PHYLOGENETIC RELATIONSHIPS OF THE BASAL DINOSAURS, THE HERRERASAURIDAE

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ABSTRACT. Herrerasaurids were predatory, obligatorily bipedal dinosaurs recorded in early Late Triassic rocks of South America. It has been suggested recently that the Herrerasauridae constitute a paraphyletic assemblage, but several apomorphic traits in the dorsal, sacral, and caudal vertebrae and the pectoral and pelvic girdles support the monophyly of this group. The relationships of Dinosauria with other members of Ornithodira are considered, supporting the monophyly of the newly recognized clade Dinosauriformes, constituted of *Lagosuchus* + (*Pseudolagosuchus* + (Dinosauria)). The Dinosauria, including Herrerasauridae, Saurischia, and Ornithischia, is diagnosed on the basis of six synapomorphic traits. The hypothesis that the Herrerasauridae constitute the sister-group of the remaining dinosaurs is supported here on the basis of four apomorphic traits uniquely shared by Saurischia and Ornithischia. The recently coined name Eudinosauria is used for the group of dinosaurs including the common ancestor of Saurischia, Ornithischia, and all of its descendants.

THE early diversification of the dinosaurs is documented mainly from Ischigualastian Age (approximately Carnian) beds of South America, which have yielded remains of several taxa commonly considered as the oldest known carnivorous dinosaurs. The Santa María Formation (Southeastern Brazil) has yielded material of *Staurikosaurus pricei* Colbert, 1970 (Galton 1977); and the Ischigualasto Formation (Northwestern Argentina), probably younger than the Santa María Formation (Bonaparte 1982), produced *Herrerasaurus ischigualastensis* Reig, 1963 (Novas 1989*a*; Sereno and Novas 1990). Almost complete herrerasaurid material recently collected in the latter formation (Sereno *et al.* 1988) strongly suggests that the type specimens of *Ischisaurus cattoi* Reig, 1963 and *Frenguellisaurus ischigualastensis* Novas, 1986 are cospecific with *Herrerasaurus ischigualastensis*, and these are considered as junior synonyms of this last taxon. The supposed occurrence of *Staurikosaurus* in the Ischigualasto Formation, as claimed by Brinkman and Sues (1987), is based on a very poorly preserved specimen that does not exhibit autapomorphies of *Staurikosaurus*. *Herrerasaurus* and *Staurikosaurus* were obligatorily bipedal dinosaurs, 1–5 metres long, with an unusual mixture of both plesiomorphic characters with respect to saurischians and ornithischians, and derived features similar to those of tetanurine theropods (Reig 1963; Benedetto 1973; Gauthier 1986).

Cladistic relationships between *Herrerasaurus* and *Staurikosaurus* are still debated. Both taxa are grouped together in Herrerasauridae by some authors (Benedetto 1973; Novas 1986, 1989*a*, 1989*b*), whereas others doubt this arrangement (Galton 1977; Gauthier 1986; Brinkman and Sues 1987; Paul 1988; Benton 1990; Sues 1990). The phylogenetic relationships of *Herrerasaurus* and *Staurikosaurus* with Saurischia and Ornithischia are also debatable. Herrerasaurids have been variously considered to be saurischians with theropod affinities (Benedetto 1973; Galton 1985), carnivorous sauropodomorphs (Colbert 1970), the sister group of Ornithischia + Saurischia (Gauthier 1984, 1986; Gauthier and Padian 1985), and as Dinosauria *incertae sedis* (Novas 1989*a*).

I will examine two main aspects of Herrerasauridae: do they constitute a monophyletic group, and what are their relationships within Dinosauria?

Abbreviations. FMNH, Field Museum of Natural History (Chicago); MACN, Museo Argentino de Ciencias Naturales (Buenos Aires); MCZ, Museum of Comparative Zoology, Harvard University (Boston); PVL, Paleontología de Vertebrados, Fundación 'Miguel Lillo' (S. M. de Tucumán); PVSJ, Paleontología de

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HERRERASAURIDAE AS A MONOPHYLETIC GROUP

The Herrerasauridae was erected by Benedetto (1973) to include *Herrerasaurus* and *Staurikosaurus*, based on numerous resemblances between them. Galton (1977, p. 240) considered both taxa as 'sufficiently different' to be placed in distinct families, and created the Staurikosauridae for the reception of *Staurikosaurus*, a position followed by Brinkman and Sues (1987), Paul (1988), and Sues (1990). Brinkman and Sues (1987) and Sues (1990) considered Herrerasauridae (*sensu* Benedetto 1973) as a paraphyletic assemblage, citing two characters *Herrerasaurus* shares with Saurischia and Ornithischia (exclusive of *Staurikosaurus*): tibia with a transversely expanded distal end, and three sacral vertebrae. However, a transverse expansion of the distal tibia seems to have been attained independently in *Herrerasaurus*, ornithischians, theropods, and sauropodomorphs (Novas 1989*a*), and contrary to previous interpretations (Reig 1963; Benedetto 1973) *Herrerasaurus* (PVL 2566; PVSJ 104; PVSJ 461) exhibits only two sacral vertebrae, a character probably retained also by *Staurikosaurus* (Galton 1977).

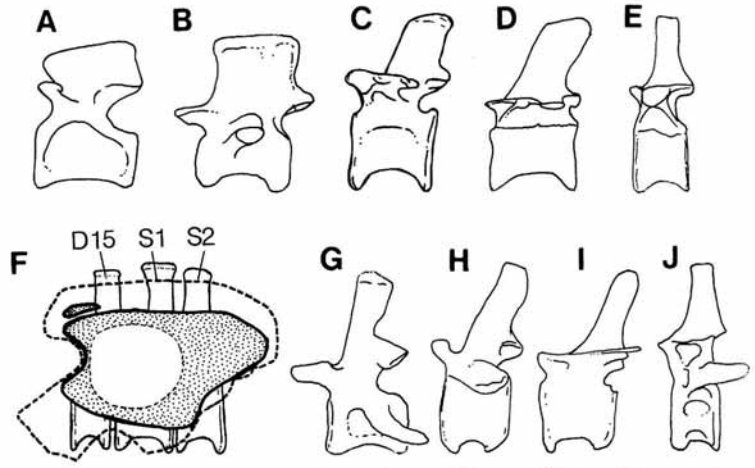
While the evidence supporting the paraphyly of the Herrerasauridae is ambivalent, the monophyletic nature of the Herrerasauridae is supported by the following derived traits uniquely shared by *Herrerasaurus* and *Staurikosaurus*:

A. *Posterior dorsal vertebrae with centra anteroposteriorly shortened (e.g. dorsal 13–15 with length/height ratio less than 0·8)*. Posterior dorsal vertebrae with long and low centra are present in *Lagosuchus* (Text-fig. 1A) with a length/height ratio (L/H) near to 1·95. Proportionately long centra (with respect to depth) seems to be plesiomorphic for Dinosauria, because that condition is present ancestrally in ornithischians (Santa Luca 1980), sauropodomorphs (Huene 1926; Bonaparte 1971; Cooper 1981), and theropods (Welles 1984; Bonaparte 1986), in which the L/H ratio for posterior dorsal vertebrae is $> 0{\cdot}9$ (Text-fig. 1B–D). On the contrary, *Herrerasaurus* and *Staurikosaurus* share posterior presacral vertebrae with short high centra, with $L/H < 0{\cdot}8$ for the thirteen dorsal vertebra (Text-fig. 1E).

B. *Posterior dorsal and first sacral vertebrae with robust neural spines axially shortened, squared shaped in cross-section*. The posterior dorsals and sacral vertebrae of *Lagosuchus* have plate-like, axially long, neural spines (Text-fig. 1A). This condition is ancestral for Dinosauria because it is present in basal ornithischians, sauropodomorphs, and theropods (Text-fig. 1B–D). *Herrerasaurus* and *Staurikosaurus* are derived in that they share posterior dorsal and first sacral vertebrae with stout, anteroposteriorly short neural spines that are quadrangular in cross-section (Text-fig. 1E).

C. *Sacral vertebrae with very deep sacral ribs especially that of the last vertebra, which cover nearly 90% of the medial surface of the iliac blade*. Lightly-built sacral ribs, with those of the last sacral vertebrae dorsoventrally flattened and fan-shaped, are present in *Chanaresuchus* (PVL 4375), *Gracilisuchus* (PVL 4597), *Lagerpeton* (PVL 4619), and *Lagosuchus* (PVL 3870), and represent the plesiomorphic condition for Archosauriformes (*sensu* Gauthier 1984). The fan-shaped ribs articulate with a horizontal ridge running medially on the posterior iliac blade. This condition was retained in Dinosauria ancestrally, being present in early sauropodomorphs (Huene 1926; Cooper 1981), theropods (Welles 1984), and ornithischians (Galton 1974). *Herrerasaurus* exhibits first and second sacral vertebrae with ribs dorsoventrally deep, especially that of the last sacral, which surpass ventrally the medial ridge of the posterior iliac blade and extend towards the rear near the posterior margin of the ilium (Text-fig. 1F). Dorsoventrally deep sacral ribs are also present in *Staurikosaurus pricei* (MCZ 1669).

D. *Proximal caudals with vertical neural spines*. Ornithischians, sauropodomorphs, and theropods appear to have retained the ancestral condition (e.g. *Lagosuchus*, PVL 3871) in that the neural spines of the proximal caudals are posteriorly inclined (Text-fig. 1G–I). Instead, *Herrerasaurus* and *Staurikosaurus* are unique in that they share proximal caudals with vertical neural spines (Text-fig. 1J).

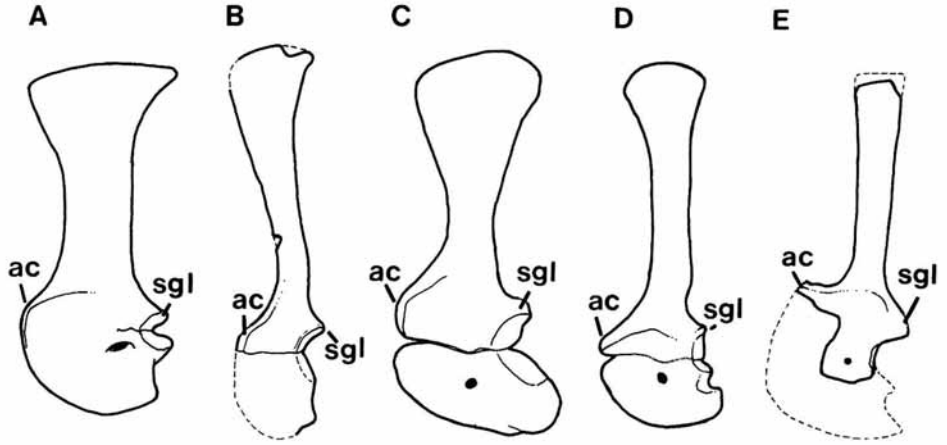


TEXT-FIG. 1. Vertebral column in lateral view of several taxa of Dinosauriformes. Not to scale. A–E, posterior dorsal vertebrae of A, *Lagosuchus*; B, *Heterodontosaurus*; C, *Plateosaurus*; D, *Dilophosaurus*; E, *Staurikosaurus*. F, dorsal fifteen and first and second sacrals of *Herrerasaurus* (PVL 2566) showing sacral rib attachment (stippled) on the ilium (dotted line). G–J, proximal caudal vertebrae of G, *Heterodontosaurus*; H, *Plateosaurus*; I, *Dilophosaurus*; J, *Herrerasaurus* (PVL 2566). A, after Bonaparte (1975); B, G, after Santa Luca (1980); C, H, after Huene (1926); D, I, after Welles (1984); E, after Galton (1977). Abbreviations: D15, fifteenth dorsal vertebra, S1, first sacral vertebra, S2, second sacral vertebra.

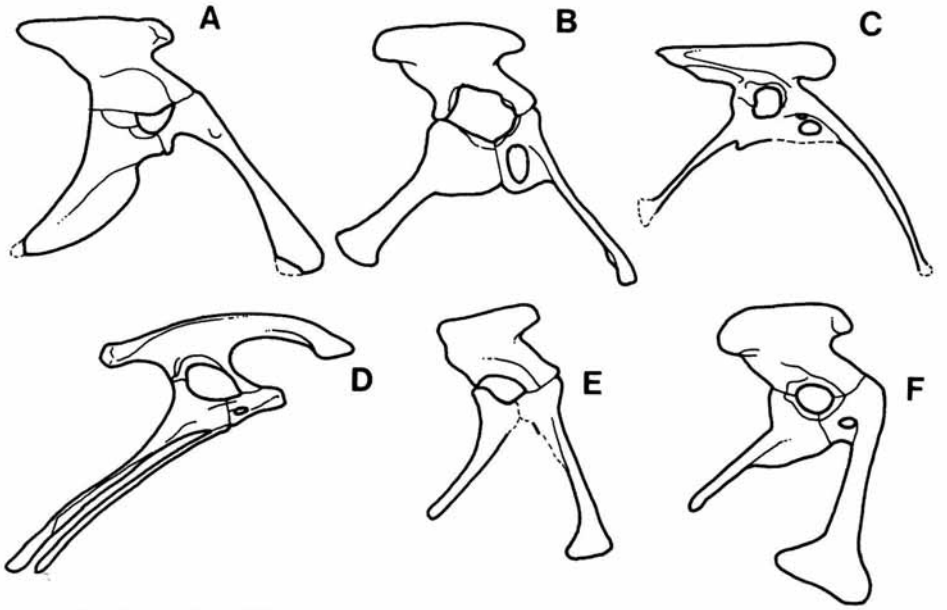
E. *Distal caudals with elongated prezygapophyses, overlapping nearly 50% of the preceding vertebra.* In Dinosauria ancestrally, distal caudals have short prezygapophyses (Gauthier 1986), surpassing slightly the anterior border of the centrum. This condition is present in *Lagosuchus* (PVL 3871), ornithischians (Thulborn 1972; Santa Luca 1980; Colbert 1981), and sauropodomorphs (Huene 1926). On the contrary, *Herrerasaurus* and *Staurikosaurus* share distal caudal vertebrae with elongated prezygapophyses, that overlap more than half of the preceding vertebrae (Galton 1977; Novas 1986). Theropods exhibit also this derived feature (see Raath 1969), but in the context of the evidence, it is interpreted that elongate prezygapophyses arose independently in Herrerasauridae and Theropoda (Gauthier 1986).

F. *Acromial process extends distally with respect to the scapular glenoid lip, and forms nearly a right angle with the scapular blade.* In *Lagosuchus* (Bonaparte 1975) and ancestrally in Sauropodomorpha (Huene 1926; Bonaparte 1971), Theropoda (Bonaparte 1986; Colbert 1989), and Ornithischia (Santa Luca 1980; Colbert 1981) the acromial process (ac, Text-fig. 2A–D) occupies approximately the same level as, or is proximal to, the scapular glenoid lip (sgl) and forms a wide curve with the scapular blade. *Herrerasaurus* exhibits an apomorphic condition with a deep acromial process extended distally with respect to the scapular glenoid lip, and defines an angle near to 90° with the scapular blade (Text-fig. 2E). This set of derived features is also seen in an undescribed, fragmentary right scapula of the type specimen of *Staurikosaurus pricei* (MCZ 1669).

G. *Distal expansion of the scapular blade strongly reduced.* In Dinosauria ancestrally the scapular blade is distally expanded anteroposteriorly (Gauthier 1986), representing more than 27% of the length of the scapula. *Herrerasaurus* (Text-fig. 2E) exhibits a distinct morphology of the scapula (Brinkman and Sues 1987; Novas 1989*b*), with slender scapular blade anteroposteriorly narrow distally, representing approximately 16% of the length. Colbert (1970, fig. 2) illustrates a distal end of a scapula of *Staurikosaurus*, but the morphology and proportions of this fragmentary bone do



TEXT-FIG. 2. Scapular girdle in lateral view of different taxa of Dinosauriformes. Not to scale. A, *Lagosuchus* (after Bonaparte 1975). B, *Heterodontosaurus* (after Santa Luca 1980). C, *Riojasaurus* (after Bonaparte 1971). D, *Piatnitzkysaurus* (after Bonaparte 1986). E, *Herrerasaurus* (reconstruction based on PVSJ 53 and MCZ 7064). Abbreviations: ac, acromial process, sgl, scapular glenoid lip.



TEXT-FIG. 3. Pelvic girdle of different taxa of Dinosauriformes. Not to scale. A, *Lagosuchus* (after Bonaparte 1975). B, *Plateosaurus* (after Huene 1926). C, *Syntarsus* (after Raath 1969). D, *Heterodontosaurus* (after Santa Luca 1980). E, *Staurikosaurus* (after Galton 1977). F, *Herrerasaurus* (reconstruction based on PVL 2566 and PVSJ 373).

not coincide with the proximal portion of the scapula cited above. The available evidence suggests that the distal end of the scapular blade in *Staurikosaurus* was anteroposteriorly narrow like that of *Herrerasaurus*.

H. *Pubis with distal half anteroposteriorly expanded.* Ancestrally in Ornithodira (e.g. *Lagerpeton*, *Lagosuchus*, and *Pseudolagosuchus*; Bonaparte 1975; Arcucci 1986, 1987) the distal half of the pubis has anterior and posterior margins subparallel in lateral view (in *Lagosuchus* the apparent distal expansion of the pubis in lateral view is due to a light lateral folding of the pubic plate; Text-fig. 3A). Dinosaurs retained such a condition since it can be seen in Sauropodomorpha, Theropoda, and Ornithischia (Text-fig. 3B–D). On the other hand, *Herrerasaurus* and *Staurikosaurus* exhibit unusual pubes with the distal half anteroposteriorly expanded, with anterior and posterior margins distally divergent (Text-fig. 3E–F), defining 'U-shaped' pubes in cross-section at the mid-length.

I. *Distinct pubic 'foot' anteroposteriorly expanded, more than 25% of pubic length.* In Ornithodira ancestrally the distal end of the pubis is anteroposteriorly flat (e.g. *Lagosuchus* and *Pseudolagosuchus*), a condition retained in Ornithischia (Santa Luca 1980), and early saurischians, which exhibit the distal end of the pubis almost unexpanded (Huene 1926; Welles 1984; Text-fig. 3A–D). One outstanding synapomorphy of the Herrerasauridae is the presence of an enlarged distal pubic 'foot' (Text-fig. 3E–F), representing more than 25% of the pubic length (Benedetto 1973).

Based on this analysis, the family Herrerasauridae is considered to be a monophyletic group, which includes *Herrerasaurus* and *Staurikosaurus* and their most recent common ancestor. Since the Staurikosauridae is monotypic, a cladistic diagnosis of this taxon is redundant with that of *Staurikosaurus*, and consequently is phylogenetically uninformative.

SYSTEMATIC PALAEONTOLOGY

Family HERRERASAURIDAE Benedetto, 1973

Diagnosis. Dinosaurs with posterior dorsal vertebrae with centra anteroposteriorly shortened (e.g. dorsal 13–15 with length/height ratio less than 0·8); posterior dorsal and sacral vertebrae with robust neural spines axially shortened, square-shaped in cross-section; sacral vertebrae with very deep sacral ribs, especially that of the second sacral, which covers almost the entire medial surface of the iliac blade; proximal caudals with vertical neural spines; distal caudals with elongated prezygapophyses, overlapping nearly 50% of the preceding vertebra; acromial process extends distally with respect to the scapular glenoid lip, and forms nearly a right angle with the scapular blade; distal expansion of the scapular blade strongly reduced; pubis with distal half anteroposteriorly expanded; distinct pubic 'foot' axially broadened, more than 25% of pubic length.

Comments. None of the synapomorphic traits diagnostic of the Herrerasauridae is seen in *Walkeria* (Maleri Formation, India; Chatterjee 1987), thus dismissing opinions that it is a member of the Herrerasauridae, as claimed by Paul (1988). On the contrary, the available information supports its referral as Dinosauria *incertae sedis* (Novas 1989*a*). *Aliwalia* (Elliot Formation, South Africa), scantily represented by portions of a femur, was interpreted by Galton (1985) as closely related to *Herrerasaurus* and *Staurikosaurus*, and as a member of the Herrerasauridae by Paul (1988). Nevertheless, the fragmentary femur not only does not share apomorphies with *Herrerasaurus* and *Staurikosaurus* (Sues 1990), but exhibits a prominent anterior trochanter, a derived feature shared by Saurischia and Ornithischia, exclusive of the Herrerasauridae (see below). In my opinion, the type specimen of *Aliwalia rex* is referable as Dinosauria indet., but in the absence of autapomorphic (diagnostic) features, *Aliwalia rex* is best regarded as a *nomen nudum*.

PHYLOGENETIC RELATIONSHIPS OF BASAL DINOSAURS

The phylogenetic relationships and the diagnosis of the Dinosauria have been substantially altered as a result of cladistic studies (e.g. Gauthier 1984, 1986; Brinkman and Sues 1987; Novas 1989*a*;

Benton 1990; Sereno and Novas 1990). Nevertheless, information resulting from recent studies and the discovery of better preserved specimens and new taxa, challenge those hypotheses and promote re-examination of the characters supporting them. Gauthier (1984, 1986) offered extensive evidence to support the view that Dinosauria, Pterosauria, and *Lagosuchus* constitute a monophyletic assemblage, which he termed Ornithodira. Although this hypothesis gained acceptance among some authors (e.g. Padian 1984; Gauthier and Padian 1985; Sereno and Novas 1990), disagreement remains about the position of *Lagosuchus*. Gauthier (1984, 1986, p. 46) grouped pterosaurs and dinosaurs in the ornithodiran subclade 'Ornithotarsi', with *Lagosuchus* as the immediate outgroup, but the evidence supporting such an interpretation is founded on several apomorphic similarities which are untestable in the available material of *Lagosuchus*. Other characters which Gauthier (1984) cited in favour of a monophyletic 'Ornithotarsi' (e.g. distal tibia transversely broadened; absence of calcanear tuberosity; simplified intratarsal joint) are absent in the Herrerasauridae, and the tarsal characters in early sauropodomorphs (Novas 1989*a*); consequently these features are considered apomorphic resemblances independently acquired by pterosaurs, ornithischians, and theropods. A preliminary study of ornithodiran relationships (Sereno and Novas 1990) strongly supports the Pterosauria and *Lagerpeton* (Arcucci 1986) as successively closer sister-groups of the remaining ornithodirans.

In order to study the phylogenetic relationships among dinosaurs and their more immediate outgroups, seventeen derived features in five terminal taxa were analysed using parsimony (see data matrix, Table 1). The character analysis is presented below and the result depicted as a cladogram in Text-figure 6.

TABLE 1. Character data matrix for five terminal taxa of Dinosauriformes. Character states scored for Ornithischia and Saurischia are hypothesized as ancestral for each group. Character numbers correspond to those listed in the text.

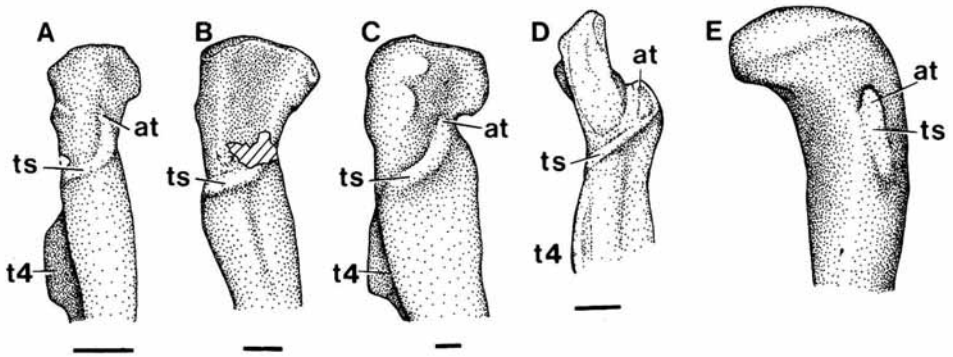
Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Lagosuchus	1	1	1	1	1	0	0	?	0	0	0	0	0	0	0	0	0
Pseudolagosuchus	1	1	1	1	1	1	1	?	0	?	0	0	0	0	0	0	0
Herrerasauridae	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Ornithischia	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Saurischia	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Lagosuchus, *Pseudolagosuchus*, and Dinosauria share the following set of derived traits, absent in Ornithodira ancestrally:

1. subrectangular, distally projected deltopectoral crest on the humerus;
2. presence of a trochanteric shelf on the lateroproximal surface of the femur (Text-fig. 4A–C; see character 17 for comments);
3. anterior trochanter on femur;
4. tibia with prominent cnemial crest;
5. distal tibia with lateral longitudinal groove.

These apomorphies suggest a monophyletic group, **Dinosauriformes** (Novas 1991), that comprises the most recent common ancestor of *Lagosuchus*, Dinosauria, and all taxa stemming from it. Within Dinosauriformes, *Pseudolagosuchus* and the Dinosauria are grouped together in an unnamed taxon, which exhibits the following apomorphies:

6. elongated pubis, nearly as long as the femur;
7. presence of a pyramidal-shaped ascending process of the astragalus, with a posterior subvertical facet and presence of an elliptical depression behind this process.



TEXT-FIG. 4. Proximal portion of the right femur of different taxa of Dinosauriformes. A, *Lagosuchus* (PVL 3871; scale 5 mm). B, *Pseudolagosuchus* (left femur reversed; UPLR-PV 53; scale 5 mm). C, *Herrerasaurus* (PVL 2566; scale 20 mm). D, *Syntarsus* (after Rowe 1989; scale 20 mm). E, *Massospondylus* (after Cooper 1981; not to scale). Abbreviations: at, anterior trochanter, ts, trochanteric shelf, t4 fourth trochanter.

Based on recent studies on dinosaur phylogeny (Gauthier 1986; Brinkman and Sues 1987; Novas 1989*a*, 1989*b*; Sereno and Novas 1990), and as a result of the present analysis, the following features are considered synapomorphic for Dinosauria:

8. increased asymmetry of the hand (phalangeal formula, 2-3-4-5-2);
9. perforated acetabulum;
10. ischium with slender shaft and with ventral 'keel' (obturator process) restricted to the proximal third of the bone;
11. femoral head more distinctly set off from shaft of femur;
12. tibia overlaps anteroproximally and posteriorly the ascending process of the astragalus (i.e. ascending process inserts beneath the tibia), with consequent ventral projection of the posterior process of the tibia;
13. calcaneum with a concave proximal articular surface, fixed to the distal end of the fibula.

The relationships of the Herrerasauridae with the Saurischia and Ornithischia are debatable. Commonly they were included in the Saurischia (e.g. Reig 1963; Colbert 1970; Benedetto 1973; Galton 1977, 1985), based primarily on pelvic morphology. Herrerasaurids share with sauropodomorphs and theropods an elongate, anteroventrally oriented pubis, perforate acetabulum, and an elongate ischium, features frequently used to define a 'saurischian pelvis' (e.g. Romer 1956). Nevertheless, none of these characters constitutes a synapomorphy of Saurischia: the anteroventral orientation of the pubis 'is a basic archosaur patent' (Romer 1956, p. 323), an elongate pubis (nearly as long as the femur) is present also in *Pseudolagosuchus* (Arcucci 1987), here considered as the immediate outgroup of the Herrerasauridae + (Saurischia + Ornithischia) clade; a perforate acetabulum and an elongate ischium are shared not only by herrerasaurids and saurischians, but also by ornithischians. In short, the 'saurischian pelvis' is an assemblage of plesiomorphic characters for Dinosauria (or even more inclusive groups), and does not support close relationships among Herrerasauridae, Sauropodomorpha, and Theropoda.

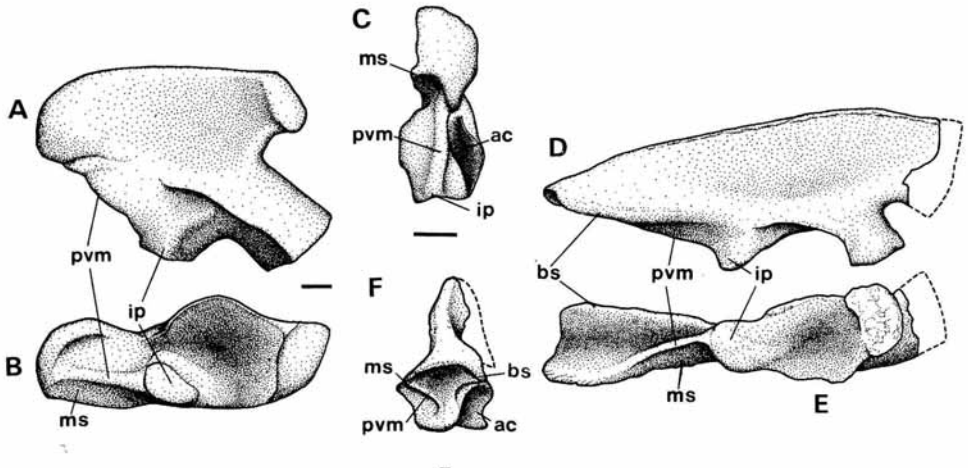
More recently, Gauthier (1984, 1986) and Gauthier and Padian (1985) considered herrerasaurids as the sister taxon of Ornithischia plus Saurischia, but no characters were cited by them in support of such an interpretation. Nevertheless, this hypothesis gained support among other authors (Brinkman and Sues 1987; Sereno and Novas 1990; Sues 1990; this paper), and Brinkman and Sues 1987, Text-fig. 7) listed in favour of such a phylogenetic arrangement 'medial wall to acetabulum less well developed', and 'pedal digit V small'. However, these characters are doubtful.

The geometry and relative development of the medial acetabular wall (expressed as a percentage of dorsoventral depth with respect to the anteroposterior length of the medial acetabular opening) is similar in *Staurikosaurus* (27%), *Herrerasaurus* (32%), and basal ornithischians (33%; Santa Luca 1984, fig. 13); only sauropodomorphs and theropods exhibit a higher ratio (nearly, or more than 50%; Bonaparte 1971; Cooper 1981; Welles 1984), and probably constitutes a synapomorphy of Saurischia. The assertion of Gauthier (1986, p. 46) that the acetabulum becomes fully perforate independently more than once in dinosaur evolution is probably true.

As for the reduction of pedal digit V (because of preservation only metatarsals, exclusive of phalanges, are considered here), a metatarsal V shorter than I is present in ornithischians (Galton 1974) and theropods (Welles 1984; Colbert 1989), but the distribution is problematic in early sauropodomorphs since some of them exhibit a metatarsal V subequal to, or even longer than, metatarsal I (Cooper 1981, table 4). Also, some specimens of *Herrerasaurus* exhibit a metatarsal V slightly shorter than metatarsal I.

Four synapomorphic features shared by Saurischia and Ornithischia are recognized here in support of the outgroup position of Herrerasauridae with respect to the remaining dinosaurs, as depicted in Text-figure 6:

14. *At least three sacral vertebrae*. The sacrum of *Herrerasaurus* (PVL 2566; PVSJ 104; PVSJ 461) is composed of two sacral vertebrae, widely attached to the ilia through the sacral ribs, a condition probably present in *Staurikosaurus* (Galton 1977). In *Herrerasaurus* the last dorsal vertebra (dorsal fifteen) is placed behind the tip of the anterior iliac spine (Text-fig. 1F), but its transverse processes, laterally projected above the first sacral rib, do not articulate with the inner surface of the ilia. On the contrary, saurischians and ornithischians can be distinguished from more remote outgroups in that they exhibit a sacrum with three or more sacrals, a condition convergently acquired in Pterosauria among ornithodirans (Padian 1984). It is hypothesized here that in the common ancestor of Saurischia and Ornithischia, the vertebra that increased the sacral count to three was incorporated from the presacral series, because in several non-dinosaurian archosauromorphs (e.g. *Lagosuchus*, *Lagerpeton*, *Gracilisuchus*, *Chanaresuchus*) and early dinosaurs

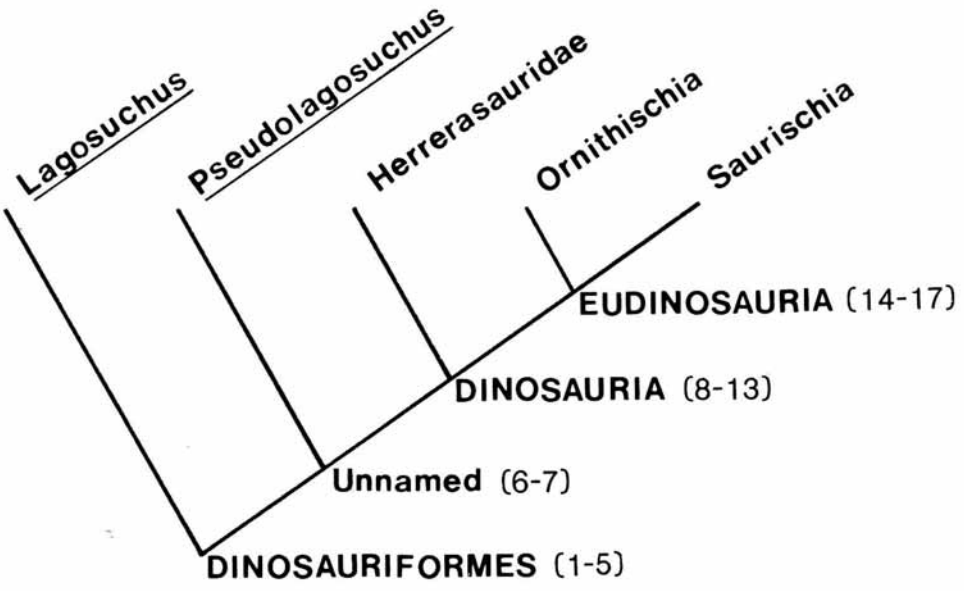


TEXT-FIG. 5. Right ilia in A, D, lateral; B, E, ventral; and C, F, posterior views. A–C, *Herrerasaurus* (A–B, PVL 2566; C, MACN 18.688); D–F, *Torvosaurus* (after Galton and Jensen 1979). Abbreviations: ac, acetabulum, bs, brevis shelf, ip, ischiadic peduncle, ms, medial shelf for sacral rib articulation, pvm, posteroventral margin of ilium. Scale 20 mm.

(*Herrerasaurus*) the placement of the two sacral vertebrae with respect to the ilia is coincident with that of sacrals 2 and 3 of basal sauropodomorphs. In addition, in the archosauromorphs and early dinosaurs mentioned above, the sacral rib of the last sacral vertebra has a similar fan-shaped morphology and it articulates along the medial surface of the posterior iliac blade (Novas 1987, 1989*b*). This evidence refutes the interpretation that in early sauropodomorphs the third sacral vertebra is of caudal origin (Charig *et al.* 1965; Charig 1982).

15. *Presence of a prominent brevis shelf on the lateroventral side of the postacetabular blade of the ilium.* Gauthier (1986, p. 43) recognized this character as a synapomorphy of Ornithodira, but the distribution of the brevis shelf is restricted to Saurischia and Ornithischia among ornithodirans. In Ornithodira ancestrally (e.g. *Lagerpeton*, *Lagosuchus*) the postacetabular portion of the iliac blade is transversely compressed, with the posteroventral margin running from the ischiadic peduncle towards the posterior end of the blade, a condition retained by herrerasaurids (Text-fig. 5A–C). In contrast, saurischians (e.g. Galton and Jensen 1979) and ornithischians (Thulborn 1972; Galton 1974), aside from the posteroventral margin running from the ischiadic peduncle to the posterior end of the blade (pvm), exhibit a distinct and prominent shelf on the lateroposterior margin of the iliac blade, the brevis shelf (bf, Text-fig. 5D–F).

16. *Presence of a prominent anterior (lesser) trochanter on the femur.* In Dinosauriformes ancestrally (e.g. *Lagosuchus*, *Pseudolagosuchus*, *Herrerasaurus* and *Staurikosaurus*) the anterior trochanter is represented by a tiny vertical prominence (at, Text-fig. 4A–C). On the contrary, ornithischians (Thulborn 1972; Santa Luca 1980), sauropodomorphs (Huene 1926; Bonaparte 1971), and theropods (Raath 1969; Rowe 1989) share a prominent proximally projected anterior trochanter. The presence of the anterior trochanter in Ornithosuchidae (Bonaparte 1971) is considered homoplastic with that of Saurischia and Ornithischia.



TEXT-FIG. 6. Cladogram depicting phylogenetic relationships among dinosauriform ornithodirans. Numbers correspond to those listed in the text and scored in the data matrix (Table 1).

17. *Trochanteric shelf reduced to a slight prominence.* In Dinosauriformes ancestrally (e.g. *Lagosuchus*, *Pseudolagosuchus* and Herrerasauridae) the 'trochanteric shelf' (Gauthier 1986) constitutes a prominent posterodistally oriented ridge on the lateroproximal surface of the femur (ts, Text-fig. 4A–C). Ornithischians and saurischians exhibit a derived condition with respect to other dinosauriforms, consisting in a reduction (or even absence) of the trochanteric shelf. In ornithischians, the trochanteric shelf is lacking (Thulborn 1972; Galton 1974), in early sauropodomorphs the trochanteric shelf is represented by a slight, subvertical ridge placed distally to the anterior trochanter (Cooper 1981, fig. 67A), and ancestrally in tetanurine theropods (e.g. *Allosaurus*, FMNH 1505 and P25114) the trochanteric shelf is probably represented by a slight prominence anterodistally oriented. Ceratosaurian theropods (Abelisauridae and robust individuals of *Syntarsus*, *Coelophysis*, *Dilophosaurus*, *Ceratosaurus*; Gauthier 1986; Rowe 1989; Novas 1991; Text-fig. 5D) constitute an exception among saurischians because they show a very prominent trochanteric shelf, even more developed than in Dinosauriformes ancestrally. The distribution of the trochanteric shelf among dinosaurs suggests that in the common ancestor of saurischians and ornithischians this structure was reduced with respect to the plesiomorphic dinosauriform condition, and that among theropods the presence of a strongly developed trochanteric shelf, even more than in Dinosauriformes ancestrally, constitutes a synapomorphy of Ceratosauria (Gauthier 1986; Rowe 1989; Novas 1991).

In short, the character distribution suggests that the Herrerasauridae are the sister-group of Saurischia + Ornithischia, as originally proposed by Gauthier (1984, 1986). In agreement with the analysis presented above, the name **Eudinosauria** (Novas 1991) is proposed for the clade including the common ancestor of Saurischia and Ornithischia and all of its descendants.

DISCUSSION

Cladistic analysis supports the hypothesis that the Herrerasauridae constitute the sister-group of Ornithischia + Saurischia, a clade traditionally named Dinosauria Owen, 1841 (Owen 1842). Implicitly based on that conception Gauthier *et al.* (1989) excluded the Herrerasauridae from the Dinosauria, preserving in such a way the original usage of the term. Nevertheless, since the herrerasaurids were described, virtually all authors have considered them to be dinosaurs (e.g. Reig 1963; Colbert 1970; Benedetto 1973; Bakker and Galton 1974; Bonaparte 1975; Galton 1977; Brinkman and Sues 1987; Paul 1988; Novas 1989*a*; Benton 1990; Sues 1990). In an influential work, Gauthier himself (1986, p. 44) offered a new combination of Dinosauria, defining them to include Herrerasauridae, Saurischia, and Ornithischia. This last position is maintained here, maximizing the stability and the phylogenetic informativeness of the name of the taxon, the composition of which most authors accept.

Preserving the Dinosauria to include the common ancestor of Herrerasauridae and Saurischia + Ornithischia, and all of its descendants, the name Eudinosauria (Novas 1991) was coined to encompass the common ancestor of Saurischia, Ornithischia, and all of its descendants, the diagnosis of which is based on the presence of at least three sacral vertebrae, a brevis shelf on the lateroventral side of the postacetabular blade of the ilium, a prominent anterior trochanter on the femur, and a reduced trochanteric shelf.

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