal end of rostral process of maxilla versus height of alveolar ramus of maxilla at first alveolus caudal to rim of internal antorbital fenestra: less than 1 (0); equal or more than 1 (1). (Tykoski 2005).
22. Rostromedial process of maxilla: dorsoventrally deep and short to moderate in length, being slightly visible in lateral view (0); rostrocaudally long and dorsoventrally low, being well rostrally extended and far visible in lateral view (1). (Ezcurra & Novas 2006).
23. Medial surface of rostromedial process of maxilla: smooth (0); bears longitudinal ridges (1). (Sereno *et al.* 1998).
24. Caudal-most maxillary vascular foramen: the same size, or smaller than, all other maxillary vascular foramina (0); larger than all other maxillary vascular foramina (1). (Yates 2003).
25. Direction that the caudal-most neurovascular foramen at the lateral maxillary row opens: rostrally, ventrally, laterally (0); caudally (1). (Yates & Kitching 2003).
26. Ascending process of the maxilla: confluent with rostral rim of maxillary body and gently sloping caudolaterally (0); offset from the rostral rim of maxillary body, with rostral projection of maxillary body shorter than high (1); offset from rostral rim of maxillary body, with rostral projection of maxillary body as long as high or longer (2). (Sereno *et al.* 1996; Rauhut 2003; ordered).
27. Ascending process of maxilla angulation with horizontal process: between 35° and 50° (0); less than 35° (1); more than 50° (2). (Tykoski 2005; unordered).
28. Caudal tip of ascending process of maxilla: blunt or tapering (0); strongly forked (1). (Ezcurra & Novas 2006).
29. Maxillary antorbital fossa rostral to internal antorbital fenestra: narrow and extending little beyond rostral rim of internal antorbital fenestra (0); broad and rostrocaudally well extended (1). (Sereno *et al.* 1994).
30. Rostral end of the antorbital fossa in late ontogeny: caudal to caudal end of external naris (0); ventral to caudal end of external naris (1). (Sereno 1999).
31. Rostral margin of maxillary antorbital fossa: rounded or pointed (0); squared (1). (Rauhut 2003).
32. Medial wall of the antorbital fossa: does not reach the caudoventral corner of the internal antorbital fenestra

- (0); extends through the entire ventral border of the internal antorbital fenestra as a very narrow lamina (1); extends through the entire ventral border of the internal antorbital fenestra as a broad lamina (2). (Galton 1990; Witmer 1997; Carrano *et al.* 2002; Langer 2004; Ezcurra & Novas 2006; ordered).
33. Ventral rim of the antorbital fossa: ventrally sloped in its caudal part (0); parallel to tooth row (1). (Sereno 1986).
 34. Dorsoventrally compressed ridge on lateral surface of maxilla, forming the ventral border of the antorbital fossa: absent (0); present (1). (Rowe & Gauthier 1990).
 35. Maxillary antorbital fossa: deep and with sharp margins (0); shallow, margins formed by low ridges, a sharp rim may be present only rostrally (1). (Sues 1997; Rauhut 2003).
 36. Lateral surface of maxillary antorbital fossa at the base of the ascending process: smooth (0); with deep, large, and subcircular or oval blind pocket(s) (1). (Carrano *et al.* 2002).
 37. Promaxillary foramen: absent (0); present (1). (Carpenter 1992).
 38. Maxillary fenestra: absent (0); present (1). (Gauthier 1986).
 39. Maximum length of internal antorbital fenestra: less than 25% of skull premaxilla-quadrata length (0); 25% or greater than maximum skull premaxilla-quadrata length (1). (Rowe & Gauthier 1990).
 40. Maxillary tooth row caudal extension: extends caudally to approximately half the length of the orbit (0); ends at the rostral rim of the orbit (1); completely antorbital, tooth row ends rostral to the vertical strut of the lacrimal (2). (Gauthier 1986; Rauhut 2003; ordered).
 41. Number of maxillary teeth in adults: 18 or less (0); more than 18 (1). (Ezcurra & Novas 2006).
 42. Lateral surface of rostral end of nasal along margin of external naris: relatively flat (0); with deep concave fossa (1); with laterally convex hood covering caudal part of external naris (2). (Carrano *et al.* 2002; unordered).
 43. Nasal contributes to border of antorbital fossa: absent (0); present (1). (Holtz 2000).
 44. Pneumatic foramen in the nasals: absent (0); present (1). (Rauhut 2003).
 45. Pronounced lateral rims of the nasals and dorsolateral margins of lacrimal: absent (0); forming a low and laterally projected pair of crests (1). (Rauhut 2003).
 46. Lacrimal shape: block-shaped or roughly triangular in lateral view (0); with well defined inverted L-shaped and dorsoventrally elongated ventral process (1). (Gauthier 1986; Rauhut 2000).
 47. Lacrimal exposition on dorsal skull roof: absent, only exposed on the lateral side of the skull (0); present, exposed on the dorsal skull roof (1). (Gauthier 1986).
 48. Lacrimal folds over the caudal/dorsocaudal part of antorbital fenestra: absent (0); present (1). (Sereno 1999; Langer 2004).
 49. Lacrimal dorsally projected horn: absent (0); present (1). (Russell & Dong 1993).
 50. Lacrimal rostral ramus: shorter than the ventral ramus in length (0); subequal or longer than the ventral ramus (1). (Sereno *et al.* 1996; unordered).
 51. Lateral lamina of bone of the lacrimal: almost covering most of the bone (0); with no interruption of the lacrimal antorbital fossa and restricted to the caudal margin of the ventral ramus along its dorsoventral extension (1); only interrupting the lacrimal antorbital fossa near the proximal end of the ventral ramus and ventrally restricted to caudal margin of the ventral ramus (2). (Ezcurra & Novas 2006; ordered).
 52. Lacrimal antorbital pneumatic foramen (into central body of lacrimal): absent (0); present (1). (Molnar *et al.* 1990; Novas 1992b).
 53. Lateral longitudinal ridge traversing rostral and caudal processes of jugal: absent (0); present (1). (Sereno & Novas 1993; Tykoski 1998).
 54. Rostral process of jugal: contributes to the caudoventral margin of the internal antorbital fenestra (0); excluded from the internal antorbital fenestra (1); expressed at the rim of the internal antorbital fenestra and with a distinct process that extends rostrally underneath it (2). (Holtz 1994; Rauhut 2003; unordered).
 55. Sublacrimal part of jugal: tapering (0); bluntly squared rostrally (1); squared rostrally with a very small dorsally directed prong, slightly overlapping the lacrimal (2); expanded with a well developed dorsally directed prong, strongly overlapping the lacrimal (3). (Rauhut 2003; Ezcurra & Novas 2006; ordered).
 56. Rostral-most tip of rostral process of jugal with three distinct prongs: absent (0); present (1). (Ezcurra & Novas 2005).
 57. Angle between ascending process and caudal process of jugal: right or obtuse (0); acute, with an ascending process strongly dorsocaudally oriented (1). (Ezcurra & Novas 2006).
 58. Ventral border of infratemporal fenestra: mostly constituted by the jugal or equal participation of both jugal and quadratojugal (0); mostly constituted by the quadratojugal (1). (Ezcurra & Novas 2006).
 59. Prefrontal: widely exposed on the rostradorsal rim of the orbit in lateral view with a slender ventral process along the mediocaudal rim of the lacrimal (0); reduced, with little participation on the rostradorsal rim of the orbit in lateral view, being displaced caudally and/or medially, ventral process absent (1). (Rauhut 2003; Ezcurra & Novas 2006).
 60. Paired frontals shape: subrectangular, rostrocaudally elongated (0); squared, rostrocaudally shortened (1). (Holtz 1994; Ezcurra & Novas 2006).
 61. Orbit size: subequal to or longer than internal antorbital fenestra length (0); shorter than internal antorbital fenestra length (1). (Holtz 1994).
 62. Orbit shape: subcircular (0); oval (1). (Holtz 2000).
 63. Postfrontal: present (0); absent (1). (Sereno & Novas 1993).
 64. Postorbital part of the skull roof: as high as the orbital region (0); ventrally deflected in adult individuals (1). (Holtz 1994).
 65. Rostral process of postorbital: sharply upturned (0); at about the same level as or slightly higher than the squamosal process, resulting in a T-shaped postorbital (1). (Currie 1995).
 66. Rostral process of postorbital length: longer or subequal to caudal process (0); shorter than caudal process (1). (Ezcurra & Novas 2006).
 67. Rostral tip of rostral process of postorbital: rostrally tapering (0); rounded (1). (Ezcurra & Novas 2006).
 68. Large rough protuberance on laterodorsal surface of

- postorbital: absent (0); present (1). (Ezcurra & Novas 2006).
69. Postorbital participation in the supratemporal fossa: present (0); absent (1). (Sereno 1999).
 70. Infratemporal fenestra shape: strongly rostrocaudally compressed, which maximum length versus maximum length of the orbit ratio is less than 0.8 (0); rostrocaudally wide and subrectangular or oval-shaped, which maximum length versus maximum length of the orbit ratio is between 0.8 and 1.5 (1); strongly widened, resulting in a maximum length 1.5 times the maximum length of the orbit with a long jugal-quadratojugal bar (2). (Rauhut 2003; Ezcurra & Novas 2006; unordered).
 71. Ventral process of squamosal: tapering (0); broad, and usually somewhat expanded (1). (Rauhut 2003).
 72. Ventral process of the squamosal length: forms more than half of the caudal border of the infratemporal fenestra (0); less than half of the caudal border of the infratemporal fenestra (1). (Rauhut 2000; Langer 2004).
 73. Ventral ramus of the squamosal: wider than a quarter of its length (0); narrower than a quarter of its length (1). (Yates 2003).
 74. Squamosal-quadratojugal contact: present, but small contact between the bones (0); present, broad contact (1); absent (2). (Holtz 1994; Ezcurra & Novas 2006; unordered).
 75. Squamosal caudal process: short and not well caudally extended (0); strongly caudally extended and longer than the rostral process, sometimes exceeding the caudal level of the quadrate condyle in lateral view (1). (Ezcurra & Novas 2006).
 76. Dorsal ramus of the quadratojugal: longer than the rostral ramus (0); of the same length, or shorter, than the rostral ramus (1). (Sereno 1986; Langer 2003).
 77. Lateral exposure of quadrate head: hidden by squamosal (0); laterally exposed (1). (Sereno & Novas 1993).
 78. Caudal curvature of the proximal end of quadrate: absent or slight, proximal half of quadrate almost straight (0); present, with quadrate head caudodorsally oriented (1). (Ezcurra & Novas 2006).
 79. Quadratojugal and quadrate in adults: remain separate (0); fuse (1). (Holtz 1994, 2000).
 80. Quadrate foramen: developed as a distinct opening between the quadrate and quadratojugal (0); almost entirely enclosed in the quadrate (1); absent (2). (Holtz 1994; Rauhut 2003; unordered).
 81. Mandibular joint: approximately straight below the quadrate head (0); significantly caudal to the quadrate head (1). (Rauhut 2003).
 82. Shape of palatine in ventral view: plate-like trapezoidal or subrectangular (0); tetradriate (1). (Harris 1998).
 83. Pterygoid-ectopterygoid articular relation: ectopterygoid ventral (0); ectopterygoid dorsal (1). (Sereno & Novas 1993).
 84. Ectopterygoid flange of the pterygoid: flat (0); marked by fossa (1). (Gauthier & Padian 1985).
 85. Ectopterygoid: slender, without ventral fossa (0); expanded, with a deep ventral depression medially (1); as above, but with a deep groove excavated into the body of the ectopterygoid from the medial side (2). (Gauthier 1986; Sereno *et al.* 1996; Rauhut 2003; unordered).
 86. Basisphenoid between basal tubera and basiptyergoid processes: approximately as wide as long, or wider (0); significantly elongated, at least 1.5 times longer than wide (1). (Rauhut 2003).
 87. Transverse intertuberal lamina of basisphenoid: simple wall (0); bears small median spur that projects rostrally along roof of basisphenoideal recess (1). (Tykoski 2005).
 88. Basisphenoid recess: absent or poorly developed (0); deep, well developed (1). (Rauhut 2003).
 89. Basispterygoid processes: well developed, rostrocaudally short and finger-like (approximately as long as wide) (0); significantly elongated rostrocaudally (longer than wide) (1). (Sues 1997; Rauhut 2003; unordered).
 90. Rostral tympanic recess in the braincase: absent (0); present (1). (Makovicky & Sues 1998; Rauhut 2003).
 91. Exit of nerve V in lateral view: positioned at the level of the caudal half of the basisphenoid (0); positioned at the level of the rostral half of the basisphenoid (1). (Ezcurra & Novas 2006).
 92. Exit of nerves X and XI: laterally through the jugular foramen (0); caudally through a foramen lateral to the exit of the nerve XII and the occipital condyle (1). (Chatterjee 1993; Rauhut 2003).
 93. Exit of mid-cerebral vein: included in trigeminal foramen (0); vein exits braincase through a separate foramen anterodorsal to the trigeminal foramen (1). (Rauhut 2003).
 94. Temporal musculature: not extended (0); or extended cranially (1) onto skull roof. (Gauthier 1986).
 95. Caudally placed, knob-like dorsal projection of the parietals: absent (0); present (1). (Bonaparte 1991).
 96. Foramen between supraoccipital and parietal knob: present (0); absent (1). (Carrano *et al.* 2005).
 97. Size of posttemporal opening: fenestra (0); foramen (1). (Sereno & Novas 1993).
 98. Supraoccipital in caudal view: as vertical strap-shaped ridge (0); triangular-shaped by a proximally widen ridge (1). (Ezcurra & Novas 2006).
 99. Paraoccipital processes in caudal view: laterally or dorsolaterally directed (0); ventrolaterally directed (1); strongly ventrolaterally directed, with distal end entirely below the level of the occipital condyle (2). (Rauhut 1997, 2003; Ezcurra & Novas 2006; ordered).
 100. Ventral rim of the basis of the paroccipital processes: above or level with the dorsal border of the occipital condyle (0); situated at mid-height of occipital condyle or lower (1). (Rauhut 2003).
 101. Orientation of paroccipital processes to each other in ventral view: more than 110° (0); equal or less than 110° (1); equal or less than 80° (2). (Ezcurra & Novas 2006).
 102. Rostral end of dentary dorsoventrally expanded: absent (0); present (1). (Gauthier 1986).
 103. Medirolateral width of anterior end of dentary: equal to that of caudal part (0); expanded (1). (Carrano *et al.* 2005).
 104. Caudoverventral process of dentary: extends further caudally than caudodorsal process (0); subequal in length to caudodorsal process (1). (Sereno 1999).
 105. Enlarged mesial dentary teeth (fang-like): absent (0); present (1). (Gauthier 1986).
 106. Dentary tooth count: 18 or less (0); 20-29 (1); more than 29 (2). (Russell & Dong 1993; Ezcurra & Novas 2006; ordered).

107. First dentary tooth: placed at the rostral apex of the dentary (0); inset for the distance of one alveolus from the dentary tip (1). (Serenó 1999).
108. Intra-mandibular joint: absent (0); present (1). (Serenó & Novas 1993).
109. Foramen in the ventral part of the splenial: absent (0); present (1). (Rauhut 2003).
110. Caudal end of splenial: straight (0); forked (1). (Serenó *et al.* 1996).
111. External mandibular fenestra size in lateral view: large opening, representing its length between 10 and 20% of the total length of the jaw (0); strongly reduced opening, representing its length less than 10% the total length of the jaw (1); hypertrophied, representing its length less than 20% the total length of the jaw (2). (Gauthier 1986; Sampson *et al.* 1998; Ezcurra & Novas 2006; unordered).
112. Cranial end of the external mandibular fenestra: caudal to the last dentary tooth (0); ventral to the last dentary tooth (1). (Serenó 1999).
113. Coronoid process of the mandible: strongly convex and well dorsally positioned from the lips of the glenoid fossa (0); straight or slightly convex and at level with the lips of the glenoid fossa (1). (Ezcurra & Novas 2006).
114. Very strong dorsally development of the coronoid process of the mandible: absent (0); present (1). (Serenó 1986).
115. Angular reaches caudal end of mandible, blocking surangular from ventral margin of the jaw in lateral view: absent (0); present (1). (Tykoski 2005).
116. Retroarticular process of the mandible: narrow and rod-like (0); broad with muscle scar (1). (Serenó *et al.* 1996; Harris 1998; Rauhut 2003).
117. Attachment of the M. depressor mandibulae on retroarticular process of mandible: facing dorsally (0); facing caudodorsally (1). (Serenó *et al.* 1996).
118. Constriction between tooth crown and root: absent (0); present in all maxillary and dentary teeth (1). (Holtz 1994).
119. Lanceolate tooth crowns: absent (0); encompass all dental elements of maxilla and dentary (1). (Gauthier 1986; modified from Langer 2004; unordered).
120. Maxillary and dentary tooth crowns: curved caudally (0); not curved caudally (1). (Serenó 1986).
121. Paradental plates: obscured or moderate in height (0); very tall (1). (Carrano *et al.* 2002).
122. Length of the atlantal intercentrum: greater than that of the axial intercentrum (0); less than that of the axial intercentrum (1). (Yates 2003).
123. Axial intercentrum length: 25-40% of axial centrum length (0); 40-70% of axial centrum length (1). (Serenó 1999).
124. Caudal face of cranial presacrals: flat (0); concave (1). (Gauthier 1986; Carrano *et al.* 2002).
125. Cervical zygapophyses: close to midline (0); displaced laterally (1). (Makovicky 1997).
126. Axial pleurocoels: absent (0); present (1). (Rowe & Gauthier 1990; Ezcurra & Novas 2006).
127. Median ventral keels on the axis: present (0); absent (1). (Currie & Zhao 1993).
128. Axial parapophysis: well developed (0); strongly reduced or absent (1). (Rowe 1989).
129. Axial diapophysis: present (0); absent (1). (Rowe 1989).
130. Axial zygapophyses: prezygapophyses and postzygapophyses equidistant from the midline of the axis (0); postzygapophyses set wider than the prezygapophyses (1). (Gauthier 1986).
131. Axial neural spine: broad and blade-shaped (0); laterally invaginated and craniocaudally reduced and rod-like (1). (Molnar *et al.* 1990; Ezcurra & Novas 2006).
132. Axial neural spine caudal to prezygapophyses: absent (0); present (1). (Tykoski 2005; Ezcurra & Novas 2006).
133. Length of the centra of the postaxial cervical vertebrae vs. length of the axial centrum: cervicals 3-7 subequal to, or shorter than, the axial centrum (0); cervicals 3-7 longer than the axial centrum (1); all postaxial cervicals longer than the axial centrum (2). (Gauthier 1986; modified from Yates 2003 and Langer 2004).
134. Postaxial cervical centra pneumatization: not pneumatized (0); pneumatized by a single pair of fossae, that not pierce the centra (1); pneumatized by two pair of fossae, that not pierce the centra (2); pneumatized by two pair of foramina, that pierce the centra (3); pneumatized by a single pair of foramina, that pierce the centra (4). (Gauthier 1986; Ezcurra & Novas 2006; ordered).
135. Interior pneumatic spaces in cervicals: absent (0); present, structure camerate (1); present, structure camellate (2). (Britt 1993; unordered).
136. Postaxial cervical neural arches: solid (0); house pneumatic cavities lateral to neural canal (1). (Tykoski 1998, 2005).
137. Postaxial cervicals neural spines: dorsoventrally high (0); dorsoventrally low (1). (Russell & Dong 1993; Carrano *et al.* 2002).
138. Hyposphene-hypantrum intervertebral articulation in dorsal vertebrae: absent (0); present (1). (Gauthier 1986).
139. Presacral dorsal neural arches: not laminated (0); impressed with deep semi-conical fossae separated by thin laminae (1). (Yates 2003).
140. Cranial face of cervical and cranial dorsals: amphiplatyan or amphicoelous (0); slightly convex (1); strongly convex, having ball-like articulation (2). (Gauthier 1986; ordered).
141. Cranial articular facet of cranial cervical vertebrae: approximately as high as wide or higher (0); wider than high (1). (Gauthier 1986; Rauhut 2003).
142. Mid-cervical (C3-C6) centrum proportions: equal or less than 3 times the height of the cranial articular surface (0); between 3 and 4 times the height of the cranial articular surface (1); more than 4 times the height of the cranial articular surface (2). (Serenó 1999).
143. Cranial cervical epiphyses: absent or poorly developed (0); long, thin and not well developed (1); long and well developed, overhanging the postzygapophyses (2); craniocaudally lengthened and extremely developed, strongly overhanging the postzygapophyses (3). (Novas 1993; Rauhut 2003; Ezcurra & Novas 2006; ordered).
144. Centrum shape in presacrals 6-9 (or 10): subrectangular (0); parallelogram-shaped (1). (Bonaparte 1975).
145. Shape of the transverse processes of caudal cervical and dorsal vertebrae in dorsal view: subrectangular (0); subtriangular (1). (Rowe & Gauthier 1990).
146. Transverse processes of the dorsal vertebrae:

- craniocaudally narrow (0); broad, extending to lateral margin of the prezygapophyses (1). (Rowe & Gauthier 1990).
147. Cranial and mid-dorsal centrum length: subequal to centrum height (0); more than 2 times centrum height (1). (Serenó 1999; Ezcurra & Novas 2006).
 148. Caudal dorsal vertebrae: strongly shortened, centrum length less than 1.33 times the height of the cranial articular surface (0); relatively short, centrum length equal or more than 1.33 times the height of the cranial articular surface (1); significantly elongated, centrum length equal or more than 2 times the height of the cranial articular surface (2). (Rauhut 2003; Tykoski 2005; ordered).
 149. Neural spines of caudal dorsals: broadly rectangular and approximately as high as long (0); high rectangular, significantly higher than long (1). (Rauhut 2003)
 150. Number of sacral vertebrae: two (0); three (1); four or five (2); more than five (3). (Gauthier 1986; Rauhut 2003; ordered).
 151. Fusion of sacrum (centra, transverse processes, ribs) and pelvic girdle elements: do not fuse, or they remain distinct from one another (0); fuse to one another, obliterating all sutures in adults (1). (Rowe & Gauthier 1990).
 152. Sacral ribs: slender and well separated (0); very massive and strongly expanded (1); forming a more or less continuous sheet in ventral or dorsal view (2). (Rowe & Gauthier 1990; Rauhut 2003; Ezcurra & Novas 2006; ordered).
 153. Sacral rib depth relative to iliac blade height: equal or more than 90% (0); less than 85% (1). (Novas 1992a).
 154. Ribs of the two sacrals in relation to the iliac pre- and postacetabular processes: cover the entire medial surface (0); are shorter (1). (Langer 2004).
 155. Ventral surface of cranial caudal vertebrae: smooth or weakly grooved longitudinally (0); at least some caudal vertebrae with narrow, sharply defined, longitudinal, ventral groove (1). (Rowe & Gauthier 1990).
 156. Distal caudal centrum length: less than four times centrum height (0); more than four times centrum height (1). (Serenó 1999; Ezcurra & Novas 2006).
 157. Prezygapophyses of distal caudal vertebrae: not elongated (0); strongly elongated, overhanging at least one-quarter of the length of the preceding centrum (1). (Gauthier 1986; Rauhut 2003).
 158. Cervical ribs: stout, and less than three centra long (0); very thin, and extended caudally more than three times centrum length (1); very thin, and extended caudally more than four times centrum length (2). (Holtz 1994; Tykoski 2005; ordered).
 159. Cranial process at base of chevrons: absent (0); present (1). (Molnar *et al.* 1990; Carrano *et al.* 2002; Rauhut 2003).
 160. Distal expansion of scapular blade: marked as a fan-shaped expansion (0); slightly expanded, narrow with subparallel margins or strap-like (1). (Currie & Zhao 1993).
 161. Shape of craniodorsal corner of distal scapular blade: rounded (0); acuminate (1). (Carrano *et al.* 2005).
 162. Cranial margin of scapulocoracoid at scapula-coracoid contact in adults: notched (0); continuous and uninterrupted (1). (Holtz 2000).
 163. Spacing between ventral glenoid and caudoventral coracoid process (= sternal process): more than dorsoventral depth of glenoid (0); less than dorsoventral depth of glenoid (1). (Carrano *et al.* 2005).
 164. Caudoventral process (= sternal process) of the coracoid: rounded and not projected beyond glenoid fossa (0); tapering and projected little beyond the caudal margin of the glenoid fossa (1); tapering and strongly caudally projected well beyond the caudal margin of the glenoid fossa. (modified from Sereno *et al.* 1996).
 165. Humerus: sigmoid in lateral view (0); straight in lateral view (1). (Holtz 1994).
 166. Humeral shaft torsion of proximal and distal ends: absent (0); present (1). (Holtz 2000).
 167. Humerus length: longer than 0.6 of the length of the femur (0); subequal or shorter than 0.6 of the length of the femur (1). (Novas 1993; Langer 2004).
 168. Humeral distal width accounts: for less than, about 0.3 of the total length of the bone (0); more than 0.3 of the total length of the bone (1). (Langer 2004).
 169. Deltopectoral crest: positioned within the proximal 30% of the humerus (0); proximodistally elongate, more than 34% of humeral length (1). (Novas 1996).
 170. Distal carpal 5: present (0); absent (1). (Serenó 1999).
 171. Large distal carpal, capping Mc I and parts of Mc II: absent (0); present (1); present, showing the shape and morphology of a semilunate carpal in proximal view, but rectangular rather than semilunate in palmar view (2). (Gauthier 1986; Rauhut 2003; ordered).
 172. Manual length (measured as the average length of digits I-III): accounts for less than 0.3 of the total length of humerus plus the radius (0), more than 0.3 but less than 0.4 of the total length of humerus plus the radius (1); or more than 0.4 of the total length of humerus plus the radius (2). (Gauthier 1986; Langer 2004; unordered).
 173. Extensor pits on the dorsal surface of the distal end of metacarpals: absent or poorly developed (0); deep, well developed (1). (Serenó *et al.* 1993).
 174. Strongly developed dorsal lip proximal to the extensor pit on the distal end of the metacarpals II and III: absent (0); present (1).
 175. Contact between metacarpal I and metacarpal II: metacarpals contact each other at their bases only (0); metacarpal I closely appressed to proximal half of metacarpal II (1). (Gauthier 1986).
 176. Width of metacarpal I at the middle of the shaft: accounts for less or 0.3 of the total length of the bone (0); between 0.3 and 0.45 of the total length of the bone (1); more than 0.45 of the total length of the bone (2). (Bakker & Galton 1974, modified from Langer 2004).
 177. Distal end of metacarpal I: condyles more or less symmetrical (0); condyles strongly asymmetrical, the medial condyle being positioned more proximally than the lateral (1). (Gauthier 1986; Yates 2003; Rauhut 2003).
 178. Metacarpal I shorter than the phalanx I-1: absent (0); present (1). (modified from Rauhut 2003).
 179. First phalanx of manual digit I: is not the longest non-ungual phalanx of the manus (0); is the longest non-ungual phalanx of the manus (1). (Gauthier 1986, modified).
 180. Twisted first phalanx in digit I: absent (0); present (1). (Benton *et al.* 2000).

181. Metacarpal II in relation to metacarpal III: shorter (0); subequal or longer (1). (Gauthier 1986).
182. Medial side of metacarpal II: expanded proximally (0); not expanded (1). (Rauhut 2003).
183. Width of the distal end of the metacarpal II: smaller or subequal to the distal end of the metacarpal III (0); larger than the distal end of the metacarpal III (1).
184. Manual digit II longer than digit III: absent (0); present (1). (Gauthier 1986).
185. Manual digits II-III: with short penultimate phalanx (0); with long penultimate phalanx (1). (Gauthier 1986; modified from Sereno *et al.* 1993).
186. Unguals of manual digits II and III: poorly curved (0); trenchant, i.e. strongly curved (1). (Gauthier 1986).
187. Ungual phalanx of digit II: the longest of the manus (0); equal in length to the ungual of digit I (1). (Gauthier 1986; Yates 2003).
188. Shaft of Mc III: subequal in width to Mc II (0); considerably more slender than Mc II (less than 70% of the width of Mc II) (1). (Rauhut 2003).
189. Proximal articular end of metacarpal III: expanded and similar in width to metacarpal II (0); not expanded, very slender when compared to metacarpal II (1). (Gauthier 1986; Rauhut 2003).
190. Shaft of metacarpal IV in relation to that of metacarpals I-III: about the same width (0), significantly narrower (1). (Sereno *et al.* 1993; Langer 2004).
191. Metacarpal IV and fourth digit: proximal portion set lateral to Mc III (proximal portion of Mc V also set lateral to Mc IV if it is present) and with more than one phalanx (0); proximal portion set lateral to Mc III (idem Mc V) and with only one or lacking phalanges (1); proximal portion at the palmar surface of Mc III (idem Mc V) and with only one or lacking phalanges (2); absent (3). (Gauthier 1986, modified from Ezcurra & Novas 2006; ordered).
192. Metacarpal V: with phalanges (0); vestigial and lacking phalanges (1); absent (2). (Gauthier 1986; ordered).
193. Dorsal margin of the iliac blade: concave (0); straight or gently convex (1).
194. Preacetabular process of ilium: stout and thick (0); relatively thin and blade-like (1). (Tykoski 2005).
195. Ventral margin of the preacetabular processes of the ilium: over the level of the supraacetabular crest (0); at level or below the level of the supraacetabular crest (1).
196. Ventral rim of preacetabular process of the ilium: horizontal (0); with a pronounced ventral hook on cranial expansion of ilium (1). (Gauthier 1986; Rauhut 2003; Tykoski 2005).
197. Acetabular wall: imperforate (0); perforate (1). (Bakker & Galton 1974; Novas 1996).
198. Iliac preacetabular process length: to edge of cranial-most pubic peduncle (0); far past cranial-most pubic peduncle (1). (Gauthier 1986; Carrano 2000).
199. Iliac postacetabular process length versus acetabular length: less or equal to 1 (0); greater than 1 (1). (Forster 1999, modified from Carrano *et al.* 2002).
200. Lateral surface of caudal end of ilium: smooth (0); distinct caudal rim on ilium for *M. iliofemoralis* (1). (Rowe & Gauthier 1990).
201. Caudal margin of postacetabular process of ilium in lateral view: rounded (0); squared-shaped (1); concave (2). (Sereno *et al.* 1994; Yates 2003).
202. Supraacetabular crest of ilium: present as a weakly developed ridge (0); present as a well developed raised shelf (0); flares lateroventrally to form a hood-like overhang that hides craniodorsal half of acetabulum in lateral view (1). (Langer 2004; Tykoski 2005).
203. Supraacetabular crest and latroventral border of the postacetabular process (lateral brevis shelf) continuity: absent (0); continuous as a weakly developed ridge (1); continuous as a well developed ridge, with non-distinct separation between both structures (2). (Ezcurra & Novas 2006; ordered).
204. Supraacetabular crest of the ilium: is at its widest halfway between the pubic and ischial contacts (0); is widest above the base of the pubic peduncle (1). (Yates 2003).
205. Brevis shelf: absent (0); present (1). (Gauthier 1986).
206. Brevis fossa: absent (0); narrow with subparallel margins or slightly expanded (1); strongly caudally expanded (2). (Molnar *et al.* 1990; Novas 1993; Rauhut 2003; Ezcurra & Novas 2006).
207. Pubic peduncle of the ilium size: equal to ischial peduncle (0); much greater than ischial peduncle (1). (Sereno *et al.* 1994).
208. Pubic peduncle of the ilium: longer than half the space between the preacetabular and postacetabular embayments of the bone (0); subequal to half the space between the preacetabular and postacetabular embayments of the bone (1) (Galton 1976; Langer 2004).
209. Pubic peduncle of the ilium: less than twice the length of its distal articular surface (0); greater than twice the length of its distal articular surface (1). (Sereno 1999).
210. Articulation facet of pubic peduncle of ilium: facing more ventrally than cranially, and without pronounced kink (0); with pronounced kink and cranial part facing almost entirely cranially (1). (Rauhut 2003).
211. Ischial peduncle of the ilium: mainly vertical (0); well expanded caudally to the cranial margin of the postacetabular embayment (1). (Langer 2004).
212. Pubis length: less than 50% (0); or more than 70% of femoral length (1). (Novas 1996).
213. Ischio-acetabular groove on the proximal articular surface of the pubis: absent (0); present (1).
214. Proximal end of the pubis with acetabular depression: well developed (0); very poorly developed or absent (1).
215. Pubic plate: solid below obturator foramen (0); perforated by a large circular pubic fenestra below the obturator foramen (1); with obturator foramen open ventrally (2); without obturator foramen (3). (Rowe & Gauthier 1990; Holtz 1994; Rauhut 2003; Ezcurra & Novas 2006; unordered).
216. Pubis between proximal end and shaft: straight or gently caudally bowed (0); sharply caudally deflected (1).
217. Pubic shaft: caudally bowed (0); nearly straight (1). (Sereno 1999; Ezcurra & Novas 2006).
218. Mediollateral width of pubic midshaft: equal or more than 20% of pubic blade length (0); less than 20% of pubic blade length (1). (Tykoski 2005; Ezcurra & Novas 2006).
219. Distal expansion of the pubis: non-expanded or slightly

- craniocaudally expanded (0); strongly craniocaudally expanded, resulting in a pubic boot (1). (Gauthier 1986; Sereno 1999; Ezcurra & Novas 2006).
220. Distal tip of pubis in distal view: elongate rectangular or subequant (0); subtriangular (1). (Rauhut 2003, Tykoski 2005).
221. Pubic apron: completely closed (0); with medial opening distally above the pubic foot (1). (Rauhut 1995, 2003).
222. Ischium length: at least three-quarters the length of pubis (0); two-thirds or less the length of the pubis (1). (Gauthier 1986).
223. Ischial antitrochanter: large, extending along all the ilium-ischial contact (0); reduced, excluded from the caudal portion of the ilium-ischial contact (1); craniolaterally prominent into acetabulum, giving "notched" profile to caudoventral margin of acetabulum (2). (Rowe & Gauthier 1990, modified from Sereno 1999).
224. Ischial obturator process: proximodistally extended (0); proximodistally short, restricted to the proximal third of the bone (1). (Novas 1996).
225. Ventral notch between obturator process or flange on ischium: absent (0); present (1). (Sereno *et al.* 1996; Rauhut 2003).
226. Cross-sectional shape of paired ischial midshafts: heart-shaped (0); oval (1); rectangular (2). (Sereno 1999; unordered).
227. Distal end of ischium: unexpanded (0); slightly expanded, with its craniocaudal length equal or less than 3 times the minimum craniocaudal width of ischial shaft (1); strongly expanded (2). (Novas 1993; Rauhut 2003; Tykoski 2005).
228. Distal outline of the ischium: roughly semicircular (0); subtriangular (1). (Sereno 1999).
229. Femoral dimorphism: absent (0); present, expressed in muscle scars, attachments, and processes (robust versus gracile morphs) (1). (Rowe & Gauthier 1990).
230. Femur: longer than the tibia (0); subequal to the tibia (1); shorter than the tibia (2). (Galton 1976).
231. Femoral head: weakly developed and slightly inturned, oriented at more than 120° from the main axis of the femoral shaft (0); strongly inturned, being oriented at less than 120° from the main axis of the femoral head, and distinctively separated from the shaft by a well developed femoral neck (1). (Modified from Paul 2002).
232. Femoral shape in proximal view: wedged or oval in contour (0); femoral head craniomedially oriented, with a proximal articular surface subtriangular in contour (1).
233. Proximal surface of femur: smooth (0); with a transversely extended groove (1).
234. Tuberosity that laterally bounds the ligament of the femoral head: prominent (0); reduced (1). (Novas 1996).
235. Fossa trochanterica on femoral head: absent (0); present (1). (Novas 1996).
236. Oblique ligament groove on caudal surface of femoral head: absent or very shallow (0); deep, bound medially by a well developed caudal lip (1). (Rauhut 2003).
237. Femoral greater trochanter, shape: rounded (0); angular (1). (Sereno 1999).
238. Cranial trochanter: absent (0); present as a low ridge (1); present, spike-like or pyramidal prominence (2); present, mediolaterally compressed flange ("wing like") projecting cranially from the femur, and placed at the distal end of the femoral head (3); present, mediolaterally compressed flange ("wing like") projecting cranially from the femur, and more proximally placed than the distal end of the femoral head level, but below the greater trochanter (4). (Gauthier 1986; Rauhut 2003; Tykoski 2005; ordered).
239. Femoral trochanteric shelf: absent (0); present (robust individuals regarding to coelophysoid theropods) (1). (Gauthier 1986).
240. Fourth trochanter: symmetrical with the distal and proximal margins forming similar low angles to the shaft (0); asymmetrical with the distal margin forming a steeper angle to the shaft (1). (Langer 2004).
241. Crest on the craniomedial surface of the distal end of the femur: absent (0); proximal to condyles, blend smoothly together (1); a hypertrophied craniomedial crest on the distal femur separates cranial and medial surfaces of femur (2). (Holtz 1994; ordered).
242. Large, subelliptical, craniomedially placed depression for origin of *Mm. femorotibialis* on distal femur: absent (0); present (1). (Novas 1993).
243. Cranial intercondylar groove (broad groove on cranial surface of distal femur): absent (0); poorly developed (1); strongly developed, separating both lateral and medial distal condyles (2). (Rauhut 2003; Ezcurra & Novas 2006).
244. Tibiofibular crest of distal femur: smoothly continuous with fibular condyle (0); sharply demarcated from fibular condyle by a sulcus or concavity (1). (Rowe 1989).
245. Femoral popliteal fossa in adults: smooth (0); transversed by infrapopliteal ridge between tibial condyle and tibiofibular crest (1). (Tykoski 1998).
246. Cnemial crest on proximal tibia: absent (0); low (1); moderately developed (2); hypertrophied (3). (Novas 1996; Rauhut 2005).
247. Lateral surface of cnemial crest of the tibia: flat or slightly concave (0); laterally excavated by deep longitudinal fossa, giving tibia laterally hooked profile in proximal view (1). (Sampson *et al.* 1998; Ezcurra & Novas 2006).
248. End of cnemial crest: rounded (0); proximodistally expanded (1). (Forster 1999).
249. Fibular condyle on proximal end of tibia: confluent with cnemial crest cranially in proximal view (0); strongly offset from cnemial crest (1). (Rauhut 2003).
250. Caudal cleft between medial part of the proximal end of the tibia and fibular condyle: absent (0); present (1). (Rauhut 2003).
251. Ridge on lateral side of tibia for connection with fibula: absent (0); present, extending from the proximal articular surface distally (1); present, clearly separated from proximal articular surface (2). (Gauthier 1986; Rauhut 2003; ordered).
252. Lateral extension of the lateral malleolus in the distal tibia: poor (0); moderate (1); strongly extended, caudally overlapping the distal end of fibula and calcaneum (2). (Sereno *et al.* 1994; Ezcurra & Novas 2006).
253. Distal tibial lateral malleolus: lobe-shaped (0); polygonal-shaped (1). (Sereno 1999).
254. Distal articular surface of tibia: subrectangular in outline and only slightly wider transversely than rostrocaudally

- (0); subrectangular with small lateral process (1); narrow triangular in outline and strongly mediolaterally expanded (2). (Rauhut 2003; ordered).
255. Facet for the reception of the ascending process of the astragalus in the distal tibia: craniocaudally as well as transversely well developed (0); subtriangular, not well developed cranially (1); subrectangular, cranially poorly developed (2); nearly absent (3). (Ezcurra & Novas 2006; ordered).
256. Facet for the reception of the ascending process of the astragalus in the distal tibia in cranial view: almost horizontal and ventrally facing (0); oblique (proximolateral to distomedial) and craniolaterally facing (1). (Molnar *et al.* 1996; Tykoski 2005; Ezcurra & Novas 2006).
257. Craniomedial corner of the distal tibia: forms a rounded low or right angle (0); forms an acute angle (1). (Langer 2004).
258. Caudolateral corner of the distal tibia: convex (0); concave (1). (Ezcurra & Novas 2005).
259. Caudomedial notch in the distal tibia (with respective bump in the proximal astragalus): absent (0); present (1). (Langer 2004).
260. Ridge on medial side of proximal end of fibula, that runs craniodistally from the caudoproximal end: absent (0); present (1). (Rowe & Gauthier 1990).
261. Medial surface of proximal fibula: flat or slightly concave (0); caudodistally opening sulcus on medial surface of the proximal fibula (1). (Rowe & Gauthier 1990).
262. Craniocaudal width at fibular mid-shaft: equal or more than 30% of the width the proximal end (0); less than 30% of the width of the proximal end (1). (Serenio 1999; Ezcurra & Novas 2006).
263. Fibular M. iliofibularis insertion: weak or indiscernible (0); as distinct tubercle (1); large craniolaterally projecting tubercle or process (2). (Mader & Bradley 1989; Rauhut 2000; Carrano *et al.* 2002; Tykoski 2005; ordered).
264. Tibia and fibula fused to astragalocalcaneum: remain separate elements throughout ontogeny (0); fuse to each other by later stages of ontogeny, forming a functional tibiotarsus (1). (Welles & Long 1974; Rowe & Gauthier 1990).
265. Tibial-astragalur articulation: tibia articulates with proximal astragalur surface medial to the ascending process (0); tibia overlaps cranioproximally and caudally the ascending process of the astragalur, and consequent ventral projection of the caudal process of the tibia (1). (Novas 1989).
266. Astragalur fused to calcaneum in adults: absent (0); present (1). (Welles & Long 1974).
267. Ascending process of astragalur: lower than astragalur body (0); equal or higher than the astragalur body (1). (Welles & Long 1974).
268. Astragalur ascending process thickness: transversely narrow and craniocaudally extended ridge (0); pyramidal-shaped, dorsal margin inserting into tibia (1); low plate, 2-5 times taller than thick craniocaudally at midpoint (2); tall plate, more than 5 times taller than thick at midpoint (3). (Gauthier 1986; Novas 1989; Serenio *et al.* 2004; Ezcurra & Novas 2006; ordered).
269. Deep fossa on the craniolateral surface of the ascending process of the astragalur: absent (0); present (1). (Ezcurra & Novas 2006).
270. Horizontal shelf cranial to ascending process of astragalur: absent (0); present (1). (Langer 2004; Remes & Rauhut 2005).
271. Horizontal groove across the cranial surface of the tibial condyle of the astragalur: absent (0); present (1). (Welles & Long 1974).
272. Tibial facet of calcaneum: absent (0); small on the caudomedial-most corner of the bone (1); large, reaching the lateral margin of the bone (2). (Rauhut 2003; Ezcurra & Novas 2006; ordered).
273. Fibular articulation surface of calcaneum: convex (0); flat or concave (1). (Novas 1989).
274. Calcaneum: proximodistally compressed with marked calcaneal tuber and medial projections (0); transversely compressed with reduced calcaneal tuber and medial projections (1). (Novas 1989; Langer 2004).
275. Distal tarsal III: remain a separate element throughout life (0); fuses to the proximal end of metatarsal III (1). (Rowe & Gauthier 1990).
276. Distal tarsal 4: proximodistally deep and trapezoidal shaped in proximal view (0); depressed and triangle shaped in proximal view (1). (Novas 1996).
277. Caudomedial prong of the lateral distal tarsal: blunt (0), pointed (1). (Novas 1993; Langer 2004).
278. Metatarsal I: contacts the ankle joint (0); reduced, elongated splint-like, attached to Mt II and not reaching the ankle joint (1); broadly triangular and attached to the distal part of Mt II (2). (Gauthier 1986; Rauhut 2003; ordered).
279. Metatarsal I length: equal or more than 50% of the length of metatarsal II (0); less than 50% of the length of metatarsal II (1). (Gauthier 1986).
280. Metatarsals II and III: are separate (0); fusion of proximal ends of metatarsals II and III to each other (1). (Rowe & Gauthier 1990).
281. Proximal end of metatarsal III position: does not back to the ventral side of metatarsals II and IV (0); backs metatarsals II and IV ventrally, resulting in a T-shaped proximal profile ("antarcotometatarsus") (1). (Carrano *et al.* 2002; Tykoski 2005).
282. Metatarsal IV in cranial view: straight (0); sigmoidally curved (1). (Novas 1996).
283. Proximal metatarsal IV possesses an elongated lateral expansion that overlaps the cranial surface of metatarsal V: absent (0); present (1). (Serenio 1999; Langer 2004).
284. Metatarsal V: with rounded distal articular facet (0); strongly reduced and lacking distal articular facet (1); short, without articular surface, transversely flattened and bowed cranially distally (2); absent (3). (Gauthier 1986; Rauhut 2003; ordered).
285. Metatarsal V length: more than 50% metatarsal IV length (0); less than 50% metatarsal IV length (1). (Gauthier 1986; Harris 1998).
286. Transverse width of the proximal face of metatarsal V: less than 30% of its depth, from the extensor to flexor surfaces (0); greater than 30% of its depth (1). (Serenio 1999; Yates 2003).
287. Pedal digit V: presents phalanges (0); lacks phalanges (1). (Galton 1976, reversed from Langer 2004).

APPENDIX 2

Taxon-character state matrix used in the current phylogenetic analysis (see Appendix 1 for codings). The characters are coded with 0 for the plesiomorphic state; 1, 2, 3, etc, for the apomorphic state; and ? for non-preserved, unknown, or indetermined characters in a taxon.

Lagerpeton chanarensis

????? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????
 ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
 ????? ?2110 ?200? ????? ????? ????? ????? ????? ????? ????? ?2000 00000 00010 0????
 0000? 00000 00000 00??2 00000 00000 0?0?? 0??20 00000 0011? ?2200 10000 00101 00?10
 00011 11

Marasuchus lilloensis

????? ???? ???? ???? ???? ?1?? ?2?? ?0?? ???? ???? ???? ???? ???? ????
 ????? ????? ????? ????? 10?? ???? ???? ???? ???? ?2000 ?0?? 0?000 0010? 00000
 ?001? 0[01]?? 000?? 10?00 0?000 ?000? ????? ?????? ?????? ?2000 00000 00000 01000
 0000? 0000? 00100 00?02 00001 00110 0?0?? 10000 000?? ?2?? ?0?00 00000 00000 00000
 00010 11

Pseudolagosuchus major

????? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????
 ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
 ????? ?2?? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????
 ?1?? ?2?? ???? ???? ?2?? 0?001 0111? 0?0?? 1?0?? ?0000 0000? ?2?00 00100 0000? ????
 ?1?? ??

Eucoelophysis baldwini

????? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????
 ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
 ????? ?0?? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????
 ?211? 01?? ???? ???? 01111 01200 0?0?? 10000 0???? ???? ???? ???? ???? ????
 ?1?? ??

Silesaurus opolensis

????? 00?0? 00?00 00010 10010 0?000 ?[01]000 ????? 00?0? ????? ?0?? ?0?00 ????? ????
 ????? ?2000 0??1? 00000 0???? ?2000 000?0 01?? ?0000 ??100 00000 000?0 00[12]0? 00000
 00000 00110 000?? 00100 0?111 1000? ????? ?????? ?????? ?????? ?2000 00000 00011 1010?
 01000 0000? 01110 00?00 01111 01210 00000 21000 21000 0000? ?0001 0010? ?0100 ?????
 01010 11

Lesothosaurus diagnosticus

00111 10000 00210 00011 00?00 00010 02100 00000 00000 00000 00000 00000 00101 10000
 00000 01100 10100 00000 10010 01000 00000 01001 10000 00101 0??00 00110 00?00 0?000
 ?00?0 00102 0?0?0 ?2??0 ?2??0 0001? ?2000 00000 100?0 0?000 ?01?0 011?0 00001 ?0110
 01?10 11100 ?2110 0?0? 10111 01401 00000 10000 01023 0??1? ?00?? ????? ????0 10000
 0103? ??

Scutellosaurus lawleri

??12 00?? 000?? ????? ????? ????? ????? ????? ?2?? ?2?? ?2?? ?2?? ?2?? ?2?? ?2??
 ????? ????? ????? ????? ????? ????? ?0?? 0???? ?2?? ?2101 0??0? ????? ?2?00 0?000
 ????? 10?? 0??0 000?0 0?000 0001? ?200? ????? ?0?20 ?200? 0??2? 0?1?? ????? ?2?00
 ?1010 1?000 ?21?0 ?000? 1?1? 01401 00000 1?000 01023 0??1? ?0001 00110 00?10 ?????
 0?03? ??

Heterodontosaurus tucki

00111 010?0 00?1? 00001 00?00 00010 00100 00000 00000 00000 00000 00000 00110 11001
 00010 01101 0???? ????? ?2?10 ?1200 ?1?11 010?? 10010 ?2101 ????? 00100 10000 00000
 ?0010 00103 00?1? 00?00 0?000 00010 02000 00??0 110?0 01000 00100 01110 00000 101?0
 01010 11?0? ?0110 00?02 1?1? 0?401 00000 1000? 01?23 01?? ?1001 0???? ?21?0 ?0000
 ?113? ??

Saturnalia tupiniquim

?1?? ???? ???? ???? ???? ???? ???? ???? ???? ?21?? ????? ????? ???? ???? ????
 0?1?? ????? ????? ????? ????? ????? ?0?00 00?? ?0?? ?2111 ????? ?0?? ?2200 ?211?
 ????? ?2?? 00?0? ?0?00 0?2?0 ?011? ????? ?????? ?????? ?????? ?2?00 00?10 ?1001 10000
 01110 11001 00110 ?11?1 10111 01111 00000 10000 01000 00100 00101 00101 00100 11000
 01100 01

Thecodontosaurus

01110 01002 00000 10001 10?[01][01] 10000 00000 00001 0??01 11100 00000 00?00 00110
 00000 00100 01000 0?101 00000 0??10 ??010 [01]0000 010?? 00000 ?0111 00?00 01101 00200
 01110 ?[01]110 00??? 00010 00000 01100 0011? 11000 11111 ??110 10000 01[01]00 01[01]00
 11011 10010 1???? ??001 ?0110 ?111? 1???? 0?101 00001 10000 01000 0??00 00001 00101
 001?0 ??000 01000 11

Plateosaurus

01001 01001 00000 11001 10011 20010 00000 00000 12100 01100 00000 00000 00110 00000
 00100 01001 10100 00000 00110 ?1000 10?10 11011 00000 00111 00000 01101 00200 01110
 0[01]10[01] 00001 00010 ?0000 01000 00111 ?1000 11111 10110 01000 00100 01000 11011
 11010 11110 0100? 00110 ?1100 1??1[01] 01101 00100 10000 01001 01000 00001 00101 00100
 11000 01100 11

Herrerasaurus ischigualastensis

10020 01000 00000 10001 1??00 00000 00000 00000 00000 01100 00123 00000 00110 10000
 11000 11001 1011? 00000 ???10 01010 00010 001?? 20001 00000 01000 00001 01100 00110
 00100 00010 01000 01??1 0?020 01011 02100 00111 01001 11001 21100 01000 01001 00000
 01000 11010 00100 10100 10011 01111 01000 10000 00000 00000 00101 00101 00100 11000
 01100 00

Staurikosaurus pricei

????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
 ????? ????? ????? ????? ????? ?00?? ??1?? 0?101 00000 ????? ?????? ?0100 01000
 ?0100 00011 0?00? 11??0 0???? ?????? ?????? ?????? ?????? ?????? ?0100 01000 01001 01000
 01??0 01010 00110 ?0??2 10111 01010 0?000 10000 00000 00000 ?0?0? ?????? ?????? ??????
 ????? ??

Eoraptor lunensis

00101 11002 01000 10200 1??11 10010 11010 00000 00101 11100 10111 01000 00110 ?0?0?
 01?00 0?101 0?1?? ?0??? ???10 0???? ??00? ??0?? 00?00 ??000 ????0 0???? ????0 0?100
 ?0110 00101 0?000 ????0 ?1?0? 110?? ?2100 11111 00000 01001 11110 01000 12101 10000
 ?1011 ??000 00110 ?10?1 10111 ?1101 ?000? 20001 0???? ?0?0? 0??01 01100 0?1?? ??000
 01??? ??

Liliensternus liliensterni

????? ?????? ?????? ????0 ?????? ?????? ??111 ?????? ?????? ?????? ?????? 0???? ?????? ?????[12]
 1?0?? ?10?1 ?????? ?????? ?????? ??1?1 10??0 ?0??0 ??000 0?000 0???? ?????? ?1110
 0111? 101?? ?01?1 11??0 ??100 1101? ??11? ?????? ?01?? 0???? ??111 01110 12101 10101
 ?101? 01101 0121? 110?1 10011 112?0 10[02]0? 210[01]1 11111 10110 111?1 10111 0011?
 ????? 111?? ??

Coelophysis bauri

10112 [01]0002 11111 00210 01?00 01011 [01]1111 10010 10101 11101 10111 01100 10110
 00010 01021 0111? 0?1?? ??10? ????1 11??0 11011 101?? 00000 00000 ?1010 0?111 00221
 11110 02110 11202 12111 10210 11120 11011 12110 11111 10111 01101 22111 01111 12201
 20101 11010 00101 01211 11012 10111 11210 1?0[01][01] 21001 11111 10111 11111 10111
 00111 10111 11111 ?1

Coelophysis rhodesiensis

10112 10002 11111 00210 11000 11011 11111 10010 10101 11101 101?0 01100 10100 00010
 01021 0111? 01111 11101 00011 ?1110 11?11 10110 00000 00000 0???? 0011? 00?21 ?1110
 ????1 11202 12111 112?0 1?010 11011 12110 11111 10111 01111 22111 01111 22201 20101
 11011 0010? 01211 21011 10111 11210 1101? 21001 11111 10111 11111 10111 01111 ??111
 11111 ?1

Syntarsus kayentakatae

10[01]12 111?2 11111 00210 01000 10011 12111 01010 10101 11101 20112 10110 10111 00000
 11001 01110 1???? ?11?? 10?11 ?1110 ?1001 101?? 00001 ??000 ?????? 0?11? 0022? 11110
 ?21?1 ????? 1???1 ??2?0 1?11? ????1 ?????? ?????? ?????? 0???1 2???1 ?1?11 ?2201 ?010?
 ?101? 00100 01211 21??2 10011 11210 21011 2100? 11?22 11111 1??11 10111 01111 101?1
 1?12? ?1

Dilophosaurus wetherilli

10?12 201?? 11?11 00102 01100 00010 02001 0101[12] 0?1?? 11?0[01] ??023 0000? 111?1 11??1
 11020 110?1 1???? 00101 111?? 1??10 11101 001?0 10101 01000 01010 00111 00[12][23]1
 01110 1021? 10112 ?0111 11?10 0?010 11011 121?0 11101 10011 01101 22111 01110 22101
 10101 11010 01101 1??11 12?11 10011 112?0 10110 20001 11011 10110 101?1 ?1111 1011?
 ??11? 01121 01

Carnotaurus sastrei

00120 20001 00200 11000 0??00 12000 00000 01000 02100 11?00 0[01]023 00011 11101 01001
 110[02]0 11112 1???0 0???? ????11 11111 10000 00110 21100 ??000 ?0011 10001 0003? 11111
 103[01]0 00013 12110 ????11 01021 0101? ?????? 2???0 100?? ????0? 22111 11110 22201 11???
 11010 01111 1?211 12??? 1???? 01300 21111 31101 1???? ?????? ?????? ?????? ??????
 ????? ??

Ceratosaurus

00020 20?02 00200 11001 10100 10010 02001 11000 02110 11110 21013 00011 11111 11002
 11010 01012 1???0 0010? ????11 11121 10000 00110 00100 10000 11111 10001 [01][01]032
 00111 1031? 10013 12111 00?11 01010 0101? ????10 ?????? 101?? ????101 22111 11110 ??201
 10100 110?1 0011? 10211 12?10 10?11 11300 21101 31111 12022 11111 11211 10201 12110
 ????0 111?? ??

Torvosaurus tanneri

??201 21??? 00000 1?002 10100 20?1? 0?001 000?? ?????? 11100 110?? ?0??? ????1 ????0?
 ?????? ?0000 ?????? ?????? ?????? ?????? ?00?? ?0??? ?????? ?????? 0??10 ?????? ????41 00112
 10200 0001? ????0 ????1? ?????1 1?01? ????11 21??1 111?? ????1? 32111 11110 12101 11100
 0?010 01111 00110 110?? ?????? ?????? ?????? 21011 22022 11110 11101 01201 12110 ?????0
 111?? ??

Spinosauridae

?0112 20??2 00111 10112 10100 2[01]000 00?00 01002 10100 11110 211?3 00011 11111 010?1
 ????10 0?000 1???? 00111 11??1 ?1011 ?1101 1011? ?0?0? ????0 0??10 11001 1124? 00112
 1[01]210 0001? ?????0 ????1? ????21 1?01? ?????? ?????? ?????? 11??? ????1? 11110 12101 11100
 1????? ?1101 10111 ?1??? 10?11 11400 10200 2?011 22?22 ?????0 1110? 01??? ?211? ??????
 ????? ??

Sinraptor dongi

00020 21011 00200 10001 10100 02110 02011 11112 01111 11100 21023 00111 11111 01102
 11010 11001 11?12 00111 1??11 11121 20?00 00111 00100 11000 11110 11?01 11241 ?0112
 10300 10012 00110 ????1 0????? ????? ????1? ?????? 1?1?1 1?111 ????11 11110 12101 10100
 11012 01111 10111 ?1??0 11011 11400 11200 21011 22122 11110 10201 01201 12110 10210
 11121 01

Allosaurus fragilis

00000 21012 00200 10001 10100 10110 02001 01102 01111 11110 21013 00011 11111 11001
 10010 11001 11112 00111 11111 11121 20010 00111 10100 11000 11110 11001 11241 00112
 10210 00012 00110 01011 00020 11011 22111 21111 10111 1111? 32111 11110 11101 11000
 01012 01111 10111 11000 10011 11400 11200 21011 22022 11110 11101 01301 12110 ??200
 1112? 11

Acrocanthosaurus atokensis

00[01]20 21011 ?0[01]00 10001 1??00 00010 01011 01112 01110 11100 21123 00011 11111
 01101 10010 11001 11??2 ?????? ????11 ?1??? 10?1? ????11 00?00 ????00 ????10 10001 11[12]42
 ?0112 ?021? ?00?? 0???0 01011 00020 1?011 22110 21111 10111 ?110? 32???? ?????? ??????
 ?????? ?1??? 0111? 1?111 ?1??0 10011 ?1400 11200 ?????? ?20?? ?????0 ????1 0????? ????10
 ??210 0?121 11

APPENDIX 3

Characters supporting each branch of the most parsimonious tree obtained in the current phylogenetic analysis (homoplasies in italic, clade name followed by the taxa that represents them in the present cladogram between parentheses). Bootstrap values greater than 50% are indicated after the clade.

Dinosauriformes (*Marasuchus* + *Acrocanthosaurus*)

Ambiguous apomorphies

ACCTRAN: 223(0>1), 235(0>1), 239(0>1), 246(0>1).

DELTRAN: none.

ACCTRAN: 14(0>1), 84(1>0), 111(0>1), 133(1>0), 154(0>1), 199(0>1), 218(0>1), 230(1>2), 257(0>1), 269(0>1), 274(0>1).

DELTRAN: 5(0>1), 29(0>1), 118(0>1), 128(0>1), 149(1>0), 208(0>1).

Unnamed node (*Pseudolagosuchus* + *Acrocanthosaurus*) (89%)

Unambiguous apomorphies: 212(0>1), 230(2>1,0), 237(0>1), 268(0>1), 282(0>1).

Ambiguous apomorphies

ACCTRAN: 118(0>1), 205(0>1), 206(0>1), 208(0>1), 224(0>1), 232(0>1), 233(0>1), 276(0>1).

DELTRAN: none.

Genosauria (*Scutellosaurus* + *Heterodontosaurus*)

Unambiguous apomorphies: 114(0>1).

Ambiguous apomorphies

ACCTRAN: 67(0>1), 70(0>1), 74(0>1), 81(1>0), 99(1>2), 104(0>1), 105(0>1), 114(0>1), 131(0>1), 205(1>0).

DELTRAN: none.

Unnamed node (*Silesaurus* + *Acrocanthosaurus*) (65%)

Unambiguous apomorphies: 234(0>1), 238(1>2), 252(0>1), 265(0>1).

Ambiguous apomorphies

ACCTRAN: 273(0>1).

DELTRAN: 205(0>1), 206(0>1), 224(0>1), 233(0>1).

Saurischia (*Herrerasaurus* + *Acrocanthosaurus*)

Unambiguous apomorphies: 7(0>1), 16(0>1), 107(1>0), 130(0>1), 138(0>1), 139(0>1), 143(0>1), 202(0>1), 226(0>1), 238(2>1), 270(0>1), 283(0>1).

Ambiguous apomorphies

ACCTRAN: 47(0>1), 48(0>1), 54(0>1), 55(0>1), 72(0>1), 85(0>1), 93(0>1), 109(0>1), 118(1>0), 148(1>0), 157(0>1), 167(0>1), 170(0>1), 173(0>1), 178(0>1), 179(0>1), 180(0>1), 190(0>1), 191(0>1), 192(0>1), 208(1>0), 228(0>1), 263(0>1), 277(0>1), 284(1>0).

DELTRAN: 80(0>1), 99(0>1).

Unnamed node (*Eucoelophysis* + *Acrocanthosaurus*)

Unambiguous apomorphies: 214(0>1), 217(0>1), 239(1>0).

Ambiguous apomorphies

ACCTRAN: 4(0>1), 5(0>1), 20(0>1), 29(0>1), 80(0>1), 81(0>1), 99(0>1), 122(0>1), 128(0>1), 149(1>0), 150(0>1), 169(0>1), 193(0>1), 197(0>1), 230(0>1), 286(1>0).

DELTRAN: none.

Herrerasauridae (*Herrerasaurus* + *Staurikosaurus*) (58%)

Unambiguous apomorphies: 108(0>1), 115(0>1), 144(1>0), 206(1>0), 219(0>1), 239(0>1), 252(1>0).

Ambiguous apomorphies

ACCTRAN: 1(0>1), 1(0>1), 3(1>0), 4(1>2), 5(1>0), 29(1>0), 53(0>1), 54(1>2), 55(1>2), 71(0>1), 76(0>1), 104(0>1), 128(1>0), 132(0>1), 149(0>1), 152(0>1), 164(0>1), 181(1>0), 182(0>1), 185(0>1), 186(0>1), 191(1>2), 214(1>0), 242(0>1), 287(1>0).

DELTRAN: 157(0>1).

Dinosauria (*Heterodontosaurus* + *Acrocanthosaurus*)

Unambiguous apomorphies: 231(0>1), 240(0>1).

Ambiguous apomorphies

ACCTRAN: 232(1>0).

DELTRAN: 4(0>1), 20(0>1), 150(0>1), 169(0>1), 193(0>1), 197(0>1), 230(0>1), 276(0>1).

Eusaurischia (*Plateosaurus* + *Acrocanthosaurus*)

Unambiguous apomorphies: 10(0>1,2), 26(0>1), 43(0>1), 66(1>0), 101(0>1), 133(1>2), 171(0>1), 176(0>1), 177(0>1), 201(0>1), 227(0>1).

Ambiguous apomorphies

ACCTRAN: 45(0>1), 46(0>1), 137(0>1), 183(0>1), 184(0>1),

Ornithischia (*Lesothosaurus* + *Heterodontosaurus*) (97%)

Unambiguous apomorphies: 21(1>0), 33(0>1), 78(0>1), 120(0>1), 150(1>2), 198(0>1), 216(0>1), 238(2>4), 254(0>2), 255(0>3), 259(0>1), 284(1>3).

Ambiguous apomorphies

211(0>1), 220(0>1), 229(0>1), 258(0>1).

DELTRAN: 93(0>1), 109(0>1).

Sauropodomorpha (*Saturnalia* + *Plateosaurus*)

Unambiguous apomorphies: 2(0>1), 73(0>1), 119(0>1), 120(0>1), 168(0>1), 213(0>1).

Ambiguous apomorphies

ACCTRAN: 42(0>1), 54(1>0), 55(1>0), 72(1>0), 84(1>0), 91(1>0), 118(0>1), 122(1>0), 157(1>0), 167(1>0), 172(2>1), 173(1>0), 190(1>0), 191(1>0).

DELTRAN: 220(0>1), 228(0>1), 277(0>1), 284(1>0).

Unnamed node (*Thecodontosaurus* + *Plateosaurus*) (55%)

Unambiguous apomorphies: 107(0>1), 127(0>1), 154(0>1), 204(0>1), 209(0>1), 263(1>0).

Ambiguous apomorphies

ACCTRAN: 24(0>1), 25(0>1), 42(1>2), 230(1>0), 257(0>1), 258(1>0), 286(0>1).

DELTRAN: 84(1>0), 91(1>0), 128(0>1), 137(0>1), 172(2>1), 183(0>1), 184(0>1), 211(0>1).

Theropoda (*Eoraptor* + *Acrocanthosaurus*)

Unambiguous apomorphies: 6(0>1), 32(0>1), 51(0>1), 166(0>1), 194(0>1), 202(1>2), 203(0>1), 246(1>2), 250(0>1).

Ambiguous apomorphies

ACCTRAN: 10(1>2), 12(0>1), 18(0>1), 23(0>1), 82(0>1), 88(0>1), 90(0>1), 92(0>1), 98(0>1), 110(0>1), 113(0>1), 141(0>1), 148(0>1), 158(0>1), 215(0>1), 228(1>0), 236(0>1), 241(0>1), 254(0>1), 255(0>1), 256(0>1), 262(0>1), 267(0>1), 274(0>1), 277(1>0), 284(0>1), 285(0>1).

DELTRAN: 29(0>1), 46(0>1), 54(0>1), 55(0>1), 72(0>1), 167(0>1), 173(0>1), 190(0>1), 191(0>1).

Neotheropoda (*Acrocanthosaurus* + *Coelophysis*) (97%)

Unambiguous apomorphies: 13(0>1), 35(0>1), 37(0>1), 61(0>1), 65(0>1), 70(0>1), 71(0>1), 74(0>1), 96(0>1), 108(0>1), 124(0>1), 134(0>2), 135(0>1), 150(1>2), 153(0>1), 154(0>1), 159(0>1), 164(0>1), 174(0>1), 185(0>1), 188(0>1), 191(1>2), 192(1>2), 195(0>1), 198(0>1), 199(0>1), 208(0>1), 218(0>1), 225(0>1), 233(1>0), 238(1>2), 240(1>0), 251(0>1), 259(0>1), 261(0>1), 278(0>1).

Ambiguous apomorphies

ACCTRAN: 6(1>2), 7(1>0), 32(1>2), 51(1>2), 55(1>2), 62(0>1), 67(0>1), 79(0>1), 95(0>1), 143(1>2), 149(0>1), 151(0>1), 221(0>1), 243(0>1), 247(0>1), 264(0>1), 266(0>1), 271(0>1), 279(0>1), 281(0>1), 284(1>2).

DELTRAN: 81(0>1), 82(0>1), 88(0>1), 90(0>1), 98(0>1),

122(0>1), 184(0>1), 211(0>1), 220(0>1), 236(0>1), 241(0>1), 254(0>1), 255(0>1), 256(0>1), 258(0>1), 274(0>1), 285(0>1).

Averostra (*Carnotaurus* + *Acrocanthosaurus*) (96%)

Unambiguous apomorphies: 52(0>1), 59(0>1), 60(0>1), 100(0>1), 116(0>1), 126(0>1), 134(2>3), 140(0>1), 160(0>1), 176(1>2), 196(0>1), 219(0>1), 230(1>0), 238(2>3), 252(1>2), 254(1>2), 255(1>2), 257(0>1), 268(1>2), 272(0>2).

Ambiguous apomorphies

ACCTRAN: 5(1>0), 12(1>0), 13(1>2), 18(1>0), 42(0>1), 45(1>0), 121(0>1), 123(0>1), 128(1>0), 137(1>0), 148(1>0), 164(1>2), 171(1>2), 186(0>1), 207(0>1), 242(0>1), 249(0>1), 278(1>2), 286(0>1).

DELTRAN: 6(1>2), 23(0>1), 55(1>3), 62(0>1), 67(0>1), 95(0>1), 113(0>1), 141(0>1), 143(1>2), 221(0>1), 243(0>1), 247(0>1), 262(0>1), 271(0>1), 281(0>1).

Ceratosauria (*Ceratops* + *Carnotaurus*) (94%)

Unambiguous apomorphies: 4(1>2), 17(0>1), 42(0,1>2), 80(1>2), 125(0>1), 133(2>0), 143(2>3), 150(2>3), 152(0>2), 166(1>0), 203(1>2), 227(1>2), 241(1>2), 245(0>1), 246(2>3), 248(0>1).

Ambiguous apomorphies

ACCTRAN: 85(1>0), 135(1>2), 157(1>0), 180(1>0), 201(1>2), 260(0>1), 263(1>2), 267(1>0).

DELTRAN: 7(1>0), 13(1>2), 79(0>1), 110(1>0), 151(0>1), 223(1>2), 242(0>1).

Tetanurae (*Torvosaurus* + *Spinosauroida* + *Acrocanthosaurus*) (65%)

Unambiguous apomorphies: 40(0>2), 89(0>1), 127(0>1), 131(0>1), 132(0>1), 134(3>4), 140(1>2), 189(0>1), 191(2>3), 238(3>4), 243(1>2), 251(1>2).

Ambiguous apomorphies

ACCTRAN: 7(0>1), 9(0>1), 72(1>0), 79(1>0), 85(1>2), 101(1>2), 110(0>1), 117(0>1), 151(1>0), 158(1>0), 162(1>0), 175(0>1), 215(1>2), 223(2>1), 229(1>0), 264(1>0), 266(1>0).

DELTRAN: 92(0>1), 164(1>2), 183(0>1), 186(0>1), 267(0>1).

Spinosauroida (*Torvosaurus* + *Spinosauridae*)

Unambiguous apomorphies: 20(1>2), 26(1>2), 80(1>0), 165(0>1).

Ambiguous apomorphies

ACCTRAN: 5(0>1), 13(2>1), 32(2>0), 41(0>1), 42(1>0), 98(1>0), 105(0>1), 106(0>1), 121(1>0), 182(0>1), 242(1>0).

DELTRAN: 207(0>1).

Avetheropoda / Allosauroida (*Allosaurus* + *Acrocanthosaurus*) (63%)

Unambiguous apomorphies: 3(1>0), 38(0>1), 44(0>1), 76(0>1), 99(1>2).

Ambiguous apomorphies

ACCTRAN: 28(0>1), 45(0>1), 104(0>1).

DELTRAN: 9(0>1), 42(0>1), 51(1>2), 85(0>2), 117(0>1), 121(0>1), 123(0>1), 157(0>1), 162(0>1), 171(1>2), 215(0>2), 242(0>1), 278(1>2).

Unnamed node (*Sinraptor* + *Acrocanthosaurus*)

Unambiguous apomorphies: 4(1>2), 10(2>1), 26(1>0), 34(0>1), 39(0>1), 54(1>2), 68(0>1).

Ambiguous apomorphies

ACCTRAN: 146(0>1), 175(1>0), 207(1>0), 262(1>0), 263(1>2).

DELTRAN: 279(0>1).

Coelophysoidea (*Dilophosaurus* + *Coelophysis*)

Unambiguous apomorphies: 1(0>1), 5(0,1>2), 11(0>1), 14(0>1), 15(0>1), 16(1>0), 21(1>0), 22(0>1), 39(0>1), 102(0>1), 105(0>1), 129(0>1), 146(0>1), 155(0>1), 156(0>1), 210(0>1), 269(0>1).

Ambiguous apomorphies

ACCTRAN: 8(0>1), 50(0>1), 74(1>2), 103(0>1), 115(0>1), 145(0>1), 158(1>2), 215(1>0), 222(0>1), 239(0>1), 244(0>1), 275(0>1), 280(0>1).

DELTRAN: 12(0>1), 18(0>1), 110(1>0), 128(0>1), 137(0>1), 157(0>1), 229(0>1), 279(0>1).

Unnamed node (*Liliensternus* + *Coelophysis*) (63%)

Unambiguous apomorphies: 18(1>2), 33(0>1), 34(0>1), 106(0>1),

142(0>1), 163(0>1), 253(0>1).

Ambiguous apomorphies

ACCTRAN: 6(2>1), 20(1>0), 23(1>0), 30(0>1), 31(0>1), 41(0>1), 53(0>1), 55(2>1), 58(0>1), 62(1>0), 67(1>0), 75(0>1), 86(0>1), 87(0>1), 92(1>0), 93(1>0), 113(1>0), 136(0>1), 141(1>0), 143(2>1), 149(1>0), 161(1>0), 221(1>0), 243(1>0), 245(0>1), 267(1>0), 271(1>0).

DELTRAN: 85(0>1), 183(0>1), 222(0>1), 223(1>2), 247(0>1), 262(0>1), 266(0>1), 281(0>1).

Coelophysidae (*Syntarsus* + *Coelophysis*) (99%)

Unambiguous apomorphies: 19(0>1), 70(1>0), 78(0>1), 142(1>2), 200(0>1), 203(1>2), 217(1>0), 242(0>1), 260(0>1).

Ambiguous apomorphies

ACCTRAN: 80(1>0), 103(1>0), 147(0>1), 148(1>2), 152(0>1), 206(1>2), 226(1>2), 230(1>2), 272(0>1).

DELTRAN: 20(1>0), 30(0>1), 31(0>1), 41(0>1), 45(0>1), 50(0>1), 53(0>1), 58(0>1), 75(0>1), 79(0>1), 87(0>1), 95(0>1), 136(0>1), 151(0>1), 158(0>2), 161(0>1), 239(0>1), 244(0>1), 264(0>1), 275(0>1), 280(0>1).

***Coelophysis* (*Coelophysis bauri* + *Coelophysis rhodesiensis*) (91%)**

Unambiguous apomorphies: 27(0>1), 36(0>1), 37(1>0), 57(0>1), 65(1>0), 69(0>1), 71(1>0), 81(1>0), 104(0>1), 233(0>1), 284(2>1).

Ambiguous apomorphies

ACCTRAN: 8(1>0), 32(2>1), 51(2>1), 91(1>0), 115(1>0), 152(1>2).

DELTRAN: 7(1>0), 74(1>2), 147(0>1), 148(1>2), 149(1>0), 152(0>2), 206(1>2).