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The phylogenetic relationships of early dinosaurs: a comparative report

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Abstract

Surprising new anatomical information has come to light for the early dinosaurs *Eoraptor lunensis* and *Herrerasaurus ischigualastensis*. *Eoraptor* has a mid mandibular jaw joint, and *Herrerasaurus* has a promaxillary fenestra at the anterior end of the antorbital fossa. Initial cladistic interpretation placed *Herrerasaurus* outside Dinosauria. Since then, *Eoraptor* and *Herrerasaurus* have been placed at the base of Saurischia or within Theropoda in two large-scale quantitative analyses. A comparative approach is taken here to show, first, that character choice is a major factor behind differing results; only half of the character data critical for each interpretation is incorporated into the opposing analysis. In that shared portion of data, furthermore, nearly 40 percent of character state scores vary for identical, or comparable, ingroup taxa. Resolving these conflictive interpretations is clearly where future progress will be made in understanding early dinosaur phylogenesis.

Keywords: Dinosauria, *Eoraptor*, *Herrerasaurus*, phylogenetic taxonomy, cladistics

Introduction

The origin and early radiation of dinosaurs has long been of interest as one of the great transitions among terrestrial vertebrate faunas (Benton 1988; Rogers et al. 1993; Sereno 1997, 1999). Only a handful of fossil-rich locales have yielded skeletons complete enough to help outline phylogenetic patterns at the base of Dinosauria.

Initiated in the late 1980s, a pair of Argentine-American expeditions re-opened field work in the richly fossiliferous outcrops of the Ischigualasto Formation in San Juan Province, Argentina, which earlier had yielded the most complete view of early Late Triassic vertebrate life (Bonaparte 1982). Now dated more precisely to the earliest Carnian (ca. 228 Ma; Rogers et al. 1993; Gradstein et al. 2004), the first complete skeletons of Triassic dinosaurs came to light in the course of this work, including the diminutive *Eoraptor lunensis* (Sereno et al. 1993) and larger-bodied *Herrerasaurus ischigualastensis* (Sereno 1993; Sereno and Novas 1993; Novas 1993).

Eoraptor and *Herrerasaurus* remain the pivotal taxa for studies of the early radiation of Dinosauria and have been subject to much commentary and analysis over the last two decades. Prior to the discovery of

more complete material, *Herrerasaurus* was positioned outside Dinosauria proper (Saurischia plus Ornithischia) in the first cladistic analyses of basal dinosaurs (Gauthier 1986; Brinkman and Sues 1987; Novas 1992). With newly discovered material from the Argentine-American expeditions and more extensive character sampling, *Herrerasaurus* and *Eoraptor* were reinterpreted as basal theropods (Figure 3A; Sereno and Novas 1992; Sereno 1993; Sereno et al. 1993; Novas 1993).

Analyses in the last decade have offered three views of these taxa: Sereno (1999) and Rauhut (2003) maintained their position as basal theropods (Figure 3B); Langer et al. (1999) and Fraser et al. (2002) returned to the initial phylogenetic view of *Herrerasaurus* as a potential dinosaurian outgroup; and Langer (2004) and Langer and Benton (2006) favored positioning both *Eoraptor* and *Herrerasaurus* inside Dinosauria as basal saurischians (Figure 3C).

The present paper is not an exhaustive comparative analysis covering all of these hypotheses. Rather, the evidence presented in favour of each of the three phylogenetic viewpoints presented above is evaluated, and the two most comprehensive analyses with available datasets and contrasting results (Sereno 1999; Langer and Benton 2006) are compared in more detail.

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Institutional abbreviations

PVL, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan.

Phylogenetic taxonomy

The taxonomic meaning (content) of Dinosauria and other basal dinosaurian taxa has varied, and so a phylogenetic taxonomy is adopted in this paper (Figure 1, Table I; de Queiroz and Gauthier 1992; Sereno 2005). These definitions aim to maximize the criteria upon which phylogenetic taxonomy is measured—*stability*, *simplicity*, and *prior use* (Sereno 1998, 1999, 2005). For simplicity and stability of taxonomic content, specifiers were chosen that are deeply nested, well known and that maintain taxonomic content under alternative phylogenetic arrangements. I have avoided form-qualified (apomorphy-based) definitions, as they inevitably introduce interpretational complexity. Finally, the relationship between three taxa at a dichotomy is best maintained by a node-based taxon linked by definition to a pair of subordinate stem-based taxa. Called a node-stem triplet, this configuration anchors Dinosauria and its subordinate clades Ornithischia and Saurischia.

The definitions presented here are recommendations. Contrary to the view taken by the PhyloCode (Cantino and de Queiroz 2004), they are not intended to function as an “established” taxonomic solution. Nonetheless, they may provide a heuristic framework for taxonomists working at the base of Dinosauria. The historical development of these definitions and all previous phylogenetic definitions for these taxa are

available online (Sereno et al. 2005; www.taxon-search.org).

New anatomical evidence

Eoraptor lunensis and *Herrerasaurus ischigualastensis* are central to the phylogenetic arguments that follow. In the current literature, they are known in very unequal detail. The skull and skeleton of *Herrerasaurus* and its close relative *Staurikosaurus* are well described (Colbert 1970; Brinkman and Sues 1987; Sereno and Novas 1992, 1993; Novas 1993; Sereno 1993; Galton 2000). *Eoraptor*, in contrast, is known only from a preliminary description (Sereno et al. 1993). Although the original fossil material or casts have been available, misinformation has entered the literature. The comments below are directed at clarifying a few features of phylogenetic import for both *Eoraptor* and *Herrerasaurus*.

Eoraptor lunensis

Eoraptor lunensis is based on the nearly complete holotypic skeleton and several unpublished referred individuals. The skull was originally figured prior to final preparation (Sereno et al. 1993; Figure 1), and several details were not fully exposed at that time. There are two rows of rudimentary palatal teeth on the pterygoid, a remarkably primitive feature recorded definitively here in *Eoraptor* for the first time within Dinosauria. The lower jaw, on the other hand, has an intramandibular joint between the usual elements (splenial, angular). The joint has a concavoconvex articulation as occurs in neotheropod dinosaurs (splenial process transversely concave), as opposed to the reversed condition present in herrerasaurids (splenial process transversely convex) (Sereno and Novas 1993). This character was previously thought to be restricted to herrerasaurids and neotheropods.

The sacrum is composed of three vertebrae. A sacral is defined here as a vertebra which has an articular contact with the pelvic girdle (with or without a distinguishable associated rib). The first sacral vertebra is a dorsosacral, which has a relatively slender transverse process (and/or fused rib) with a distal attachment to the base of the preacetabular process. The next posterior two vertebrae are the primordial sacral pair, each with a broad fused rib and a substantial distal articulation with the iliac blade.

Elongate prezygapophyses in the distal caudal vertebrae, previously reported in herrerasaurids (Novas 1993) and neotheropods, remain unknown in *Eoraptor*, because the distal tail is not preserved. The distal tail, however, is preserved in a closely related (unnamed) species from the same formation (Ischigualasto) that has elongate prezygapophyses projecting anteriorly beyond the centrum. ‘Elongate’ is a relative measure that depends on how the character is defined.

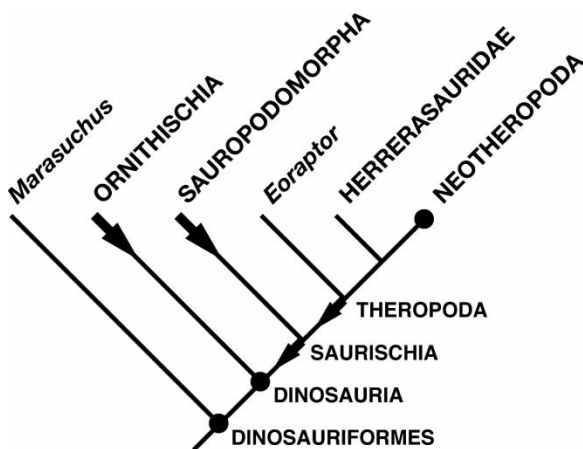


Figure 1. Cladogram of basal Dinosauria showing the position of node-based (dot) and stem-based (arrow) phylogenetic definitions (see Table I for phylogenetic definitions). None of the definitions at the base of Dinosauria cite or are linked in any special way to the position of *Eoraptor* or Herrerasauridae.

Table I. Phylogenetic definitions for key taxa used in this paper (for background information, see Sereno in press or www.taxonsearch.org).

Taxon	Phylogenetic definition	Definitional type
Dinosauriformes Novas 1992	The least inclusive clade containing <i>Passer domesticus</i> (Linnaeus 1758) and <i>Marasuchius lilloensis</i> (Romer 1972)	Node
Dinosauria Owen 1842	The least inclusive clade containing <i>Triceratops horridus</i> Marsh 1889 and <i>Passer domesticus</i> (Linnaeus 1758)	Node
Ornithischia Seeley 1888	The most inclusive clade containing <i>Triceratops horridus</i> Marsh 1889 but not <i>Passer domesticus</i> (Linnaeus 1758) or <i>Saltasaurus loricatus</i> Bonaparte and Powell 1980	Stem
Saurischia Seeley 1888	The most inclusive clade containing <i>Passer domesticus</i> (Linnaeus 1758) but not <i>Triceratops horridus</i> Marsh 1889 and including <i>Saltasaurus loricatus</i> Bonaparte and Powell 1980	Stem
Sauropodomorpha Huene 1932	The most inclusive clade containing <i>Saltasaurus loricatus</i> Bonaparte and Powell 1980 but not <i>Passer domesticus</i> (Linnaeus 1758), <i>Triceratops horridus</i> Marsh 1889	Stem
Theropoda Marsh 1891	The most inclusive clade containing <i>Passer domesticus</i> (Linnaeus 1758) but not <i>Saltasaurus loricatus</i> Bonaparte and Powell 1980	Stem
Neotheropoda Bakker 1986	The least inclusive clade containing <i>Coelophysis bauri</i> (Cope 1889) and <i>Passer domesticus</i> (Linnaeus 1758)	Node

If the projection of the prezygapophyses beyond the centrum is measured relative to centrum length, the percentage is low (about 15 percent of centrum length) because the centra themselves are considerably more elongate than in *Herrerasaurus*.

Herrerasaurus ischigualastensis

The antorbital fossa of *Herrerasaurus* had been shown as a narrow band devoid of invaginations or openings (Sereno and Novas 1993). Two anterior pneumatic openings in the wall of the fossa, the promaxillary and maxillary fenestrae, are known only among neotheropods. This region is well preserved in only one specimen, which shows a narrow slit-shaped opening at the anterior end of the fossa (Figure 2). Here identified as the promaxillary fenestra, it opens anteriorly into a matrix-filled space. It cannot be explained away as an artifact of preservation; the slit-shaped opening is present on both sides of the skull. The same area of the fossa is well preserved in *Eoraptor*, which does not exhibit any depression or opening.

Other details of the palate have been recently exposed in this skull of *Herrerasaurus* and include a modest fossa on the ventral aspect of the ectopterygoid. Termed the ectopterygoid pocket, this is a derived feature long associated with theropods. *Eoraptor* is the only dinosaur known to maintain rudimentary rows of palatal teeth on the pterygoid, which was presumably lost independently in several early lineages of dinosaurs. *Herrerasaurus* does not have any palatal teeth.

The number of sacral vertebrae in *Herrerasaurus* and *Staurikosaurus* has remained controversial. Do they have at least three vertebrae, as characterizes *Eoraptor* and other dinosaurs, or only the primordial pair? To answer that question, well-preserved specimens are needed, because one would anticipate that the additional sacral, if present, would be a dorsosacral with a comparatively weak attachment to the preacetabular process of the ilium. Colbert (1970) had originally described three sacral vertebrae, but only two vertebrae are clearly modified as sacrals, and the primordial pair (Galton 2000). Galton (2000) and several previous authors have stated that *Staurikosaurus* has only these two sacral vertebrae. The presence or absence of a dorsosacral vertebra, however, cannot be determined in my opinion, given the disarticulation and state of preservation of the specimen.

In *Herrerasaurus*, two partial skeletons preserve in articulation the relationship of the last dorsal and primordial sacral pair: the holotype, collected by V. Herrera and J. F. Bonaparte in 1961 (Reig 1963) and mounted in the collections of the Fundación Miguel Lillo in Tucumán, Argentina (PVL 2566), and a referred specimen, collected by my team in 1988 and

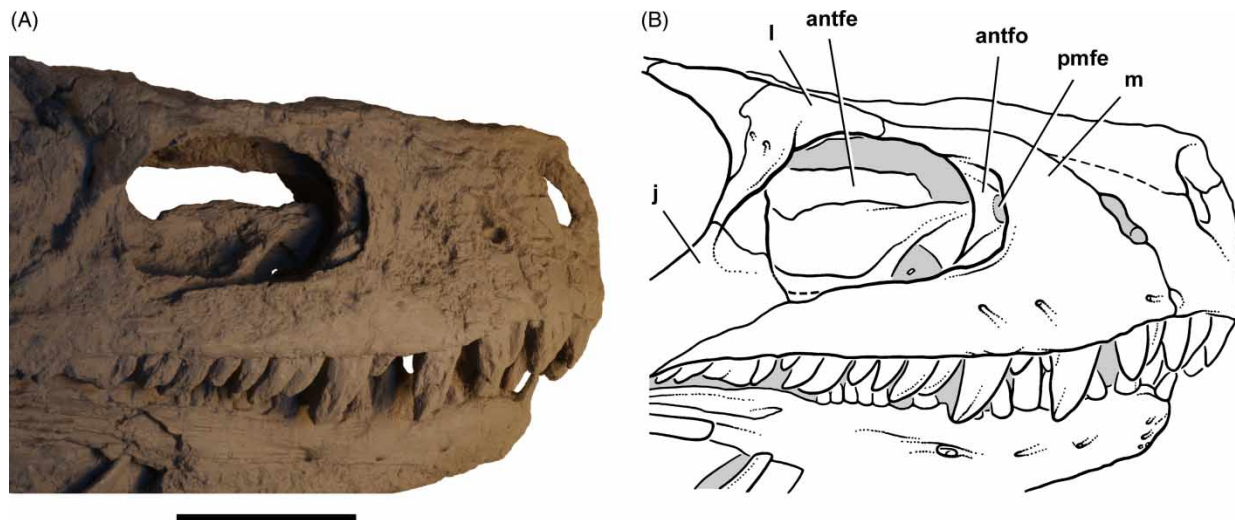


Figure 2. Skull of *Herrerasaurus ischigualastensis*. A, B, Posterolateral view of the slit-shaped promaxillary fenestra located on the anterior wall of the antorbital fossa of the maxilla (cast of PVSJ 407). Abbreviations: antfe, antorbital fenestra; antfo, antorbital fossa; j, jugal; l, lacrimal; m, maxilla; pmfe, promaxillary fenestra. Scale bar = 5 cm.

now in the collections of the Museo de Ciencias Naturales in San Juan, Argentina (PVSJ 461). Sereno and Novas (1992: 1139) described the sacral series as composed of two “fully incorporated” sacral vertebrae. Novas (1993), in a more detailed account, described the presence of only two sacral vertebrae with contact with the ilium and did not comment in particular on the last dorsal vertebra, which was shown between the blades of the ilia. As preserved, its transverse process projects toward the base of the preacetabular process. Although it fails to contact the ilium in the holotypic specimen, it could not have articulated with a separate dorsal rib given its location. As this specimen was prepared and mounted many years ago, the original condition of this vertebra and its potential attachment to the preacetabular process of the ilium remain uncertain.

The referred specimen (PVSJ 461), which includes an articulated pelvic girdle, clarifies this relation. The vertebra in question is a dorsosacral with a transverse process no larger than that in posterior dorsal vertebrae. Its transverse process contacts the base of the preacetabular process as in *Eoraptor* and many other dinosaurs. Given this new information, Galton (2000: 411) suggested that it be identified as a dorsal vertebra anyway, because “the form of the transverse process is not modified for attachment to the ilium”. Although this definition may be convenient for identifying sacral vertebrae in disarticulated specimens, the number of vertebrae with bony attachments to the pelvic girdle is the evolutionary modification associated with this character. A sacral in this view is a vertebra that articulates distally with the ilium by its transverse process and/or a shortened rib. It does not have a free distal transverse process or rib. Dinosaurian outgroups, such as *Marasuchus* (Sereno and Arcucci 1994), clearly only have two sacral vertebrae,

the primordial pair. By this definition and evidence, *Herrerasaurus* appears to have three, rather than two, sacral vertebrae. Enlargement of the iliac attachment of the dorsosacral vertebra is a further modification.

Previous phylogenetic interpretations

Setting aside pre-cladistic commentary regarding herrerasaurids (Reig 1963; Colbert 1970), cladistic commentary can be divided into analyses based on qualitative versus quantitative hypotheses. Qualitative hypotheses list characters but are not based on parsimony analysis of a character-taxon matrix. Analyses of this sort that cover early dinosaur phylogeny include Gauthier and Padian (1985), Gauthier (1986), Gauthier et al. (1989), Benton (1990) and Fraser et al. (2002). Seven quantitative analyses have been published with a wide range in the number of characters and ingroup taxa considered (Table II).

Herrerasauridae as a dinosaurian outgroup

Gauthier (1984, 1986) was first to place *Herrerasauridae* in phylogenetic context on a cladogram—as an outgroup to Dinosauria (as defined above). Several subsequent authors followed this lead (Gauthier and Padian 1985; Gauthier 1989; Padian and May 1993), although no supporting character evidence was presented. In Gauthier’s (1986) saurischian analysis, for example, there are no synapomorphies given for dinosaurs (Saurischia + Ornithischia) excluding herrerasaurids.

Brinkman and Sues (1987) were first to propose synapomorphies to unite *Herrerasaurus* and other dinosaurs and were followed by Benton (1990), Novas (1992) and Fraser et al. (2002). The character

Table II. Profile of phylogenetic analyses that consider relationships at the base of Dinosauria.

Authors	Matrix							Character Documentation		
	Analysis	Printed	e-Archived	No. Ingroups	No. Characters	Character listed	Character states listed	Original author cited	Character description	Character figured (%)
1	Novas 1992	+	-	5	17	-	+	-	-	24
2	Novas 1993	+	-	6	51	+	+	+	-	0
3	Sereno et al. 1993	-	-	12	132	-	+	-	-	0
4	Sereno 1999	-	+	13	146	+	+	-	-	0
5	Rauhut 2003	+	-	58	224	+	+	-	-	0
6	Langer 2004	-	+	9	107	+	+	-	-	80
7	Langer and Benton 2006	+	-	10	98	-	+	+	+	~10

evidence (listed below in order of publication) has not been convincing, in part because many of the characters are based on ill-defined relative size differences:

- (1) Medial acetabular wall, less well developed (Brinkman and Sues 1987).
- (2) Pedal digit V small (Brinkman and Sues 1987).
- (3) Three or more sacral vertebrae (Benton 1990).
- (4) Femoral anterior trochanter prominent (Benton 1990).
- (5) Distal tibia transversely expanded (Benton 1990).
- (6) Brevis shelf prominent (Novas 1992).
- (7) Femoral trochanteric shelf reduced to a prominence (Novas 1992).

Fraser et al. (2002), the most recent paper supporting this hypothesis, presented a short character list and cladogram but lacked a character-state matrix or quantitative analysis. The ingroups shown on their cladogram are limited to *Herrerasaurus*, *Agnostiphys*—a newly named taxon based on a few isolated elements of uncertain association, and Dinosauria. Seventeen “principal diagnostic characters of Dinosauria” were listed in an appendix (Fraser et al. 2002:95). The placement for six of these was given in a figure legend to a cladogram, two of which unite *Agnostiphys* and Dinosauria to the exclusion of *Herrerasaurus*. Both of these are potentially problematic. The first, three or more sacral vertebrae, I argued above characterizes both *Eoraptor* and *Herrerasaurus*, the sacra of which are composed of two primordial sacrals and one dorso-sacral vertebra that attaches to the preacetabular process. The second feature, the presence of a brevis fossa, is weakly expressed in *Herrerasaurus*, which has an autapomorphic swollen postacetabular process. A better-developed brevis fossa, however, is present in another herrerasaurid, *Staurikosaurus* (Colbert 1970), and in the probable herrerasaurid *Chindesaurus* (Long and Murry 1995).

Despite limited character analysis and no matrix, Fraser et al. (2002:91) claimed that “the position of *Herrerasaurus* is at best equivocal,” citing a published abstract (Holtz and Padian 1995). They recommended, further, “its characteristics should not be used as a basis for diagnosing Dinosauria, Saurischia or Theropoda.” No quantitative hypothesis has ever been published that positions either *Eoraptor* or *Herrerasaurus* outside Dinosauria as the most parsimonious solution. Langer et al. (1999) came the closest, showing *Herrerasaurus* in an unresolved basal polytomy. The matrix for this analysis, however, was not published.

Eoraptor and Herrerasauridae as basal Saurischia

Langer et al. (1999) positioned *Herrerasaurus* as a basal saurischian. Said to be based on 40 characters,

the analysis “excluded features of the skull and hand” as they were not preserved in the new taxon (*Saturnalia*) they were describing (Langer et al. 1999:515). Given that the skull and hand provided many of the synapomorphies central to the theropod hypothesis (Sereno and Novas 1992; Sereno et al. 1993), this result is not surprising. In a subsequent analysis of 107 characters, Langer (2004) confirmed the most general phylogenetic result of Sereno et al. (1993), that positioning either *Eoraptor* or *Herrerasaurus* outside Dinosauria is not a parsimonious option. Doing so increased tree length by 14 steps. Langer (2004) then argued that positioning *Eoraptor* and *Herrerasaurus* as basal saurischians was slightly more parsimonious (two steps) than placing them within Theropoda. Although Langer (2004) discussed several characters, no global comparisons were made to the character list and matrix of Sereno (1999; Figure 3B), and so the reasons for this new result are not clear. Was it due to new character data, excluded character data, alternative character-state scores, or new ingroup taxa?

More recently, Langer and Benton (2006) analyzed a dataset of 98 characters (Figure 3C), drawing the same conclusions—that *Eoraptor* and *Herrerasaurus* are best positioned, albeit tenuously, as basal saurischians rather than basal theropods. The majority of the 98 characters were used previously by Langer (2004); 16

of the original 107 characters were omitted, seven characters are new, and *Silesaurus opolensis* is added to ingroup taxa. Only character states were given (Table II). To make a comparative tabulation of character data (Table III), I needed to infer the character (numbers 17–25) from the character states, a proposition that risks misinterpretation. Morphologic character data mandates clear delineation of characters composed of mutually exclusive character states (Hawkins et al. 1997; Sereno in press).

Re-analyzing this published dataset (with six of seven multistate characters ordered) did not yield a single, fully resolved most-parsimonious tree as reported (Langer and Benton 2006:Figure 15). Rather there are six minimum length trees with no resolution among ‘eusaurischian’ taxa (Figure 3C). The loss of resolution is due to an apparent scoring error in character 78, in addition, of the published matrix; *Guaibasaurus* was scored as polymorphic with states 0 and 1 rather than states 1 and 2 (M. Langer, personal communication). Character 78 provides a good example of the perils of listing character states by themselves: “Distal pubis nearly as broad as (0) or significantly narrower than (1) proximal part of the blade lateromedially compressed and not broader than deep (2)” (Langer and Benton 2006: 30). States 0 and 1 involve the width of the distal end of the pubic blade relative to the proximal end; state 2 involves the shape

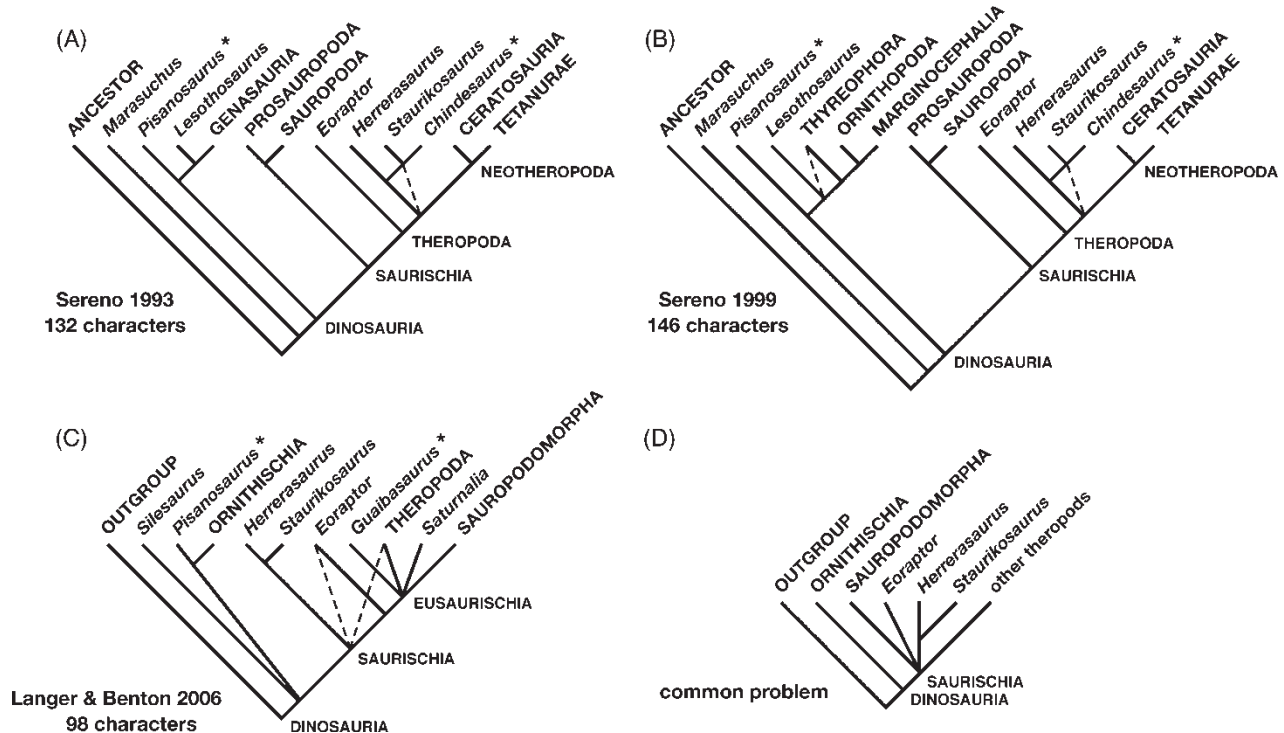


Figure 3. Cladograms showing the interrelationships of basal dinosaurs. (A) Sereno (1993), (B) Sereno (1999), (C) Langer and Benton (2006), and (D) a reduced, unresolved cladogram retaining only those taxa that are central to conflicting interpretations. Asterisks identify poorly known taxa that are particularly unstable. Dashed lines indicate loss of resolution with increase in tree length of two steps above minimum length (taxa with asterisks were removed prior to this calculation, because the additional collapse these taxa generate masks the general level of support measured by decay).

Table III. Characters listed as synapomorphies at key nodes for the interpretation of *Eoraptor* and *Herrerasaurus*. Characters 1–16 were listed by Sereno (1999) as synapomorphies linking *Eoraptor* and/or *Herrerasaurus* with other theropods; characters 17–25 (inferred from character states) were used by Langer and Benton (2006) as “eusaurischian” synapomorphies linking saurischians to the exclusion of *Eoraptor* and *Herrerasaurus*. Shading indicates the presence of 12 characters in both analyses (see Table IV for character state comparison). Abbreviations: S = Sereno (1999); LB = Langer and Benton (2006).

No	Character No	Character
1	S89	Cervical epiphyses, shape: crest or rugosity (0); prong-shaped process (1)
2	S90	Internal cavitation of centra and long bones: moderate (0); extreme (1)
3	S91	Metacarpals I-III, intermetacarpal articular facets: absent (0); present (1)
4	S94	Ischial obturator process: absent (0); present (1)
5	S96	Axial intercentrum width: less (0), or more (1), than maximum width of axial centrum
6	S98	Scapular blade, length versus distal width: less (0), or more (1), than 3 times distal width
7	S102	Femoral distal end, anterior attachment depression: absent (0); present (1)
8	S69	Manus length (measured along digit II or III, whichever is longest): 20–30% (0), approximately 40% (1), or 50–70% (2) length of humerus + radius. (state 1 > 2)
9	S87	Ectopterygoid fossa: absent (0); present (1)
10	S88	Intramandibular joint: absent (0); present (1)
11	S92	Metacarpals I-III, asymmetrical extensor depressions: absent (0); present (1)
12	S95	Pubic blade, distal width: subequal to (0), or 65% or less than (1), proximal width of blade
13	S97	Distal caudal prezygapophyses: short (0); elongate (1)
14	S99	Manual digits I-III, penultimate phalanx (digits II, III) length and ungual (digits I-III) form: shorter or subequal to preceding phalanx, short moderately recurved unguals (0); longer than preceding phalanx, long strongly recurved unguals (1)
15	S100	Metacarpals IV and V, diameter: short (0); vestigial, less than 50% diameter of metacarpal III (or metacarpal II) (1)
16	S101	Pubic foot: absent (0); present (1). (loss of broad blade-shaped distal end)
17	LB5	Premaxilla, tip of posteroventral ramus, location: posterior (0), or ventral (1), to the external naris
18	LB35	Posterior cervical centra, length: longer (0), or shorter than (1), anterior dorsal vertebrae
19	LB42	Sacrocaudal vertebra(e): absent (0); present (1)
20	LB51	Radius, length: more (0), or less (1), than 80% of humeral length
21	LB87	Tibia, medial corner of distal end, shape: 90° or more (0); less than 90°
22	LB89	Tibia, medial margin of distal end, anteroposterior width: subequal to (0), or broader than (1), the lateral margin
23	LB57	Metacarpal 1, length: longer (0), or subequal or shorter (1), than digit I-ungual
24	LB61	Metacarpal 2, length: shorter (0), or subequal or longer (1), than metacarpal 3
25	LB80	Ischium, distal end, transverse width: equal (0), or dorsoventrally expanded (1), relative to the shaft

of the proximal portion of the blade. States 0 and 1 and state 2, thus, do not appear to be mutually exclusive and therefore belong to independent characters.

The difference with the single fully resolved published tree, however, is minor. All resolution among saurischian clades collapses with one additional step with either score for character 78 in *Guaibasaurus* (Figure 3C). Removal of the poorly known genera *Pisanosaurus* and *Guaibasaurus* does not alter this one-step collapse. Ordering the seven multistate characters also has little effect; all resolution within Saurischia collapses with one or two additional steps with ordered or unordered characters. The basal position of herrerasaurids and *Eoraptor* relative to other saurischians and the need for naming this less inclusive taxon ‘Eusaurischia’ thus appear to be illusory.

Nine unambiguous synapomorphies, nonetheless, unite theropods and sauropodomorphs to the exclusion of herrerasaurids and *Eoraptor* (Table III, numbers 17–25), five of which do not exhibit homoplasy (numbers 17, 18, 23–25). Langer and Benton (2006: 41) mentioned these five and two others (numbers 20, 22) but did not cite the final two

(numbers 42, 87). Given the instability of the node that these synapomorphies support (‘Eusaurischia’), a nearly equivalent number of conflictive characters must be present.

Eoraptor and *Herrerasauridae* as basal *Theropoda*

This hypothesis was originally based on an analysis of 132 characters (Sereno et al. 1993) (Figure 3A). All synapomorphies at critical internal nodes were listed under delayed transformation (132 characters, 12 terminal taxa, CI = 0.85), although the matrix itself was not published. The same result was obtained by a subsequent analysis of 146 characters (CI = 0.81), the character list and matrix for which has been available online (Figure 3B). Both the 1993 and 1999 analyses were presented in short papers that did not discuss alternative arrangements. More than a dozen unambiguous synapomorphies in each analysis support the position of *Eoraptor* and *Herrerasauridae* outside other theropods (Neotheropoda). Eight additional steps are required before their basal position within Theropoda collapses (with *Pisanosaurus* and *Chindesaurus* removed; Figure 3B, Table III).

Rauhut (2003) also positioned *Eoraptor* and *Herrerasaurus* as basal theropods in his survey of basal theropod relationships. Repositioning either *Eoraptor* or *Herrerasaurus* as a basal saurischian (*vide* Langer and Benton 2006) required five and eight extra steps, respectively (Rauhut 2003:162). The reasons behind the varying or overlapping results obtained by Sereno (1999), Rauhut (2003), Langer (2004) or Langer and Benton (2006) remain unclear, because these analyses principally compared phylogenetic results rather than the characters or character state scores that lie behind those results.

Isolating the problem

To better understand how comparable analyses arrive at different solutions, Sereno (1999) and Langer and Benton (2006) are compared. Figure 1D shows the common phylogenetic problem (an outgroup and six terminal taxa) that these analyses resolve in different ways.

The role of fragmentary species

The different solutions are not significantly influenced by the presence or absence of a handful of fragmentary forms, including the ornithischian *Pisanosaurus*, possible saurischian *Guaibasaurus*, or possible herrerasaurid *Chindesaurus* (Figure 3; taxa with asterisks). Removal of *Pisanosaurus* and *Guaibasaurus* from the analysis of Langer and Benton (2006), for example, does not change minimum tree length, alter the relationships of *Eoraptor* or *Herrerasaurus* (Herrerasauridae) as successive groups outside “Eusaurischia,” or increase the single additional step needed to collapse their basal position within Saurischia (Figure 3C). Likewise, the presence or absence of *Silesaurus* has little effect. Langer and Benton (2006) ordered six of the seven multistate characters in the dataset; leaving these unordered also has little effect on topology. One to three steps is the greatest branch length differential between the hypothesis that *Eoraptor* and *Herrerasaurus* are basal saurischians and an alternative that links one or both to Theropoda. Sampling of fragmentary forms, like *Pisanosaurus*, *Guaibasaurus*, and *Silesaurus*, thus, does not appear to play a significant role in the differing interpretations of *Eoraptor* and *Herrerasaurus*.

Key character evidence

Given that taxon sampling does not appear to be a significant factor, the differing results are most likely due to character and character state choice. What follows is a quick assessment of those two areas in Sereno (1999) and Langer and Benton (2006). Key character evidence can be quickly ascertained by running each analysis and compiling the unambiguous synapomorphies that accrue at critical nodes (Table III). In the case of Sereno

(1999), 16 of such characters are responsible for maintaining *Eoraptor* at the base of Theropoda (S87–92, 94, 95) and Herrerasauridae at a node within that clade (S69, 96–102). In the case of Langer and Benton (2006), nine characters unite “Eusaurischia” (LB5, 35, 42, 51, 57, 61, 80, 87, 89), a clade composed of Sauropodomorpha and Theropoda that excludes *Eoraptor* and Herrerasauridae.

Character and character state choice

There are, in sum, 25 critical characters between the two analyses that have a major effect on the position of *Eoraptor* and *Herrerasaurus*. Half of these (12 out of 25; 48%) are present in both analyses (Table III). This is a significant finding. The analyses are tapping into very different character data to answer the same question. Character choice must play a major role in obtaining different phylogenetic results.

Variation in character state scores is also manifest in every one of the 12 characters that are shared between the analyses (Table IV). Most of this character state variation comprises mismatched scores, or character state mismatch, rather than a positive score opposing a question mark, or character state disparity. Nearly 40% of the character states differ between the analyses (28 mismatches out of 72; 39%). Thus, character state choice may well play a major role in generating the observed differences in phylogenetic results.

Discussion and conclusions

Most of the differences outlined above between the analyses of Sereno (1999) and Langer and Benton (2006) lie hidden within their respective data matrices. Although resolving these character issues is clearly paramount, we lack analytic tools to efficiently sort opposing character lists and character state scores to highlight the differences visualized in Tables III and IV. Such visualization is needed, in turn, to facilitate future consensus and resolution (Sereno in review).

The two areas highlighted in this study concern character choice and character state choice. It is remarkable that only half of the character data supporting critical nodes (25 characters) is shared between analyses (Table III). What phylogenetic structure does the shared partition of character evidence yield if run alone for each analysis? How about the unshared partition? Is most of the phylogenetic signal for the differing results coming from character evidence that is not included (or has been omitted/rejected)? These are important questions to resolve.

It is also remarkable how much variation exists in character state scores for the 12 characters from critical nodes that are shared between the hypotheses (Table IV). A little less than half of this variation is scored for terminal taxa represented by species. These

Table IV. Character state variation (mismatch, disparity) between Sereno (1999) and Langer and Benton (2006) for 12 characters that are present in both analyses and key to the phylogenetic position of *Eoraptor* and *Herrerasaurus*. The prefix on character numbers identify the analysis. Characters state scores are shown for six taxa present in both analyses (Figure 3D). SAU (= Sauropodomorpha) lists a composite score from Sereno (1999) for Prosauropoda and Sauropoda; NEO (= Neotheropoda) is a composite in Sereno (1999: Ceraosauria + Tetanure) and equivalent to "Theropoda" in Langer and Benton (2006). Abbreviations: S = Sereno (1999); LB = Langer and Benton (2006); ORN = Ornithischia; SAU = Sauropodomorpha; *Eor* = *Eoraptor lunensis*; *Her* = *Herrerasaurus ischigualastensis*; *Sta* = *Staurikosaurus*; NEO = Neotheropoda.

Character number	Character description	Taxa (character state scores)					
		ORN	SAU	<i>Eor</i>	<i>Her</i>	<i>Sta</i>	NEO
1	S69 Manus length (measured along digit II or III, whichever is longest): 20-30% (0), approximately 40% (1), or 50-70% (2) length of humerus + radius	0	1,0	1	2		2
	LB52	0,1	0	0	0		0
2	S87 Ectopterygoid fossa: absent (0); present (1)		0				
	LB16		?				
3	S88 Intramandibular joint: absent (0); present (1)			1			1
	LB20			0			?
4	S92 Metacarpals I-III, asymmetrical extensor depressions: absent (0); present (1)					1	
	LB55					?	
5	S95 Pubic blade, distal width: subequal to (0), or 65% or less than (1), proximal width of blade.	0		1	1	1	1
	LB78	2		0	0	0	2
6	S97 Distal caudal prezygapophyses: short (0); elongate (1)	0	0				1
	LB47	1,0	1				0
7	S99 Manual digits I-III, penultimate phalanx (digits II, III) length and ungual (digits I-III) form: shorter or subequal to preceding phalanx, short moderately recurved unguals (0); longer than preceding phalanx, long strongly recurved unguals (1)					1	
	LB63					?	
8	S100 Metacarpals IV and V, diameter: short (0); vestigial, less than 50% diameter of metacarpal III (or metacarpal II) (1)			0			
	LB64			1			
9	S101 Pubic foot: absent (0); present (1). (loss of broad blade-shaped distal end)	0			1	?	1
	LB76	1			0	0	0
10	S133 Metacarpal I length: longer (0), or shorter (1), than phalanx 1 or ungual of digit I		0				
	LB57		1				
11	S131 Manual digits and metacarpals, longest: digit III, metacarpal III (0); digit II, metacarpal II (1)		0,1				
	LB61		1				
12	S134 Ischial distal end, anteroposterior dimension: less (0), or more (1), than greatest width of either ischial peduncle (i.e., "foot" present)		0	1		0	
	LB80		1	0		?	

involve direct observation of materials, which sometimes is limited to a single specimen. Presumably, most of this conflict is resolvable by recourse to original materials. As mentioned at the outset, that is not the goal of the present manuscript, in part because the detailed morphology of *Eoraptor lunensis* is not yet available. An imperative for future study, nevertheless, ought to be resolving these outstanding observational issues.

A little more than half of the variation in character state scores, on the other hand, involves suprageneric terminal taxa, such as Sauropodomorpha or Neotheropoda. In these cases, estimating the basal condition, or groundplan (Yeates 1995; Prendini 2001), of the terminal taxon is at issue. Different ideas about basal structure within these suprageneric terminal taxa is an important, and often unstated, assumption that directly influences choice of character state. Future studies ought to include a more explicit statement of the assumed basal relationships within suprageneric taxa as well as which taxa are consulted as exemplars.

In each of the two analyses compared we have seen that a very relevant partition of data is either sidelined (omitted or rejected) or exhibits startling variation in character state scores for the same or comparable taxa. Pondering the significance of tree lengths that differ by as little as one or two steps, in this light, seems questionable. Further observations on specimens, character descriptions, and consideration of the basal condition within suprageneric outgroups will all increase the overlap and accuracy in the character evidence we employ and decrease the differences in character state scores (Jenner 2004). Indeed, we must follow this path, if the practice of morphology-based phylogenetics has a rigorous future.

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