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Early dinosaurs: a phylogenetic study

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SYNOPSIS Early dinosaur evolution has been the subject of several phylogenetic studies and the position of certain basal forms is currently debated. This is the case for the oldest known members of the group, excavated from the Late Triassic Ischigualastian beds of South America, such as *Herrerasaurus*, *Eoraptor*, *Pisanosaurus*, *Saturnalia* and *Staurikosaurus*. A new cladistic analysis of the early dinosaur radiation was performed to assess the relationships among the three major clades (Ornithischia, Sauropodomorpha and Theropoda) and to define the phylogenetic position of the basal members of the group. The most parsimonious hypothesis has *Silesaurus opolensis* as the sister taxon to a dichotomy including monophyletic Saurischia and Ornithischia. The latter includes *Pisanosaurus mertii*, and the former all other well-known Triassic dinosaurs. Saurischia is composed of two major monophyletic groups: Herrerasauridae (including *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei*) and Eusaurischia (including the theropod and sauropodomorph lineages), while *Eoraptor lunensis* appears to represent the sister taxon to Eusaurischia. *Saturnalia tupiniquim* is a stem-taxon to Sauropodomorpha and *Guaibasaurus candelariensis* might belong to the theropod branch. Some of these hypotheses are, however, not strongly supported. Especially uncertain are the affinities of *Silesaurus* and *Guaibasaurus*. The latter can only be safely regarded as a saurischian, while the former might belong to the ornithischian lineage. The dinosaurian affinities of *Eoraptor* and Herrerasauridae are strongly supported. Yet, the possibility that they (especially *Eoraptor*) represent basal theropods, rather than basal saurischians, cannot be dismissed. In fact, basal saurischian evolution is still too poorly understood for a definitive hypothesis of relationships to be presented.

KEY WORDS Dinosauria, Saurischia, Herrerasauria, Triassic, phylogeny, early radiation

Contents

Introduction

Various Triassic dinosaurs are regarded as basal members of one or other of the three major lineages of the group: ornithischians (Bonaparte 1976; Hunt & Lucas 1994; Baez & Marsicano 2001), theropods (Hunt *et al.* 1998; Rauhut & Hungerbühler 2000; Arcucci & Coria 2003), and sauropodomorphs (Galton 1990*a*; Yates & Kitching 2003). However, other well-known Triassic dinosaurs have a controversial taxonomic position. This is particularly the case for herrerasaurids (*Herrerasaurus* and *Staurikosaurus*), as well as *Eoraptor*, which have been regarded as basal to the Ornithischia–Saurischia dichotomy (Gauthier 1986; Brinkman & Sues 1987; Benton 1990; Novas 1992; Fraser *et al.* 2002), as basal theropods (Sereno & Novas 1992; Sereno *et al.* 1993; Novas 1993, 1996; Sereno 1999), or non-theropod basal saurischians (Holtz 1995; Langer 2001*a*, *b*, 2004). Herrerasaurid monophyly itself is debated, although accepted by most authors since its demonstration by Novas (1992, 1993); a more basal position for *Staurikosaurus* had been proposed in earlier studies (Brinkman & Sues 1987; Benton 1990).

The primary aim of this contribution is to provide detailed descriptions of the morphological characters used in a cladistic analysis to assess the interrelationships of the very basal members the dinosaurian clade. The study is focused on the phylogenetic positions of *Herrerasaurus*, *Staurikosaurus* and *Eoraptor*, but also tests some other assumptions of early dinosaur evolution, such as the status of *Pisanosaurus* and *Saturnalia* as the basalmost members of the ornithischian and sauropodomorph lineages, respectively. In addition, the phylogenetic positions of *Guaibasaurus candelariensis* (Bonaparte *et al.* 1999) and *Silesaurus opolensis* (Dzik 2003) are assessed cladistically for the first time.

Materials and methods

This study of early dinosaur evolution here employs standard procedures of cladistic analyses (Wiley *et al.* 1991; Forey *et al.* 1992). Despite recent criticism (Nixon & Carpenter 1993), the so-called 'first step in the two-step procedure' of Maddison *et al.* (1984) is used to define not only the character states of the composite outgroup, but also (in a 'reverse' practice) those of the three composite Operational Taxonomic Units (OTUs) of the ingroup, when internal variation in character distribution is present. In this procedure, members of each composite OTU are plotted on a predetermined phylogenetic framework (defined by previous analysis of the group). Based on the character states assigned to a set of taxa, the 'outgroup algorithm' is applied 'down the tree' for each character to determine the state of the ingroup node. These states are applied to the composite OTU and, together, represent the ancestral condition.

In order to exemplify this method, it is applied to determine the condition of the acetabular aperture in basal ornithischians (Fig. 1). The character varies within the composite taxon: *Scelidosaurus* has a closed acetabulum, while this structure is semi-perforate in all other early members of the group. The basal condition for Thyreophora is, therefore, uncertain, given that *Scelidosaurus* is the basal-most member of the clade for which a well-preserved ilium is known. Yet, since all basal neornithischians have a semi-perforate acetabulum, the basal condition for Genasauria is defined as semi-perforate. This is also the case for fabrosaurids such as *Lesothosaurus*, which corroborates a semi-perforate acetabulum as the ancestral ornithischian condition.

Source of the anatomical data

References to the source of the anatomical data are listed along with the quotation of certain taxa, including suprageneric groups of both the hypothetical outgroup (e.g. pseudosuchians, 'basal archosaurs') and composite ingroup OTUs (e.g. 'prosauropods', ornithopods). We have examined

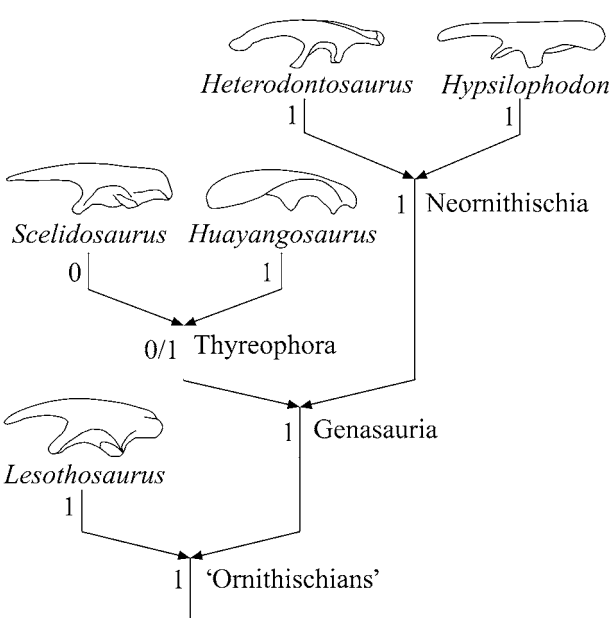

Figure 1 The 'outgroup algorithm' used to trace morphological changes and infer character states of composite ingroup operational taxonomic units (OTUs). In this case, exemplified by the acetabular aperture of ornithischians, it is based on the phylogeny of Sereno (1999). Abbreviations (character states): 0, closed acetabulum; 1, semi-perforated acetabulum.

Table 1 Source of the anatomical data for the ingroup single-taxon OTUs and some members of the outgroup.

Taxon	Source
Eoraptor lunensis	PVSJ 512; Sereno *et al.* (1993); Novas (1993); Rauhut (2003)
Guaibasaurus candelariensis	MCN PV2355, PV2356; Bonaparte *et al.* (1999)
Herrerasaurus ischigualastensis	PVL 2054, 2566; PVSJ 104, 373, 407, 461; MACN 1860; Novas (1992, 1993); Sereno & Novas (1993); Sereno (1993)
Lagerpeton chanarensis	PVL 4619; Arcucci (1986); Sereno & Arcucci 1993; Novas (1989, 1996)
Lewisuchus admixtus	Romer (1972*b*); Arcucci (1997, 1998); Hutchinson (2001*b*)
Marasuchus lilloensis	PVL 3870, 3871, 3972, 4672; Bonaparte (1975, 1999); Novas (1989, 1992, 1996), Sereno & Arcucci (1994)
Pisanosaurus mertii	PVL 2577; Bonaparte (1976); Sereno (1991*b*)
Pseudolagosuchus major	PVL 4629; Arcucci (1987, 1997, 1998); Novas (1989, 1992, 1996)
Saturnalia tupiniquim	MCP 3844-PV, 3845-PV, 3846-PV; Langer (2003)
Silesaurus opolensis	ZPAL Ab III 404/1; Dzik (2003)
Staurikosaurus pricei	MCZ 1669; Galton (1977, 2000*a*); Novas (1992, 1993); Bittencourt (2004)

specimens of most relevant taxa first-hand, including the basal dinosauromorphs in the outgroup and the single-taxon ingroup OTUs. Data sources are summarised in Table 1 and these references are generally not repeated in the text.

The abbreviations for the various institutions where material discussed in this paper is held are as follows: **BMNH**, Natural History Museum, London, UK; **BRSUG**, University of Bristol, Department of Earth Sciences, Bristol, UK; **GPIT**, Institut für Geologie und Paläontologie, Tübingen, Germany; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MB**, Humboldt Museum für Naturkunde, Berlin, Germany; **MCN**, Museu de Ciências Naturais, Fundacão Zoobotânica, Porto Alegre, Brazil; **MCP**, Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil; **MCZ**, Museum of Comparative Zoology, Cambridge, MA, USA; **PVL**, Fundación "Miguel Lillo", Tucumán, Argentina; **PVSJ**, Museo de Ciencias Naturales, UNSJ, San Juan, Argentina; **QVM**, National Museum of Natural History, Harare, Zimbabwe; **SAM**, South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **ZPAL**, Institute of Paleobiology of the Polish Academy of Science, Warsaw, Poland.

Operational taxonomic units

The outgroup

The definition of an adequate dinosaur outgroup within Archosauria (*sensu* Benton 2004) has been debated. Whereas most basal Ornithosuchia (*sensu* Parrish 1997) are poorly known (Arcucci 1997; Benton 1999; but see Sereno & Arcucci 1994), other basal archosaurs are already highly derived in their own evolutionary line, as with pterosaurs (Wellnhofer 1991) and phytosaurs (Chatterjee 1978), have a debatable phylogenetic position, as is particularly the case of pterosaurs (Bennett 1996), or are too distantly related to dinosaurs, such as *Euparkeria* (Sereno 1991*a*). Because of these difficulties, a rather extensive phylogeny of non-dinosaurian archosaurs was compiled based on previous studies (Gauthier 1986; Benton & Clark 1988; Sereno 1991*a*; Parrish 1993, 1997; Juul 1994; Bennet 1996; Gower & Wilkinson 1996; Novas 1996; Arcucci 1997; Benton 1999) and used as a template for the 'outgroup algorithm' (Maddison *et al*. 1984). It consists of a basal polytomy including proterochampsids, *Euparkeria* and the 'crown-group archosaurs', the latter being composed of pseudosuchian and dinosaurian branches. Because of the growing evidence that pterosaurs may not belong within the 'crown-group archosaurs' (Wellnhofer 1991; Bennett 1996; Peters 2000), they have not been considered in this study. This framework has suchians, phytosaurs and ornithosuchids forming a basal polytomy within Pseudosuchia (*sensu* Parrish 1997), the first of which is composed of aetosaurs, rauisuchians and crocodylomorphs. The dinosaur lineage includes *Scleromochlus* and *Lagerpeton* as successive sister-taxa to Dinosauriformes, which consists of a polytomy including *Marasuchus*, *Lewisuchus*, *Pseudolagosuchus* and the ingroup (Bonaparte 1995; Arcucci 1997, 1998). The recently described putative dinosaur sister-taxon, *Silesaurus opolensis* (Dzik 2003), is included in the ingroup.

Single-taxon OTUs of the ingroup

Seven single-taxon OTUs are used in the present study: *Herrerasaurus ischigualastensis*, *Pisanosaurus mertii*, *Staurikosaurus pricei*, *Eoraptor lunensis*, *Saturnalia tupiniquim*, *Guaibasaurus candelariensis* and *Silesaurus opolensis* (details of material listed in Table 1). Among these, the monophyletic status of *Staurikosaurus* (Colbert 1970; Novas 1993) and *Pisanosaurus* (Bonaparte 1976; but see Sereno 1991*b*) are assured because they are known from a single specimen. More than one specimen of *Eoraptor*, *Saturnalia* and *Guaibasaurus* is known, but the data used in this study derives largely from their holotypes. When this is not the case, it is noted. The monophyletic status of *Herrerasaurus* and of *Silesaurus* is more controversial. The latter is known from an accumulation of more than 400 bones, including four partially articulated skeletons, which serves as the main basis for the descriptive account by Dzik (2003). The dentary, ilium, forearm and first pedal digit bear possible autapomorphies within the dinosaur lineage, but the overlapping of these among the four skeletons is too limited to guarantee their taxonomic association unambiguously. Nevertheless, since we did not have the opportunity to examine the specimens first-hand, the association is assumed for the purpose of the cladistic analysis and the characters are revised based on the data presented by Dzik (2003). Collectively, these are sufficient (see below) to warrant the inclusion of *Silesaurus* in the ingroup here.

Herrerasaurus is also known from various specimens (Novas 1993) and several autapomorphies have been proposed to diagnose the taxon (Novas 1993; Sereno 1993; Sereno & Novas 1993). Those related to the skull scapular girdle, and forelimb are, however, ambiguous. They might, in fact, represent apomorphic conditions of

Herrerasaurus plus its sister-taxon *Staurikosaurus*, given that these anatomical parts are poorly known in the latter. Additional autapomorphies of *Herrerasaurus* are also present in other Triassic members of the dinosaur lineage. This is the case for the spine tables in the caudal trunk and sacral vertebrae (Novas 1993) which are also seen in *Eoraptor* (PVSJ 512), and the circular pit on the humeral ectepicondyle (Sereno 1993), also present in *Saturnalia*. Furthermore, the sinuous lateral margin of the pubis (Novas 1993) is the result of two distinct and independent morphological transformations. The more proximal concavity is the pathway for the proximal extension of the *M. puboischiofemoralis externus* part 1, as seen in *Saturnalia* (Langer 2003), and various sauropodomorphs (Huene 1926; Galton 1973*a*; Cooper 1984). The distal compression, however, is simply the result of the extreme folding of the lateral margin of this part of the bone. This forms the well-developed 'pubic boot' of *Herrerasaurus*, which truly represents an unique feature of the taxon. Conditions such as the sub-circular scar on the laterocranial surface of the distal femur and the cranioproximal keel of the same bone (Novas 1993) are also seen in other archosaurs (Galton 1969; Sill 1974; Cooper 1981; Norman 1986; Bonaparte *et al*. 1999; Langer 2004). These muscle-related features are probably widespread among basal dinosaurs, but often not preserved. Accordingly, they are not considered autapomorphic for *Herrerasaurus*. In fact, only two of the previously proposed characters stand as autapomorphic for that taxon: the steep angle between the dorsal margin of the iliac peduncle of the ischium and shaft of the bone and the extremely enlarged 'pubic boot' (Novas 1993). These are not seen in the pelvic elements of any other putative Triassic dinosaur. Although the distal pubis of *Staurikosaurus* is also folded (character 77), it is not to the extent seen in *Herrerasaurus*. In addition, *Herrerasaurus* also differs from other Triassic dinosaurs in the extreme axially compressed caudal trunk, sacral and proximal caudal vertebrae (character 39).

Although diagnosable based on autapomorphies, does *Herrerasaurus* encompass all material previously attributed to the genus? Some of the most important specimens (Table 1) present at least one of the above defined autapomorphies, all of which are present in the holotype. This is, however, not the case for the type specimen of *Ischisaurus cattoi* which lacks pubis and ischium and does not have trunk vertebrae as compressed as those of *Herrerasaurus*. However, it lacks features supporting an assignment to other Triassic dinosaurs and resembles *Herrerasaurus* more than *Staurikosaurus* in the longer ischiadic peduncle of the ilium, the more dorsally expanded cnemial crest and the square distal tibia. The type material of *Frenguellisaurus ischigualastensis* also lacks autapomorphies of *Herrerasaurus* and the only skeletal parts that can be compared to both *Herrerasaurus* and *Staurikosaurus* are the mandible and some vertebrae. As described by Novas (1986), the dentary of *Frenguellisaurus* is much shorter than those of the other two taxa and its caudal vertebrae bear stronger lateral ridges for tendon insertion. These might represent autapomorphies of the taxon, but could also be related to the developmental stage of its much larger type. Indeed, the longer caniniform teeth of its maxilla may also be developmentally constrained and not taxonomically significant. Despite this, the skull material of *Frenguellisaurus* shows striking similarities to PVSJ 407, including a narrow U-shaped maxillary antorbital fossa, a lateral ridge on the jugal, a squared ventral ramus of the squamosal, a dorsally narrow laterotemporal fenestra and a mediocaudally expanded quadratojugal. In conclusion, the assignment of *Ischisaurus* and *Frenguellisaurus* to *Herrerasaurus* is probable (Novas 1993), based both on topotypic principles and morphological resemblance. Yet, this is not unambiguously supported by autapomorphies.

Anatomical remarks on Guaibasaurus *and* Saturnalia

Two basal dinosaurs have been described recently from the Late Triassic of South Brazil, but several of their anatomical details are still to be addressed. *Guaibasaurus candelariensis* (Fig. 2) is based on two partial skeletons and the distal portion of a left hind limb (Bonaparte *et al*. 1999) from the Caturrita Formation. The syntypical series of *Saturnalia tupiniquim* is composed of three partial skeletons (Langer *et al*.1999; Langer 2003; Fig. 3) from the slightly older Santa Maria Formation.

Guaibasaurus was first considered to be a basal saurischian (Bonaparte *et al*. 1999), but later studies suggested a theropod affinity (Langer 2004). The original diagnosis (Bonaparte *et al*. 1999) was based mostly on characters either plesiomorphic within Dinosauria, or widely distributed among the basal members of the group. These include trunk vertebrae with parapophyseal prezygapophyseal lamina, hyposphene–hypantrum auxiliary articulations and a complex of cranial, ventral and caudal chonoe; scapular blade slender and dorsally expanded; ilium with highly extended supra-acetabular crest and almost fully closed acetabular wall; elongated pubis and ischium; femur with small 'lesser trochanter' and no 'trochanteric shelf'; transversely narrow calcaneum with pronounced ventromedial process; and reduced metatarsal V, lacking phalanges.

The pre-sacral vertebrae of the holotype of *Guaibasaurus* are estimated to represent the caudal part of the trunk. Their centra are longer than deep. The parapophyses and diapophyses are placed on the dorsal portion of the neural arch and clear hyposphene–hypantrum auxiliary articulations are present. A set of robust laminae radiates from each diapophysis in the direction of the zygapophyses, parapophysis and the caudoventral corner of the neural arch. These laminae define deep cranial, medial and caudal chonoe. A ridge extending from the parapophysis to the cranioventral corner of the neural arch is, however, absent. This is a rare condition for basal dinosaurs, since well-developed precentro–parapophyseal laminae are seen in most other members of the group, except ornithischians (Santa Luca 1980; *Scelidosaurus* – BMNH 6704) and *Eoraptor*. Furthermore, the lack of a precentro–parapophyseal lamina together with well-developed cranial and ventral chonoe is a combination of features unique to *Guaibasaurus*, given that well-developed chonoe are absent in trunk vertebrae of basal ornithischians and *Eoraptor*.

Two articulated sacral centra, of the possibly three-vertebra sacrum of *Guaibasaurus*, have been preserved. The cranial-most of these is the largest and it is broader cranially than caudally. The ribs articulate on the cranial border of both elements. The presence of sacral centra with size disparity was considered diagnostic for *Guaibasaurus* by Bonaparte *et al*. (1999). Yet, the ambiguous identification of these elements casts doubt upon their phylogenetic significance. If the preserved sacral centra of *Guaibasaurus* represent the primordial archosaur elements, their size disparity

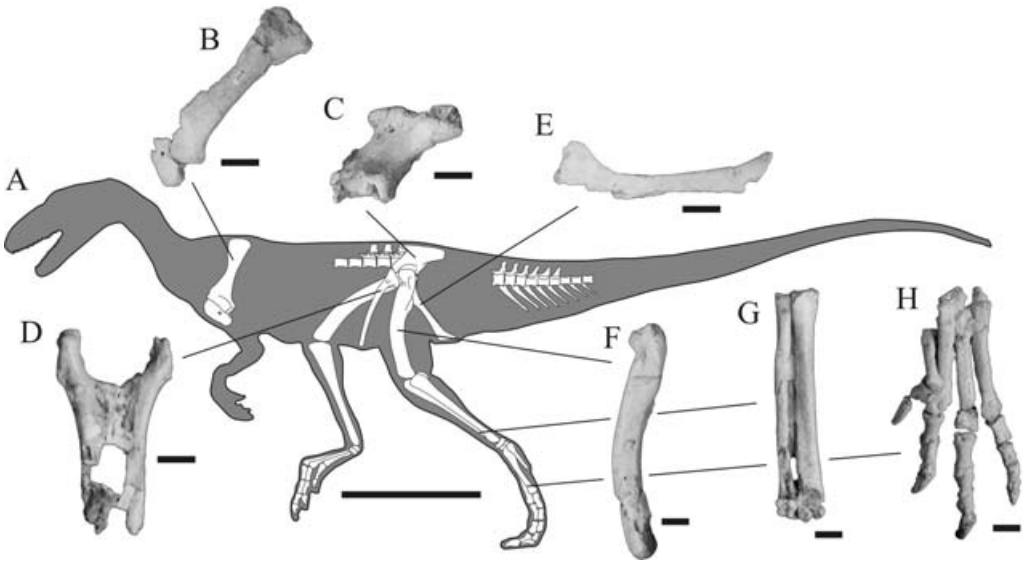

Figure 2 Skeletal reconstruction of *Guaibasaurus candelariensis*. **A**, preserved bones on shaded outline; **B**, left scapulocoracoid in lateral aspect; **C**, right ilium (reversed) in lateral aspect; **D**, pubic pair in cranial aspect; **E**, left ischium in lateral aspect; **F**, right femur (reversed) in lateral aspect; **G**, right tibia and fibula in cranial aspect; **H**, left pes in cranial aspect. **B–G** based on MCN-PV 2355 and **H** based on MCN-PV 2356. Scale bars: **A** = 250 mm; **B–H** = 25 mm.

is unique among basal dinosaurs. If, on the contrary, these are the second primordial sacral and a caudosacral, similar size disparity is known in other basal forms (Galton 1977; Novas 1993). The preserved caudal series probably represents the proximal part of the tail. Their neural spines are proximodistally short and distally inclined. The 'chevrons' are not longer than the height of the corresponding vertebra and bear fused condyles. The pectoral girdle of *Guaibasaurus* includes scapula and coracoid united in an immovable joint. The scapular blade is slender and not particularly expanded dorsally. The pelvis is propubic and the acetabulum almost fully closed. The ilium possesses a highly expanded crista supraacetabularis and a long postacetabular ala. This bears a marked brevis fossa, the medial edge of which is formed by the medioventral margin of the postacetabular ala. The pubic pair is transversely compressed distal to the ambiens processes, but its lateral margin is not caudally folded. Medially, the symphysis is formed by thin mediodorsal laminae. The ischia possess a robust and long symphysis and are markedly expanded distally. Their shafts are subtriangular in cross-section, lacking a medioventral lamina. A well-developed medial ridge is seen in the mostly flat dorsal margin of the pair, which medially bounds the origin area of the *M. ischiofemoralis*.

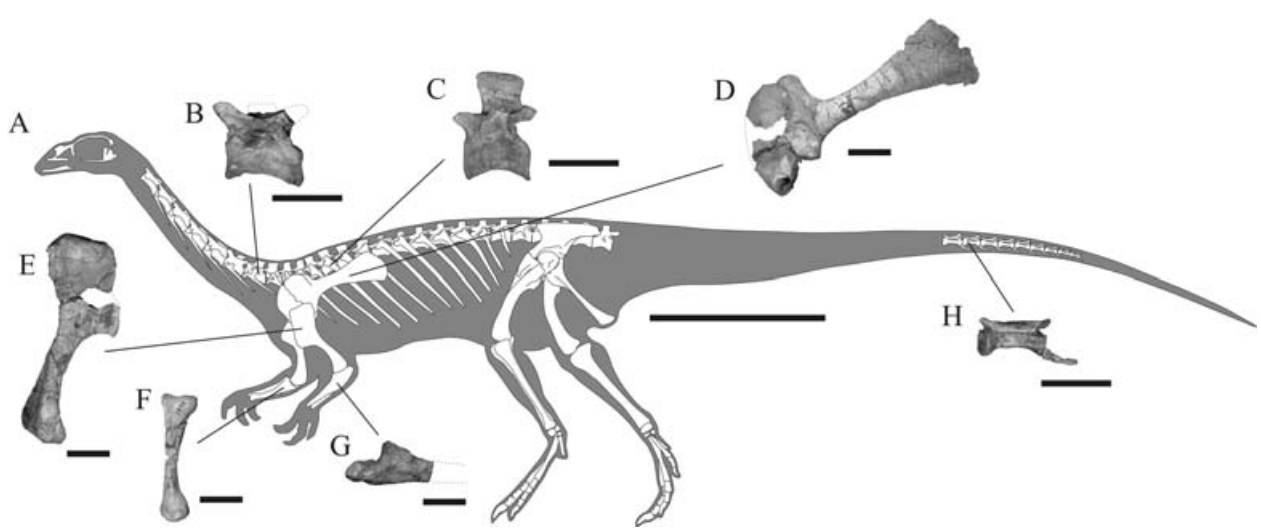

Figure 3 Skeletal reconstruction of *Saturnalia tupiniquim*. **A**, preserved bones on shaded outline; **B**, 8th cervical vertebra in lateral aspect; **C**, 4th trunk vertebra in lateral aspect; **D**, right scapulocoracoid (reversed) in lateral aspect; **E**, right humerus in lateral aspect; **F**, right radius in medial aspect; **G**, right ulna in lateral aspect; **H**, distal caudal vertebra in lateral aspect. **B–D, H** based on MCP 3845-PV and **E–G** based on MCP 3846-PV. Scale bars: **A** = 250 mm; **B–H** = 20 mm.

The femoral head is incomplete, but appears to form an angle of about 45° to the transverse axis of the distal end of the bone. A knob-like 'lesser trochanter' is present, but there is no sign of a horizontal scar for the iliofemoral musculature. This peculiar feature is autapomorphic for *Guaibasaurus*. In basal dinosauromorphs the insertion of the *M. iliofemoralis externus* usually forms a transverse scar extending caudally from the 'lesser trochanter' (or the equivalent insertion area of the *M. iliofemoralis cranialis*) along the lateral surface of the proximal femur (Hutchinson 2001*b*). In some dinosaurs this scar is raised to form the 'trochanteric shelf' (Raath 1990; Novas 1993; Langer 2003), whereas only a faint scar is seen in other forms (Langer 2004). *Guaibasaurus* is unique among basal dinosaurs, because its femur lacks traces of this muscle insertion altogether. The 'dorsolateral trochanter' described by Bonaparte *et al*. (1999) is also seen in other basal dinosaurs (Galton 1974, 1984*b*; Galton & Jensen 1973; Norman 1986; Raath 1990) and corresponds to the insertion of the *M. iliotrochanterici* (Rowe 1986). The fourth trochanter bears symmetrical and gently sloping distal and proximal margins and bounds a cranial cavity for the *M. caudofemoralis longus*. The tibia is subequal in length to the femur and the longitudinal groove lateral to the cnemial crest extends for the entire proximal half of the bone. The distal tibia is craniocaudally compressed, bearing a sharp mediocranial corner. Its descending process forms a faint post-fibular wing, which is cranially bound by a transverse groove for the articulation of the astragalar ascending process. The insertion of the *M. iliofibularis* inflects the fibular shaft laterally. The medial portion of the astragalus is wider than the lateral and a marked furrow is seen cranial to the ascending process. A marked bump is also present in the caudomedial corner of the proximal astragalar surface, which locks into a notch in the distal tibia. A similar structure is seen in various basal theropods (Welles & Long 1974; Currie & Zhao 1994*a*; Carpenter 1997; *Liliensternus* – HMN MB.R. 1275), basal ornithischians (Galton 1981; *Lesothosaurus* – BMNH RUB 17; *Scelidosaurus* – BMNH 1111) and some 'prosauropods' (*Coloradisaurus* – PVL 3967), although absent from most other basal dinosauromorphs, in which the medial part of the proximal surface of the astragalus is nearly flat (Arcucci 1987; Novas 1989; Sereno & Arcucci 1994; *Herrerasaurus* – MACN 18060, PSJ 373, *Staurikosaurus* – MCZ 1669, *Saturnalia* – MCN 3844–PV; *Thecodontosaurus* – BRSUG 23623; ?*Massospondylus* – PBI 4693, 5238). The calcaneum shows a slight transverse compression, but retains a sub-triangular shape, as well as a reduced caudal tuber and a medial process extending ventrally to the astragalus. There are two distal tarsals and three weight-bearing pedal digits. Digit V is more reduced than digit I and probably lacks phalanges.

Saturnalia tupiniquim was described in a preliminary fashion by Langer *et al*. (1999) as the basal-most sauropodomorph, a view supported since (Galton 2000*a*; Yates 2003*a*; Yates & Kitching 2003; Galton & Upchurch 2004). Although a detailed description of its pelvis and hind limb is available (Langer 2003), a comprehensive description of the three known specimens is still lacking. This is not fulfilled here and only notes on the anatomy of the skeletal parts not considered by Langer (2003) are provided along with a diagnosis.

The skull of *Saturnalia* is relatively small, accounting for less than two-thirds of the femoral length. The maxilla has a long and thin caudal ramus extending below the antorbital fenestra. The frontals are broad and form the entire portion of the skull roof between the orbits. The lacrimal is 'L-shaped', with a short rostral ramus and a long oblique ventral ramus. The latter forms about three-quarters of the preorbital height and is markedly expanded in its ventral portion, where it receives the jugal and the maxilla. The antorbital fossa excavates the lacrimal at the cranioventral portion of its ventral ramus and at the entire ventral portion of its rostral ramus. Caudal to that, a lateral expansion of the bone overhangs the dorsocaudal corner of the antorbital fenestra. The squamosal is typically tetraradiate and possesses a slender ventral ramus that is narrower than a quarter of its length. The braincase is not particularly deep. The long parasphenoid rostrum lies below the occipital condyle and bears an elongated concavity on the ventral surface of its caudal part. The short basipterygoid processes are directed rostroventrally and slightly laterally, while a tympanic recess seems to be absent. The paroccipital process projects laterally in caudal view, while the occipital condyle is 'bean-shaped' and forms a median crest on the floor of the endocranial cavity. The dentary is elongate and its cranial tip not ventrally curved. Its dorso- and ventrocaudal processes are separated by a large external mandibular fenestra. The entire tooth series of the dentary is composed of 'leaf-shaped' elements, which are more slender towards the cranial tip of the bone. Seventeen tooth positions were recognised in MCP 3845-PV, occupying about two-thirds of the entire length of the bone.

The cervical series of *Saturnalia* is composed of 10 vertebrae, the atlas–axis complex of which is unknown. Cervical vertebrae 3–9 are significantly longer than the cranial trunk vertebrae, but the tenth cervicovertebral element is shorter and subequal in length to those. All cervical vertebrae have low neural spines and ventrally keeled centra. The parapophyses shift from the cranioventral corner of the centrum in cranial cervical elements to the craniodorsal corner in more caudal vertebrae. Ribs from the middle of the cervical series are about the length of two centra and subparallel to the neck. There are 14 trunk vertebrae, the neural spines of which are deeper and more robust. The three cranial-most elements are shorter than mid-cervical vertebrae, but more caudal trunk vertebrae are longer and subequal to mid-cervical elements. Only the two cranial-most trunk centra have ventral keels, but hyposphene–hypantrum auxiliary articulations are seen through the series. The diapophyses are buttressed by strong laminae that form well-developed cranial, ventral and caudal chonoe. The parapophyses are placed at the neurocentral junction in the two first trunk vertebrae, but are restricted to the neural arch in more caudal elements. Yet, they only merge definitively with the diapophyses at the very end of the series. Caudal trunk vertebrae and proximal caudal vertebrae show no signs of axial shortening, while vertebrae from the distal part of the tail have typically short prezygapophyses.

The pectoral girdle of *Saturnalia* has the scapula and coracoid attached in an immovable articulation, with a variable degree of fusion between the bones. The angle between the acromion process and the scapular blade also varies among different specimens; from less than 90° in MCP 3845-PV to about 115° in the holotype. The more robust caudal portion of the *caput scapulae* includes a glenoid that forms an angle of about 45° to the long axis of the bone. The scapular blade is slender and gradually expands dorsally. The coracoid foramen is restricted to the homonymous bone, which is medially concave and has an ovoid outline. The coracoid

is thicker caudally, where the glenoid is ventrally bound by a caudally facing subglenoid fossa (see Yates 2003*a*). Ventral to that lies a well-developed 'caudal coracoid process' (Nicholls & Russell 1985). The humerus has a prominent deltopectoral crest, which is separated from the proximal articulation of the bone and expands along 45% of its length. The broad distal articulation accounts for 35% of the length of the humerus. The entepicondyle represents about 20% of that distal breadth and has a marked circular pit on its medial surface. The radius has an elongated shaft with expanding extremities, accounting for about 60% of the humeral length. Its proximal articulation is ovoid, while the distal articulation is more circular. The ulna of *Saturnalia* is incomplete distally and atypical for a basal dinosaur. Its proximal portion is much broader than the shaft and has a heavily striated caudal surface for the insertion of the *M. triceps*. Similar striations also occur on the caudal surface of the extremely long olecranon process. Among basal dinosaurs, a comparably enlarged olecranon has otherwise been described for theropods (Bonaparte 1986; Raath 1990). In addition, a skeleton of *Plateosaurus* (MB HMN C; Galton 2001: fig. 27) exhibits a large process emanating from the proximal margin of its left ulna (Gabriel 2001) that might represent an abnormally ossified olecranon.

Apart from the enlarged olecranon process, few autapomorphic features have been recognised in the skeleton of *Saturnalia*. Most of these are autapomorphic reversals from characters widespread among more basal archosaurs. The more conspicuous of these is the size of the ischiadic antitrochanter, which occupies the entire acetabular incisure of that bone. This is typical of basal archosaurs (Ewer 1965; Bonaparte 1972; Long & Murry 1995), including *Lagerpeton* (Sereno & Arcucci 1993), while basal dinosaurs and *Marasuchus* have a smaller antitrochanter. Other distinctive features of *Saturnalia* among basal dinosaurs are the presence of a marked distal ridge in the caudal process of the lateral distal tarsal (also seen in *Lagerpeton* and *Marasuchus*) and an almost fully closed acetabulum, as seen in *Guaibasaurus*, *Scelidosaurus* and most non-dinosaur archosaurs. In addition, *Saturnalia* shares a deeply excavated ischio–acetabular groove of the pubis with *Eocoelophysis baldwini* (Sullivan & Lucas 1999). These are interpreted as convergently acquired putative apomorphies.

Composite OTUs of the ingroup

Theropod monoplyly has been supported repeatedly in phylogenetic studies (Thulborn 1984; Gauthier 1986; Holtz 1994, 2000; Forster 1999; Sereno 1999; Carrano *et al*. 2002; Rauhut 2003). Recent revisions have shown that Ceratosauria *sensu* Rowe (1989) is paraphyletic and composed of at least two successive sister-groups to Tetanurae (Rauhut 1998, 2003; Forster 1999; Carrano *et al*. 2002) and this hypothesis is followed here. Given that Theropoda is defined as a stem-based taxon (Gauthier 1986), it might also encompass some of the single-taxon OTUs of this study, depending on their final position. Accordingly, the name Theropoda cannot be applied to a composite OTU prior to the phylogenetic analysis. Therefore, an OTU labelled 'Theropods' is used here to designate the clade Neotheropoda of Carrano *et al*. (2002: fig. 23).

In contrast to that of Saurischia, the monophyly of Ornithischia was never seriously questioned and has been corroborated by phylogenetic studies (Sereno 1984, 1986; Norman 1984; Cooper 1985; Maryanska & Osmólska 1985). The relationships within the group are controversial, but the hypothesis advocated by Sereno (1999) is followed here. As for theropods, Ornithischia is currently defined as a stem-based taxon (Padian & May 1993) and the name cannot be used to designate a composite ingroup OTU prior to the phylogenetic analysis. Thus, an OTU labelled 'Ornithischians' is used to designate the clade *Lesothosaurus* plus Genasauria of Sereno (1999: fig. 1).

The name Sauropodomorpha was coined to combine Prosauropoda and Sauropoda in a single taxon (Huene 1932), the monophyly of which was recently defined on the grounds of phylogenetic systematics (Gauthier 1986; Sereno 1999; Benton *et al*. 2000; Yates 2003*a*; Yates & Kitching 2003). For relationships within the group, the most recent hypothesis supporting a paraphyletic 'Prosauropoda' (Yates 2003*a*; Yates & Kitching 2003) is followed here. Given that Huene (1932) listed *Thecodontosaurus*, *Anchisaurus* and *Plateosaurus* within Prosauropoda, as an insight into the taxa he believed to typify the group, a node-based definition of Sauropodomorpha ought to include those three prosauropods, together with sauropods of some sort, as internal specifiers. Following the phylogenetic hypothesis of Yates & Kitching (2003: fig. 4), but not their nomenclature, the name Sauropodomorpha is applied here to the composite OTU that represents the clade encompassing *Thecodontosaurus*, *Efraasia*, Prosauropoda and Sauropoda.

Ingroup monophyly

Various phylogenetic studies have confirmed the hypothesis that the members of the present ingroup, generally termed Dinosauria (see below), form a monophylum, exclusive of the 'non-dinosaurian' archosaurs of the outgroup (Gauthier 1986; Novas 1989, 1996; Sereno & Arcucci 1993, 1994; Sereno *et al*. 1993; Benton 1999; Sereno 1999; Yates 2003*a*). However, forms such as *Guaibasaurus* and *Silesaurus* were not included in those studies and their phylogenetic position remains to be defined on the basis of thorough cladistic studies. Alternatively, in order to establish the monophyly of the ingroup, a series of putative apomorphies are evaluated below (ambiguous ones are indicated by an asterisk). These are either newly proposed or have been previously considered apomorphic for clades nearly 'equivalent' to the present ingroup. Other discussed characters (indicated by a question mark) have previously been considered apomorphic for such clades, but deserve further inquiry to determine their status. This re-evaluation is beyond the scope of this paper and succinct comments are given below. In turn, depending on the chosen topology, characters that show variation within the ingroup may also represent apomorphies, with reversals, of the ingroup as a whole. These characters are discussed as part of those used in the phylogenetic analysis.

In the character discussions below, the members of the ingroup will often be termed 'basal dinosaurs', while 'non-dinosaurian archosaurs' refers to the outgroup. It is clear, however, that the name Dinosauria cannot be strictly applied to the present ingroup, prior to the phylogenetic analysis. This is because, as defined on the grounds of Phylogenetic Nomenclature (Padian & May 1993), that name is restricted

to the monophylum including Saurischia and Ornithischia, and some of the ingroup taxa may not belong to either of these groups (Gauthier 1986; Brinkman & Sues 1987; Novas 1989; Fraser *et al*. 2002; Dzik 2003).

Ingroup apomorphies

*Postfrontal absent** (Benton 1984) – The postfrontal bone is known in all basal archosaurs (Walker 1964; Ewer 1965; Cruickshank 1972; Barberena 1978; Chatterjee 1978), as well as in pterosaurs (Wellnhofer 1985; Bennett 1996) and possibly *Scleromochlus* (Benton 1999). However, no basal dinosaur is known to possess an individualised postfrontal ossification (Galton 1984*a*; Colbert 1989; Sereno 1991*b*; Sereno & Novas 1993; Sereno *et al*. 1993). Yet, it is ambiguous whether this character represents an ingroup apomorphy, since the condition in basal dinosauromorphs is unknown (Sereno & Novas 1993; Arcucci 1997; but see Parrish 1993).

*Frontal participates in the supratemporal fossa** (Gauthier 1986) – In most members of the ingroup the supratemporal fossa extends into the frontal (Galton 1984a; Raath 1985; Rowe 1989; Haubold 1991; Sereno 1991*b*; Sereno *et al*. 1993; Sereno & Novas 1993; Chatterjee & Zheng 2002; Dzik 2003; Yates 2003*a*, *b*; but see Chatterjee 1993). The reverse situation is seen in most other archosaurs (Ewer 1965; Bonaparte 1972; Chatterjee 1978). Yet, pterosaurs apparently share the ingroup condition (Wellnhofer 1985), while that of basal dinosauriforms is unknown. Accordingly, it is ambiguous whether a supratemporal fossa entering the frontal is apomorphic for the ingroup.

Quadrate head exposed in lateral view? (Sereno & Novas 1992) – Sereno & Novas (1992) suggested that a quadrate head not covered by the squamosal is apomorphic for Dinosauria. Indeed, in most basal members of the group (Gilmore 1920; Bonaparte 1978; Galton 1984*a*; Welles 1984; Weishampel & Witmer 1990; Coombs *et al*. 1990; Dzik 2003; Yates 2003*a*, *b*), the quadrate head is enveloped by the ventral and caudal ramus of the squamosal, but is somewhat laterally exposed between these rami. This condition is very similar to that seen in various pseudosuchians (Barberena 1978; Gower 1999), as well as in *Euparkeria* (Ewer 1965). In fact, pseudosuchians only have the quadrate head extensively covered by the squamosal if the latter has a marked lateral expansion (Walker 1961, 1990; Romer 1972*a*; Chatterjee 1985). In addition, the quadrate head of *Lewisuchus* (Romer 1972*b*) also does not seem to be significantly covered by the squamosal. Therefore, the lateral exposure of the quadrate head most probably does not constitute an apomorphy of the present ingroup.

*Ectopterygoid dorsal to transverse flange of the pterygoid** (Sereno & Novas 1993) – Sereno & Novas (1993) suggested that most dinosaurs have an ectopterygoid extending dorsal to the pterygoid transverse flange, while the reverse condition characterises the dinosaur outgroup. Indeed, in most basal archosaurs (Ewer 1965; Cruickshank 1972; Sereno & Novas 1993) and pseudosuchians (Walker 1964; Doyle & Sues 1995; Gower 1999), the medial portion of the ectopterygoid overlaps the pterygoid ventrally, although a more complex articulation is seen in some members of the latter group (Walker 1961, 1990; Wu & Chatterjee 1993). Within the present ingroup, basal ornithischians have an ectopterygoid that dorsally overlaps the transverse ramus of the pterygoid (Galton 1974; Sereno 1991*b*; *Scelidosaurus* – BMNH 1111). The condition in saurischians (Galton 1984*a*; Currie & Zhao 1994*a*; Madsen & Welles 2000; Brochu 2003) is more difficult to interpret, but the distal portion of the pterygoid flange seems always to be ventral to the ectopterygoid. Nevertheless, given that the condition in basal dinosauriforms is unknown, the apomorphic status of this character is, at best, ambiguous.

*Reduced manual digits IV and V** (Gauthier & Padian 1985) – Usually, manual digits IV and V of non-dinosaurian archosauromorphs are elongated elements with, respectively, more than three and about three phalanges (Gregory 1945; Romer 1956; Gow 1975; Long & Murry 1995). However, the dinosaur manual digit IV is always subequal to, or shorter than, metatarsal III and never possesses more than three phalanges, none of which is an ungual (Gilmore 1920; Romer 1956; Raath 1969; Galton 1971, 1973*a*; Santa Luca 1980; Welles 1984; Colbert 1989; Rowe 1989; Sereno 1990, 1993; Novas 1996; Benton *et al*. 2000). Likewise, almost none of these forms has more than two phalanges in manual digit V (Galton 1973*a*, 1974; Maryanska 1977; Santa Luca 1980; Cooper 1981; Zhang 1988; Colbert 1989; Forster 1990; Sereno 1990, 1991*b*, 1993; Benton *et al*. 2000). Yet, the manus is unknown for basal dinosauriforms and for various single-taxon OTUs of the ingroup. Therefore, it is ambiguous whether these characters represent ingroup apomorphies.

Reduced ischiadic medioventral lamina (Novas 1992) – In *Lagerpeton*, *Marasuchus* and most non-dinosauromorph archosaurs (Romer 1956, 1972*c*; Walker 1964; *Leptosuchus* – Long & Murry 1995), the ischium has a well-developed medioventral lamina, forming a broad plate-like symphyseal area. Exceptions to this are poposaurids (Long & Murry 1995) in which most of the shaft is rod-like and the medioventral lamina is restricted to the cranial quarter of the bone, forming the obturator plate. This condition is similar to that of most members of the ingroup, but some basal ornithischians retain a vestigial medioventral lamina along the shaft (character 79). Accordingly, as discussed by Novas (1996), although the proximodistal reduction of the lamina is not diagnostic for the ingroup, its transversal restriction most probably is.

Inturned femoral head (Bakker & Galton 1974) – As discussed by Carrano (2000) and Langer (2003, 2004) the complete inturning of the femoral head was independently achieved in several dinosaur lineages. By contrast, the single-taxon ingroup OTUs have femoral heads forming angles of 45–90° to the sagittal line. This is also the case for basal members of the composite OTUs (Raath 1990; Sereno 1991*b*; Yates 2003*b*), the femoral heads of which are not fully inturned. However, the femoral heads of the Argentinian basal dinosauromorphs are even less inturned and form an angle of less than 45° to the sagittal line. Accordingly, a more inturned femoral head seems to represent an apomorphy of the ingroup.

Femoral head sub-rectangular and distinctly set from shaft? (Gauthier 1986) – The femoral head of basal dinosauromorphs usually has a subcircular outline and is not

projected medially. However, that of dinosaurs has a marked mediodistal 'corner' ('c' in Novas 1996: fig. 3) and a flatter proximal articulation, that forms a near right angle to the shaft. Collectively, these features give the femoral head of dinosaurs a somewhat sub-rectangular outline in cranial or caudal aspects (Galton 1973*a*, 1976; Colbert 1981; Welles 1984; Raath 1990; Novas 1993; Langer 2003). Yet, none of these traits alone seems to represent an unambiguous apomorphic condition for the ingroup. A marked mediodistal 'corner' is not seen in *Lesothosaurus* (Thulborn 1972) or *Silesaurus*, while *Pseudolagosuchus* also has an angular lateroproximal corner.

Proximal femur with reduced medial tuberosity? (Novas 1996) – The reduction of the tuberosity between the sulcus of the *Lig. capitis femoris* and the *facies articularis antitrochanterica* has been considered apomorphic for dinosaurs (Novas 1996). Indeed, this structure does not protrude in most members of the ingroup, including *Silesaurus*, *Herrerasaurus*, *Staurikosaurus*, *Saturnalia*, basal theropods (Welles 1984; Padian 1986; Rowe 1989; *Liliensternus* – MB R.1275) and sauropodomorphs (Galton 1973*a*, 1976; *Thecodontosaurus* – BRSUG various specimens). Basal ornithischians lack this structure altogether, and the femoral head has a concave caudal/medial margin (Sereno 1991*b*; *Scelidosaurus* – BMNH 1111, 6704), although a more marked medial tuberosity seems to have been reacquired in some ornithopods (Galton 1974, 1981; Forster 1990; Novas 1996). Yet, the pertinent question is whether the basal dinosauromorph condition is distinct from that of basal dinosaurs. Indeed, a more marked tuberosity is present in some specimens of *Marasuchus* (Novas 1996; fig. 3b), but not in others (Sereno & Arcucci 1994; fig. 9b; PVL 3871), as well as in the holotype of *Pseudolagosuchus*. The femoral head of *Lagerpeton* is markedly convex medially, but this is partially given by its much narrower caudal portion. Accordingly, it is not clear if the reduction of that medial tuberosity is apomorphic for the ingroup.

Tibial descending process fits caudal to astragalar ascending process (Novas 1989) – The morphology of the tibia–astragalus articulation has been extensively discussed and various characters regarding the morphology of the tibial descending process and the astragalar ascending process were proposed to diagnose Dinosauria (Novas 1989, 1996; Sereno *et al*. 1993; Sereno 1999). In fact, the tibia of basal archosaurs (Sereno 1991*a*) and basal dinosauromorphs articulates only medial to the osteological correlate of the astragalar ascending process of these reptiles. In all members of the ingroup, however, the descending process of the tibia is apomorphicaly expanded laterodistally and fits caudally to the ascending process (Huene 1926, 1934; Welles & Long 1974; Galton 1974, 1981; Bonaparte 1976; Cruickshank 1980; Colbert 1981; Novas 1989; Raath 1990; Dzik 2003).

Astragalus with a straight caudal margin – In *Marasuchus* and *Pseudolagosuchus* the astragalar caudal margin is excavated at about the level of the ascending process, so that a markedly concave surface is formed. No member of the ingroup has such an excavation (Huene 1926, 1934; Welles & Long 1974; Galton 1974; Bonaparte 1976; Cruickshank 1980; Colbert 1981; Cooper 1984; Novas 1989; Raath 1990; Dzik 2003), the caudal margin of the astragalus of which is apomorphically straight to convex.

Flat to concave proximal calcaneum (Novas 1989) – As discussed by Novas (1989), the fibular articulation facet in the calcaneum is mainly convex in basal dinosauriforms, although a transverse excavation is present in that of *Pseudolagosuchus*. By contrast, the calcaneum of *Silesaurus* seems proximally concave, a condition shared by all members of the ingroup (Huene 1926; Welles & Long 1974; Galton 1974; Cruickshank 1980; Novas 1989; Raath 1990; Langer 2003; *Scelidosaurus* – BMNH 1111). Accordingly, a flat to concave proximal calcaneum is considered an ingroup apomorphy.

Distal tarsal 4 proximally flat (modified Novas 1996) – As discussed by Novas (1996), the distal tarsal 4 of basal dinosauriforms has a proximal ridge that caudally forms a proximal projection. In 'basal dinosaurs', however, that bone is proximally flat and does not have a markedly upturned caudal margin (Santa Luca 1980; Cooper 1981; Padian 1986; Forster 1990; Raath 1990; Novas 1993; Langer 2003). This condition is considered apomorphic for the ingroup, while the shape of the distal tarsal 4 is more variable within its members (character 96).

Broad weight-bearing portion of metatarsus – *Scleromochlus* (Benton 1999), *Lagerpeton* and *Marasuchus* are extremely gracile animals and the metatarsals of their three weight-bearing digits form a structure that is about five times longer than broad. The members of the ingroup have bulkier metatarsals II–IV. These form a relatively short weight-bearing structure, that is at most four times longer than broad (Huene 1934; Galton 1976, 1981; Santa Luca 1980, 1984; Cooper 1981; Welles 1984; Colbert 1989; Novas 1993; Bonaparte *et al*. 1999; Dzik 2003). Accordingly, this condition represents an ingroup apomorphy.

Metatarsals II and IV subequal in length (Sereno 1991*a*) – In basal dinosauromorphs (Sereno & Arcucci 1993, 1994) and basal archosaurs (Ewer 1965; Bonaparte 1972; Romer 1972*b*) metatarsal IV is always significantly longer than metatarsal II. In all members of the ingroup, however, metatarsal IV is apomorphically shorter, approaching the length of metatarsal II (Huene 1926; Raath 1969; Santa Luca 1980, 1984; Welles 1984; Novas 1993; Bonaparte *et al*. 1999; Yates 2003*a*; Langer 2003; Dzik 2003).

Definition and description of the characters

The majority of the characters discussed below are modified from previous studies of early dinosaur evolution, which are quoted accordingly. Yet, some of the characters defined in those studies have been rejected after critical analysis. The main criterion for this procedure was the assessment of morphological variation within each OTU. When a significant number of OTUs have different states of a given character, the character is disregarded. However, if only a few OTUs show such internal variation, these are coded as variable for that particular character, while the other OTUs are coded accordingly. *A priori* criteria for character exclusion such as developmental constraint, or a 'smaller amount' of new information (Hecht & Edwards 1976) have not been employed.

The use of continuous characters in phylogenetic analysis has often been criticised (Pimentel & Riggins 1987;

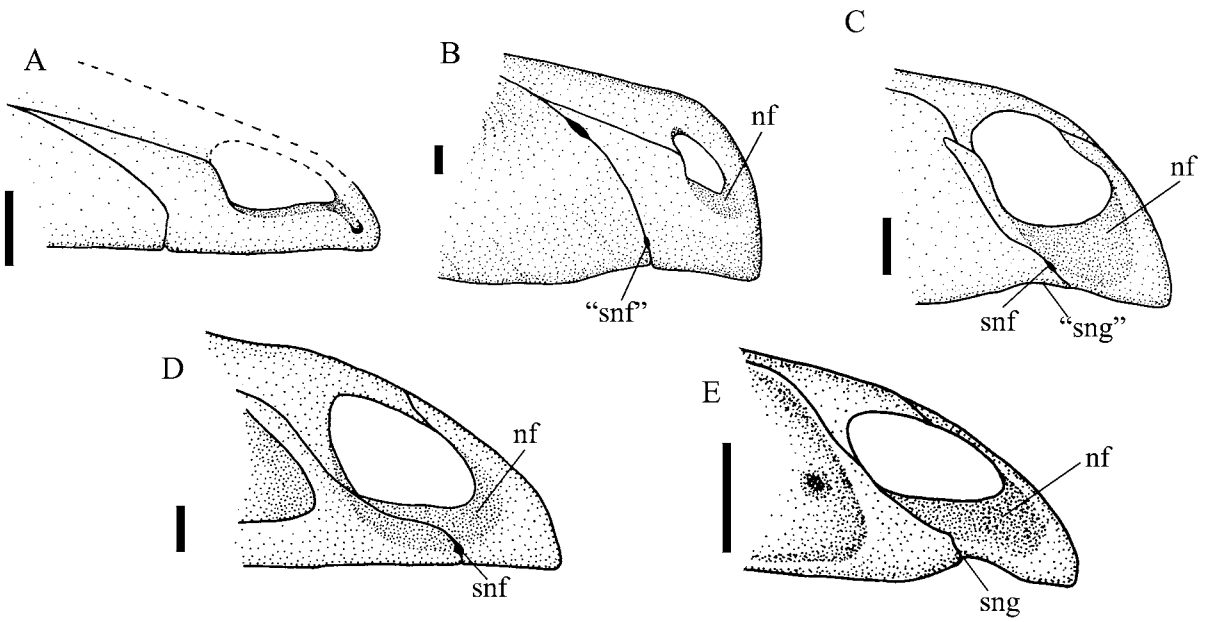

Figure 4 Lateral aspect of the rostral part of the skull of **A**, *Lesothosaurus diagnosticus*, based on BMNH R8501 and Sereno (1991*b*); **B**, *Herrerasaurus ischigualastensis*, based on PVSJ 407 and Sereno & Novas (1994); **C**, *Eoraptor lunensis*, based on PVSJ 512 and Sereno *et al.* (1993); **D**, *Efraasia diagnostica*, based on Yates (2003*b*); **E**, cf. *Syntarsus rhodesiensis*, based on BP/I/5278 and Munyikwa & Raath (1999). Abbreviations: **nf**, narial fossa; **snf**, subnarial foramen; **sng**, subnarial gap. Scale bars: **A**, **C** = 5 mm; **B**, **D**, **E** = 10 mm.

Crowe 1994). Yet, at least in morphological studies of fossils, their exclusion would represent serious loss of information. Accordingly, and following Rae (1998), ratio characters are used in the present analysis. In the same way, multistate characters are also applied. These were ordered when one or more of the derived states are transitional between the primitive and another of the derived states (Mickevich 1982; Slowinski 1993).

In the following character discussions, the morphological condition of certain OTUs is not mentioned if the relevant anatomical parts are not preserved. In turn, the term 'uncertain' is applied when the corresponding anatomical part is preserved, but the character still cannot be coded because of either a lack of clarity in the literature, or obliteration of the specimens. The same term is applied when the definition of the character state is ambiguous for the outgroup or composite ingroup OTUs based on the method outlined in the 'Materials and Methods' section, above. If more than one state of a particular character is present in different specimens of a single-taxon OTU, this is coded as 'variable', and the character is considered 'inapplicable' for a particular OTU if its morphology is modified to an extreme beyond recognition.

Skull and mandible

1. *Head longer (0) or shorter (1) than two-thirds of the femoral length* (Gauthier 1986). It has long been recognised that sauropodomorphs have a remarkably small head compared to other dinosaurs. Here, the length comparison to the femur is used to infer its relative size (Galton 1990*a*). A head that is shorter than two-thirds of the femoral length is seen in *Saturnalia* and all basal sauropodomorphs (Huene 1926; Young 1941*a*; Galton 1976; Bonaparte & Plumares 1995; Chatterjee & Zheng 2002). However, the length of the head is always greater than two-thirds of the femoral length in basal theropods (Gilmore 1920; Welles 1984; Colbert 1989) and ornithischians (Owen 1863; Thulborn 1972; Santa Luca 1980), although this condition is reversed in some derived members of both groups (Sereno & Dong 1992; Russell & Dong 1994). Likewise, the heads of *Silesaurus*, *Herrerasaurus*, *Staurikosaurus* and *Eoraptor* are longer than two-thirds of their femur lengths, a condition also estimated for *Pisanosaurus*. As for the outgroup, virtually all non-dinosauromorph archosaurs have a skull longer than half the femoral length (Walker 1961; Ewer 1965; Bonaparte 1972), and a long skull can be inferred for *Marasuchus* and *Lewisuchus*.
2. *Narial fossa absent or shallow (0) or expanded (1) in the rostroventral corner of the naris* (Fig. 4; modified Sereno 1999). Despite the fact that a similar arrangement is present in some theropods, Sereno (1999) used a ventral narial fossa that is large and encompasses the subnarial foramen to diagnose Sauropodomorpha. A poorly-developed narial fossa has been described for *Batrachotomus* (Gower 1999), but *Euparkeria* (Ewer 1965) and most pseudosuchians (Walker 1961, 1964; Bonaparte 1972; Sill 1974; Chatterjee 1985) apparently lack such a structure. Basal ornithischians (Haubold 1991; Sereno 1991*b*; Sereno & Dong 1992), as well as *Silesaurus*, also lack a well-developed narial fossa, although this is seen in some ornithopods (Charig & Crompton 1974; Sues 1980; but see Thulborn 1974). By contrast, a well-developed narial fossa is present on the cranioventral part of the external naris of *Eoraptor*, *Herrerasaurus*, basal theropods (Madsen 1976; Rowe 1989; Colbert 1989; Munyikwa & Raath 1999; Madsen & Welles 2000) and basal sauropodomorphs (Huene 1926; Bonaparte & Plumares 1995; Yates 2003*a*, *b*).

3. *Subnarial gap absent (0) or present (1)* (Fig. 4; Gauthier 1986). Gauthier (1986) regarded the presence of a subnarial gap as plesiomorphic among archosaurs. Indeed, this structure is particularly well-developed in ornithosuchids (Walker 1964; Bonaparte 1972), but absent in *Euparkeria* (Ewer 1965) and most pseudosuchians (Barberena 1978; Chatterjee 1978, 1985). Among dinosaurs, Rowe (1989) suggested that a subnarial gap is apomorphic for certain 'ceratosaurs'. Yet, based on the adopted framework of theropod phylogeny, the subnarial gap as seen in coelophysoids (Munyikwa & Raath 1999; Tykoski & Rowe 2004) is considered plesiomorphic for the group. In those forms, the gap appears as a toothless and concave area at the ventral margin of the premaxilla–maxilla contact, a subtle version of which is seen also in *Eoraptor*. By contrast, *Herrerasaurus*, *Silesaurus*, basal sauropodomorphs (Huene 1926; Bonaparte & Plumares 1995) and basal ornithischians (Haubold 1991; Sereno 1991*b*; Sereno & Dong 1992; Peng 1997), have no sign of this structure. An exception is the gap, probably not equivalent, seen in basal neornithischians (Galton 1974; Maryanska & Osmólska 1974; Thulborn 1974; Weishampel & Witmer 1990).
4. *Subnarial foramen absent (0) or present (1)* (Fig. 4; modified Sereno & Novas 1993). *Euparkeria* (Ewer 1965) and most pseudosuchians (Walker 1961; Chatterjee 1978) lack a subnarial foramen, although this structure is known in rauisuchians (Sill 1974; Chatterjee 1985; Gower 1999). Among dinosaurs, Sereno & Novas (1993) defined its presence as apomorphic for Saurischia. Indeed, most basal ornithischians lack a clearly developed subnarial foramen, although some forms bear possibly correlated structures such as the premaxillary foramina (Galton 1974; Sereno 1991*b*) and an aperture at the base of the premaxilla–maxilla contact (Sues 1980; Sereno & Dong 1992). Theropods (Currie & Zhao 1994*a*; Zhao & Currie 1994; Rauhut 1997; Currie & Carpenter 2000) and sauropodomorphs (He *et al*. 1988; Yates 2003*b*), however, have a well-developed subnarial foramen below the naris, which usually opens at the ventral margin or inside the narial fossa, a condition apparently seen also in *Eoraptor*. *Herrerasaurus* has a much smaller aperture at the base of the premaxilla–maxilla contact. It lies at some distance from the narial fossa, and its correspondence to the subnarial foramen is not certain. Large foramina are also absent from the premaxilla of *Silesaurus*.
5. *Caudoventral premaxillary process extends caudally to the external naris (0) or is restricted to its ventral border (1)* (Fig. 4). The caudoventral process of the premaxilla of *Euparkeria* (Ewer 1965) extends caudal to the external naris, forming most of its caudal margin. This condition is also present in various pseudosuchians (Sill 1974; Crush 1984; Chatterjee 1985), although the process is shorter in other members of the group (Walker 1961; Bonaparte 1972; Gower 1999). Among dinosaurs, a long process is seen in basal ornithischians (Galton 1974; Weishampel & Witmer 1990; Haubold 1991; Sereno & Dong 1992; Peng 1997), as well as in *Herrerasaurus*, *Silesaurus* and *Eoraptor*. By contrast, the premaxillary caudoventral process of basal theropods (Colbert 1989; Rowe 1989; Britt 1991; Munyikwa & Raath 1999; Madsen & Welles 2000) and basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942; Bonaparte 1978; Galton 1984*a*, 1985*a*; He *et al*. 1988; Gow *et al*. 1990) does not extend caudally to the caudal margin of the external naris.
6. *Maxilla separated from the external naris by a broad premaxilla–nasal contact (0) or approaches or enters the external naris (1)* (Fig. 4; modified Gauthier 1986). Most non-dinosaurian archosaurs (Ewer 1965; Bonaparte 1972; Sill 1974; Chatterjee 1978, 1985; Crush 1984) show a broad premaxilla–nasal contact, separating the maxilla from the external naris. Within dinosaurs, Gauthier (1986) defined the absence of the premaxilla–nasal contact as apomorphic for saurischians. Indeed, a broad premaxilla–nasal contact is seen in *Silesaurus*, *Herrerasaurus* and basal ornithischians (Galton 1974; Weishampel & Witmer 1990; Haubold 1991; Sereno & Dong 1992; Peng 1997), while in most basal theropods (Madsen 1976; Colbert 1989; Rowe 1989; Munyikwa & Raath 1999; Madsen & Welles 2000) and basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942; Bonaparte 1978; Galton 1984*a*, 1985*a*; He *et al*. 1988; Gow *et al*. 1990) the maxilla either enters the border of the external naris, or is separated from it by only a thin premaxilla–nasal contact. *Eoraptor* apparently presents an intermediate condition, in which the long caudoventral premaxillary process forms a thin separation between maxilla and naris.
7. *Rostral margin of the maxilla and its ascending process straight or convex (0) or concave, with the base of the ascending process continuous with the rostral margin of the bone, or markedly offset from it (1)* (Fig. 4; modified Gauffre 1993). In most pseudosuchians (Bonaparte 1972; Sill 1974; Barberena 1978; Crush 1984; Chatterjee 1985) and, apparently, in basal dinosauromorphs (Bonaparte 1975), the ascending process of the maxilla is continuous with the rostral margin of the bone. This forms a convex to straight rostral maxillary rim, an arrangement seen also in *Herrerasaurus* and most basal ornithischians (Weishampel & Witmer 1990; Sereno & Dong 1992; Peng 1997). However, as defined by Gauffre (1993), the maxillary ascending process of basal sauropodomorphs is markedly offset from the rostral margin of the bone, forming a distinctly concave rostral maxillary rim (Galton 1976; Bonaparte 1978; Bonaparte & Vince 1979; Attridge *et al*. 1985; Bonaparte & Plumares 1995; Madsen *et al*. 1995; but see Yates 2003*b*). An intermediate arrangement is present in *Eoraptor*, most basal theropods (Rowe 1989; Colbert 1989; Britt 1991; Zhao & Currie 1994; Munyikwa & Raath 1999; Madsen & Welles 2000), as well as in *Silesaurus*, in which the rostral rim of the maxilla is concave, but the ascending process is not so markedly offset from the rostral margin of the bone as in sauropodomorphs.
8. *Nasal does not form (0) or forms (1) part of the dorsal border of the antorbital fossa* (Fig. 5; modified Sereno *et al*. 1994). Sereno *et al*. (1994) suggested a nasal that participates in the antorbital fossa as a diagnostic feature of allosauroids. Indeed, this feature is observed in *Allosaurus* (Madsen 1976), *Acrocanthosaurus* (Currie & Carpenter 2000) and *Sinraptor* (Currie & Zhao 1994*a*). However, even when it does not contribute to the antorbital fossa, the nasal of most theropods forms a portion of its dorsal margin (Bonaparte *et al*. 1990; Zhao &

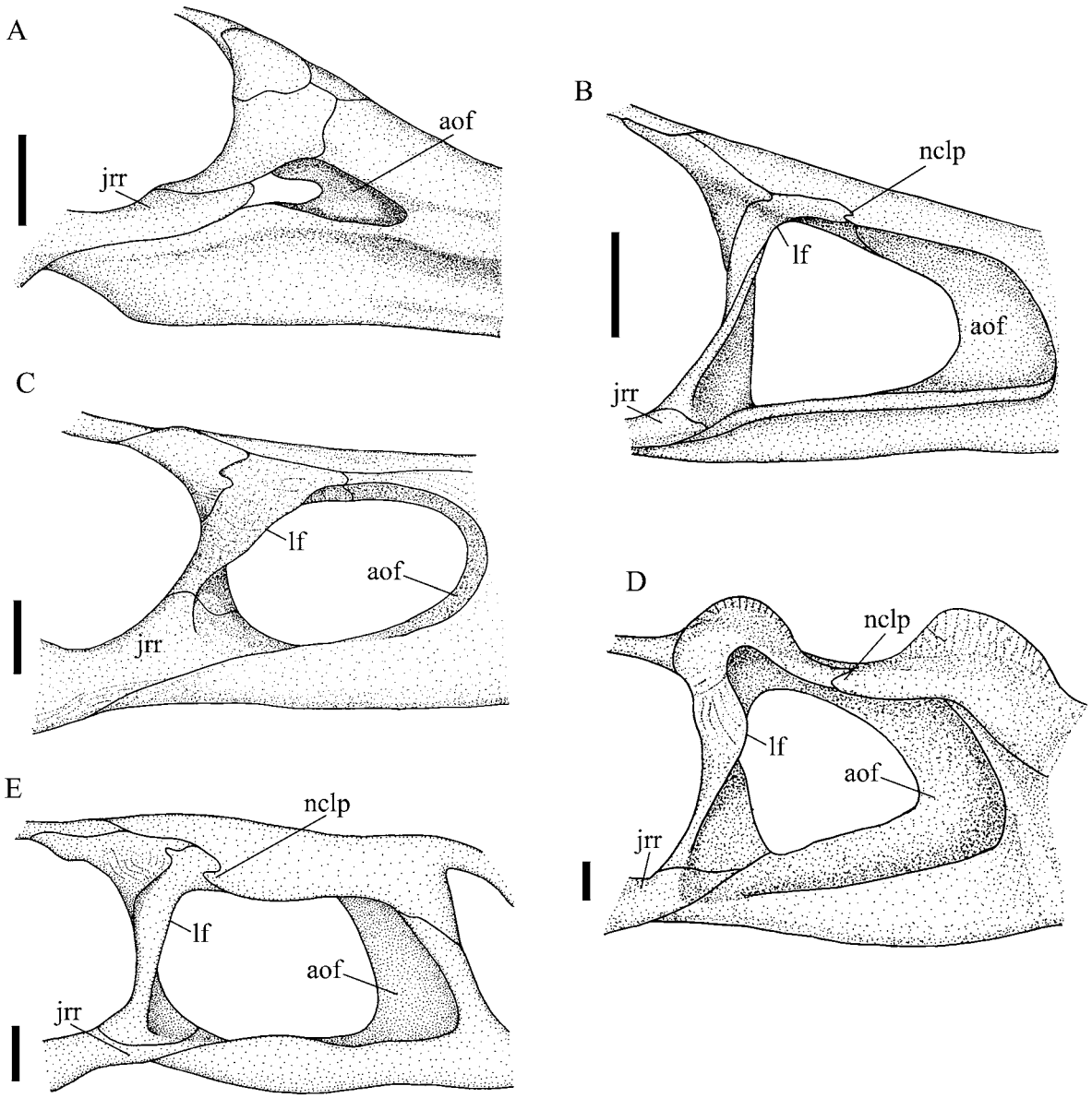

Figure 5 Lateral aspect of the orbital portion of the skull of **A**, *Scelidosaurus harrisonii*, based on BMNH 1111; **B**, *Eoraptor lunensis*, based on PVSJ 512 and Sereno *et al.* (1993); **C**, *Herrerasaurus ischigualastensis*, based on PVSJ 407 and Sereno & Novas (1994); **D**, *Ceratosaurus magnicornis*, based on Madsen & Welles (2000); **E**, *Plateosaurus engelhardti*, based on Galton (1984*a*). Abbreviations: **aof**, antorbital fossa; **jrr**, jugal rostral ramus; **lf**, lachrimal flange; **nclp**, nasal caudolateral process. Scale bars: **A**, **C–E** = 20 mm; **B** = 10 mm.

Currie 1994; Rauhut 2003). This condition is seen also in *Eoraptor*, as well as in basal sauropodomorphs (Huene 1926; Gow *et al*. 1990). In *Herrerasaurus*, however, the nasal is separated from the antorbital fenestra by the dorsocaudal maxillary process, which not only forms the craniodorsal part of the antorbital fossa, but also the dorsal margin of the antorbital fenestra for its entire length. A similar condition is seen in ornithischians (Weishampel & Witmer 1990; Haubold 1991; Sereno 1991*b*; Peng 1997), in which the reduced antorbital fenestra is dorsally bounded by a strong maxilla–lacrimal contact exposed on the lateral surface of the skull. The outgroup condition is 'uncertain'. The nasals of aetosaurs (Walker 1961; Witmer 1997), rauisuchians (Sill 1974; Gower 1999), and apparently *Euparkeria* (Ewer 1965), contribute to the dorsal border of the antorbital fenestra, while the reverse is seen in ornithosuchids (Sereno 1991*b*; Witmer 1997), sphenosuchians (Wu & Chatterjee 1993) and the longirostrine proterochampsids (Price 1946; Romer 1971).

9. *Nasal does not possess (0) or possesses (1) a caudolateral process that envelops part of the rostral ramus of the lacrimal* (Fig. 5; modified Yates 2003*a*). A strong caudolaterally directed hook-like projection is present in the lateral margin of the nasal of various saurischians, including *Eoraptor*, theropods (Bonaparte *et al.* 1990; Currie & Zhao 1994*a*; Sereno *et al*. 1994; Madsen & Welles 2000) and sauropodomorphs (Huene

1926; Yates 2003*b*). Its base is rostrally adjacent to the lacrimal, the rostral margin of which is enveloped between the medial border of that process and the lateral border of the nasal body. This projection is absent in most non-dinosauromorph archosaurs (Ewer 1965; Bonaparte 1972; Walker 1990; Gower 1999), as well as in *Herrerasaurus*, the nasal of all of which has an almost straight lateral margin. In ornithischians, the caudolateral portion of the nasal is overlapped by the prefontral, giving the impression that a process is present in the lateral margin of the bone (Galton 1974; Sereno & Dong 1992). This is surely not the aforementioned hook-like process and the lateral margin of their nasals is clearly straight where it touches the rostral tip of the lacrimal (Sereno 1991*b*).

10. *Ventral ramus of the lacrimal short and mainly inclined (0) or long, forming about 0.75 or more of the maximum preorbital skull height, and mainly vertical (1)* (Fig. 5; modified Rauhut 2003). The lacrimal of most theropods is 'L-shaped', with a long and vertically orientated ventral ramus, which forms almost the entire caudal margin of the antorbital fenestra. The rostral ramus, however, is usually much shorter, and forms an angle of 90° or less to the ventral ramus (Osborn 1916; Madsen 1976; Colbert 1989; Rowe 1989; Currie & Zhao 1994*a*; Sereno *et al.* 1994, 1996; Rauhut 1997; Madsen & Welles 2000). A lacrimal with these characteristics usually corresponds to more than three-quarters of the pre-orbital height of the skull, and that of *Eoraptor* fits into this category. The lacrimal of basal ornithischians is distinct. Its main body (mainly composed of the ventral ramus) is inclined and usually represents only about 50% of the preorbital height of the skull (Galton 1974; Weishampel & Witmer 1990; Haubold 1991; Sereno 1991*b*; Sereno & Dong 1992), as seen also in *Herrerasaurus*. In *Saturnalia* and basal sauropodomorphs the lacrimal has an intermediate morphology. Unlike those of theropods, the ventral ramus is not strictly vertical, but in most forms it comprises about three-quarters of the preorbital height (Young 1941*a*, 1942; Bonaparte 1978; Galton 1984*a*, 1985*b*; Attridge *et al.* 1985; Bonaparte & Plumares 1995; Yates 2003*a*, *b*). For the dinosaur outgroup, rauisuchians (Sill 1974; Gower 1999) have a lacrimal that is somewhat similar to that of theropods, but the bone has an inclined and short ventral ramus in most other forms (Ewer 1965; Bonaparte 1972; Wu & Chatterjee 1993).
11. *Lacrimal does not fold (0) or folds (1) over the caudal/dorsocaudal part of antorbital fenestra* (Fig. 5; modified Sereno 1999). Sereno (1999) used the presence of a 'flange' in the ventral ramus of the lacrimal as an apomorphy of Neotheropoda. Indeed, the ventral ramus of the lacrimal of most theropods presents a rostral expansion of its lateral margin, which overhangs the caudal-most portion of the antorbital fenestra (Britt 1991; Currie & Zhao 1994*a*; Witmer 1997; Madsen & Welles 2000). A similar structure is seen also in most basal sauropodomorphs (Young 1941*a*; Bonaparte 1978), but it is usually displaced dorsally and overhangs the dorsocaudal corner of the antorbital fenestra (Galton 1984*a*; Gow *et al.* 1990; Yates 2003*a*, *b*), as seen also in *Eoraptor*, *Herrerasaurus* and *Saturnalia*. By contrast, the lacrimal of ornithischians (Haubold 1991; *Lesothosaurus* – BMNH R8501) lacks a flange extending rostrally from the ventral ramus. This is also true of most non-dinosauromorph archosaurs (Walker 1961, 1990; Ewer 1965; Gower 1999), although an expansion similar to that of theropods is seen in ornithosuchids (Walker 1964).
12. *Rostral ramus of jugal expands rostrally, forming part of the rostral margin of the orbit (0) or does not expand rostrally (1)* (Fig. 5; modified Rauhut 2003). In most non-dinosauromorph archosaurs the rostral ramus of the jugal expands rostrally (Walker 1961, 1964; Ewer 1965; Bonaparte 1972; Chatterjee 1985; Gower 1999), forming part of the rostral rim of the orbit. Such an expansion is also present in *Herrerasaurus*, various theropods (Welles 1984; Currie & Zhao 1994*a*; Sampson *et al.* 1998; Currie & Carpenter 2000) and, apparently, *Silesaurus*. By contrast, that ramus either tapers rostrally or is about the same depth along its length in other theropods (Rowe 1989; Witmer 1997), as well as in *Eoraptor*, basal sauropodomorphs (Gow *et al.* 1990; Bonaparte & Plumares 1995; Yates 2003*a*, *b*) and basal ornithischians (Galton 1974; Haubold 1991; Sereno 1991*b*; Peng 1997).
13. *Ventral ramus of squamosal forms more (0) or less (1) than half of the caudal border of the lower temporal fenestra*. In non-dinosauromorph archosaurs, the ventral ramus of the squamosal is usually long and forms more than half of the caudal border of the lower temporal fenestra (Walker 1964; Bonaparte 1972; Chatterjee 1978). This character is retained in basal ornithischians (Coombs *et al.* 1990; Haubold 1991; Sereno 1991*b*) as well as in basal sauropodomorphs (Huene 1926; Young 1941*a*; Gow *et al.* 1990; Bonaparte & Plumares 1995; Yates 2003*b*). By contrast, this process is more restricted in theropods and usually forms only the dorsal third of the caudal margin of the lower temporal fenestra (Gilmore 1920; Welles 1984; Colbert 1989; Rowe 1989; Currie & Carpenter 2000; Rauhut 2003). *Eoraptor* and *Herrerasaurus* apparently show an intermediate condition. Although the ventral ramus of their squamosal is not as short as that of basal theropods, it also does not reach the ventral half of the lower temporal fenestra.
14. *Ventral ramus of the squamosal wider (0) or narrower (1) than a quarter of its length* (Yates 2003a). The ventral ramus of the squamosal of non-dinosauromorph archosaurs (Walker 1961; Romer 1971; Bonaparte 1972; Barberena 1978; Chatterjee 1978) is usually broad. This is seen also in *Herrerasaurus* and basal theropods (Gilmore 1920; Welles 1984; Rowe 1989; Currie & Carpenter 2000), in which the rostrocaudal breadth of the ventral ramus of the squamosal approaches half of its length. A distinctive derived condition is present in *Saturnalia* and basal sauropodomorphs (Galton 1984*a*; Yates 2003*b*; *Coloradisaurus* – PVL 3967). In these forms, the long ventral ramus of the squamosal is also very thin, and its rostrocaudal breadth never reaches one-quarter of its length. Ornithischians also present a primitive broad ramus, as seen in *Heterodontosaurus* (Weishampel & Witmer 1990) and *Scelidosaurus* (BMNH 1111). This is also the case for *Lesothosaurus* (Sereno 1991*b*: fig. 7) and *Emausaurus* (Haubold 1991: fig. 8), the quadrate of which partially covers the broad

ventral ramus of the squamosal, giving the impression that it is thin in lateral aspect. Accordingly, the condition in *Eoraptor* is uncertain, since it is not clear how far its quadrate covers the ventral ramus of the squamosal.

15. *Dorsal ramus of the quadratojugal longer (0) or the same length or shorter (1) than the rostral ramus* (modified Sereno 1986). Sereno (1986) used a short rostral ramus of the quadratojugal as apomorphic for Ornithischia within dinosaurs. Indeed, in most basal ornithischians the rostral ramus of the quadratojugal is shorter than the dorsal (Coombs *et al.* 1990; Haubold 1991; Sereno 1991*b*; Sereno & Dong 1992; Peng 1997). A similar condition is, however, also present in most non-dinosauromorph archosaurs (Walker 1961; Ewer 1965; Chatterjee 1978, 1985; Crush 1984) as well as in *Eoraptor*. In basal sauropodomorphs, however, the rostral ramus of the quadratojugal is either subequal or longer than the dorsal (Young 1941*a*; Bonaparte & Vince 1979; Galton 1984*a*; Attridge *et al.* 1985; Gow *et al.* 1990; Bonaparte & Plumares 1995; Chatterjee & Zheng 2002; Yates 2003*b*), as seen also in *Herrerasaurus*. The condition varies within theropods. Several forms retain a longer dorsal ramus (Colbert 1989; Rowe 1989; Rauhut 2003), while the reverse is seen in other taxa (Osborn 1916; Welles 1984).
16. *Ectopterygoid ventral recess absent (0) or present (1)* (Gauthier 1986). Gauthier (1986) defined the presence of a ventral fossa in the ectopterygoid as apomorphic for theropods. Sereno (1999) also used this feature as an apomorphy of the group including *Eoraptor*, Herrerasauridae and Neotheropoda. Indeed, most theropods bear a pneumatic recess on the ventral surface of the expanded medial portion of the ectopterygoid (Huene 1934; Colbert 1989; Currie & Zhao 1994*a*; Harris 1998; Madsen & Welles 2000). Among pseudosuchians, a very similar recess has been reported for the phytosaur *Paleorhinus* (Doyle & Sues 1995), while *Sphenosuchus* bears an excavation in the rod of its ectopterygoid (Walker 1990). Yet, most other non-dinosaurian archosaurs show no sign of similar structures (Walker 1964; Bonaparte 1972; Romer 1972*b*; Wu & Chatterjee 1993; Gower 1999). Likewise, clear recesses are absent in the ventral surface of the ectopterygoids of ornithischians, as seen in *Dryosaurus* (Janensch 1955) and *Hypsilophodon* (Galton 1974). Among basal sauropodomorphs, a faint recess is present in *Thecodontosaurus* (Yates 2003*a*), but not in *Plateosaurus* (MB R.1937). For *Eoraptor*, we follow Sereno (1999), who coded an ectopterygoid fossa as present in the taxon. Sereno & Novas (1993) noted that the ventral surface of the ectopterygoid is not exposed in the better-known skull specimen of *Herrerasaurus* (PVSJ 407) and the condition in this taxon is uncertain.
17. *Post-temporal opening is a large aperture (0), a fissure between the skull roof and braincase (1) or reduced to a foramen or an incisure almost enclosed in the latter (2)* [ordered] (Sereno & Novas 1993). Sereno & Novas (1993) considered the reduction of the post-temporal fenestra to a foramen-sized aperture as a dinosaurian apomorphy. Indeed, in most non-dinosauromorph archosaurs the post-temporal opening is a large fenestra (Walker 1961, 1964; Ewer 1965; Romer 1971; Gower & Weber 1998), which served partially for the attachment of the adductor musculature. A relatively large aperture between skull roof and braincase is retained in *Silesaurus* and, apparently, also in basal dinosauriforms (Romer 1972*b*), while the post-temporal opening of other members of the ingroup is markedly reduced in size. It is, however, always retained, probably for the exit of the occipital ramus of the ophthalmic artery, which in birds leaves the braincase to irrigate the neck area (Midtgård 1984). In *Herrerasaurus*, the post-temporal opening is a clear fissure bounded by supraoccipital, parietal and opisthotic, a condition also usually seen in basal sauropodomorphs (Bonaparte 1978; Galton 1984*a*; Attridge *et al.* 1985; Bonaparte & Plumares 1995; Madsen *et al.* 1995; Benton *et al.* 2000). In theropods, however, the post-temporal opening is reduced to a foramen, which can be enclosed within the paroccipital process (Raath 1985) or retains its original position between the braincase and the skull roof (Rowe 1989; Currie & Zhao 1994*b*). Similar to theropods, the post-temporal opening of ornithischians is also 'foramen-sized' and either restricted to the paroccipital process (Galton 1974; Sues 1980; Weishampel & Witmer 1990; Sereno 1991*b*), or placed between the braincase and the skull roof (Galton 1983, 1988, 1989; *Scelidosaurus* – BMNH 1111).
18. *Dentary lacks (0) or bears (1) a marked lateral ridge in its caudal portion, which demarcates an emargination that corresponds to half of the transverse width of the bone*. Most dinosaurs bear a lateral ridge below the alveolar socket area, which extends throughout the length of the dentary. It is usually faint, as seen in basal theropods (Huene 1934; Welles 1984; Rowe 1989), but may be enlarged to form a marked emargination. This condition, together with the lingual offset of the maxillary teeth, is often related to the presence of cheeks (Galton 1973*b*; Paul 1984). In these cases, the ridge is especially well-developed in the caudal portion of the bone, as seen in basal ornithischians (Weishampel & Witmer 1990; Sereno 1991*b*; Sereno & Dong 1992), 'prosauropods' (Bonaparte & Plumares 1995; Yates 2003*b*) and segnosaurs (Paul 1984). In ornithischians, including *Pisanosaurus*, the emargination occupies about half of the transverse width of the bone (Galton 1974; Haubold 1991; *Lesothosaurus* – BMNH RUB17, R5801; *Scelidosaurus* – BMNH 1111). That of 'prosauropods' is, by contrast, much less developed, as seen in *Thecodontosaurus* (Benton *et al.* 2000), *Plateosaurus* (Galton 1984*a*) and *Coloradisaurus* (PVL 3967). Similarly to theropods, *Silesaurus, Staurikosaurus, Herrerasaurus, Saturnalia, Eoraptor* as well as most non-dinosauromorph archosaurs (Walker 1961, 1990; Ewer 1965; Chatterjee 1985; Sereno 1991*a*, Gower 1999), do not show signs of a well-developed emargination.
19. *Dentary symphysis restricted to the rostral margin of the dentary (0) or expanded along the ventral border of the bone (1)*. The dentary symphysis of most non-dinosauromorph archosaurs is restricted to the rostral tip of the bone (Walker 1964; Romer 1971; Gower 1999). This condition is retained in most dinosaurs, including *Staurikosaurus*, *Herrerasaurus*, *Saturnalia*, basal theropods (Huene 1934; Madsen 1976; Zhao & Currie 1994; Charig & Milner 1997; Madsen & Welles 2000) and basal sauropodomorphs (Galton 1984*a*; Madsen *et al.* 1995; Benton *et al.* 2000). By contrast, the ventral margin of the rostral tip of the dentary of ornithischians,

including *Pisanosaurus*, is medially expanded, so that the symphysis is caudally extended (Ostrom & McIntosh 1966; Galton 1974; Sereno 1991*b*; *Scelidosaurus* – BMNH 1111). In *Silesaurus*, although the symphysis seems more elongated caudally, the ventral margin of the dentary does not expand medially.

20. *Intramandibular joint absent (0) or present (1)* (Sereno & Novas 1992). The mandible of *Herrerasaurus* bears a well-developed intramandibular joint, formed by sliding dentary–surangular, dentary–angular and splenial–angular articulations. In *Staurikosaurus*, despite the poor preservation of its mandible, it is possible to recognise a sliding joint at least between the splenial and a rostral process in the angular. Sliding intramandibular articulations are also known in most theropods (Bonaparte *et al*. 1990; Currie & Carpenter 2000). Yet, as discussed by Sereno & Novas (1993, see also Holtz 2000, Fraser *et al*. 2002), unlike that of *Herrerasaurus*, the splenial–angular joint of these dinosaurs is formed by a concave depression on the angular and the convex dorsal border of the splenial. Moreover, coelophysids seem to lack an intramandibular joint (Holtz 2000), as is the case of all other basal dinosaurs (Galton 1974, 1984*a*; Bonaparte 1976; Sereno 1991*b*; Sereno *et al*. 1993) and most non-dinosaurian archosaurs (Walker 1961, 1990; Ewer 1965; Barberena 1978; Chatterjee 1978), although a comparable sliding articulation between dentary–splenial and angular occurs in *Ornithosuchus* (Walker 1964).
21. *Splenial mylohyoid foramen absent (0) or present (1)* (Rauhut 2003). *Sinraptor* has a clear foramen on the ventral part of its splenial, which Currie & Zhao (1994*a*) interpreted as the exit of the mylohyoid nerve. A similar foramen is seen also in other theropods (Madsen 1976; Welles 1984; Bonaparte *et al*. 1990; Madsen & Welles 2000), as well as in *Plateosaurus* (Galton 1984*a*) and *Coloradisaurus* (PVL 3967). An equivalent foramen was not recognised in ornithischians (Galton 1974; *Lesothosaurus* – BMNH RUB17, *Scelidosaurus* – BMNH 1111), nor in most non-dinosauriforms archosaurs (Walker 1961; Wu & Chatterjee 1993; Gower 1999), although an apparently homologous aperture is seen in *Postosuchus* (Chatterjee 1985; Long & Murry 1995).
22. *Craniomandibular joint at about the same level (0), or set well below the tooth rows (1)* (modified Gauthier 1986). Gauthier (1986) used the presence of a mandibular condyle set below the tooth row to diagnose sauropodomorphs more derived than *Thecodontosaurus* and *Anchisaurus*. In fact, the condition in those two taxa (Galton 1986; Yates 2003*a*) seems to be as derived as that of most sauropodomorphs that have ventrally displaced mandibular condyles (Huene 1926; Young 1941*a*; Bonaparte 1978; Gow *et al*. 1990; Yates 2003*b*; but see Bonaparte & Plumares 1995). Yet, these are not the only basal dinosaurs to present a ventrally displaced condyle, a condition seen also in *Eoraptor* and basal ornithischians (Galton 1974; Weishampel & Witmer 1990; Coombs *et al*. 1990; Haubold 1991; Sereno 1991*b*; Sereno & Dong 1992; Peng 1997), including *Pisanosaurus*. In other basal dinosaurs, however, the condyle is in line with the tooth row, as seen in *Herrerasaurus*, *Staurikosaurus*, and basal theropods (Gilmore 1920; Welles 1984; Colbert 1989; Charig & Milner 1997; Sampson *et al*. 1998). Similarly, this arrangement also characterises most non-dinosauromorph archosaurs (Ewer 1965; Romer 1971; Barberena 1978; Crush 1984), and apparently basal dinosauromorphs (Romer 1972*b*).
23. *Labial and lingual surface of maxillary/dentary tooth crowns evenly longitudinally convex (0) or bearing a marked low eminence (1)* (modified Sereno 1984). Sereno (1984) used the presence of bosses on the cheek tooth crowns as apomorphic for ornithischians (see also Sereno 1991*b*, Gauffre 1993). Indeed, a rounded low eminence is present in the maxillary/dentary tooth crowns of most basal members of the group (Charig & Crompton 1974; Galton 1974, 1985*c*, 1986; Colbert 1981; Weishampel & Witmer 1990; Haubold 1991; Thulborn 1992; Sereno & Dong 1992; *Scelidosaurus* – BMNH 1111), including *Pisanosaurus*, and also occurs in *Silesaurus*. The labial and lingual surfaces of the cheek teeth crowns of all other basal dinosaurs are, however, flat or evenly convex longitudinally, as in basal theropods (Colbert 1989; Madsen & Welles 2000), *Staurikosaurus, Eoraptor, Herrerasaurus, Saturnalia* and basal sauropodomorphs (Attridge *et al*. 1985; Galton 1985*c*, 1986; Gow *et al*. 1990; Gauffre 1993; Benton *et al*. 2000; Barrett 2000). Likewise, this is the condition seen in non-dinosauromorph archosaurs (Ewer 1965; Chatterjee 1985; Hungerbühler 2000) and basal dinosauromorphs (Romer 1972*b*; Bonaparte 1975).
24. *Maxillary/dentary tooth crowns unexpanded (0) or rostro-caudally expanded at the base (1)* (modified Sereno 1984). Sereno (1984) used the presence of cheek teeth with a well-developed neck at the base of the crown as an ornithischian apomorphy. As discussed by Gauffre (1993; see also Cooper 1985), however, a similar condition is seen also in 'prosauropods'. Indeed, in lingual or labial aspects, most tooth crowns of *Pisanosaurus*, *Silesaurus*, *Saturnalia*, basal sauropodomorphs (Attridge *et al*. 1985; Galton 1985*c*; Gow *et al*. 1990; Gauffre 1993; Benton *et al*. 2000; Barrett 2000) and basal ornithischians (Colbert 1981; Galton 1986; Weishampel & Witmer 1990; Haubold 1991; Thulborn 1992), are expanded at the base and abruptly constricted towards the root. By contrast, tooth crowns of most other basal dinosaurs, including basal theropods (Huene 1934; Welles 1984; Colbert 1989), *Staurikosaurus* and *Herrerasaurus*, are simple conical structures: a condition also present in most non-dinosauromorph archosaurs (Walker 1964; Ewer 1965; Hungerbühler 2000) and basal dinosauromorphs (Romer 1972*b*; Bonaparte 1975). *Eoraptor* bears some basally expanded tooth crowns, but these are restricted to the premaxilla and rostral tip of the maxilla and most cheek teeth are of the primitive conical type.
25. *Maxillary/dentary tooth crowns caudally curved (0), or straight (1)* (Sereno 1986). Sereno (1986) considered the absence of caudally curved maxillary and dentary teeth as apomorphic for ornithischians. Indeed, maxillary and dentary tooth crowns are mainly straight in basal ornithischians (Colbert 1981; Galton 1985*c*; Weishampel & Witmer 1990; Haubold 1991; Thulborn 1992) and *Pisanosaurus*, lacking a caudal curvature. Caudally curved tooth crowns are, however, widespread among dinosaurs, as seen in *Herrerasaurus*,

Staurikosaurus, basal theropods (Huene 1934; Welles 1984; Colbert 1989) and in most dental elements of *Eoraptor*. A similar tooth morphology is present in most non-dinosauromorph archosaurs (Walker 1964; Ewer 1965; Romer 1972*b*; Hungerbühler 2000), as well as in basal dinosauromorphs (Romer 1972*b*; Bonaparte 1975). Sauropodomorph tooth crowns are often asymmetrical, with the rostral border longer than the caudal (Attridge *et al*. 1985; Galton 1986; Gow *et al*. 1990; Barrett 2000). This gives a slight caudal inclination to the crown (Gauffre 1993), as seen also in *Silesaurus* and *Saturnalia*, as well as in the premaxillary teeth of some ornithischians (Sereno 1991*b*). Yet, this condition is distinct from the strong caudal curvature of theropod and basal archosaur teeth.

26. *Lanceolate crowns present in none (0), some (1), or most (2) maxilla/dentary teeth* [ordered] (modified Gauthier 1986). As previously discussed, tooth crowns that are not basally expanded and caudally curved are typical of archosaurs and plesiomorphic for dinosaurs. Maxillary and dentary teeth of ornithischians are distinctive because they broaden abruptly at the base and their short crowns are sub-triangular (Colbert 1981; Haubold 1991; Sereno 1991*b*; Sereno & Dong 1992) or sub–rectangular (Bonaparte 1976; Weishampel & Witmer 1990) in lingual–labial aspect. As proposed by Gauthier (1986; see also Galton 1976), basal sauropodomorphs are characterised by lanceolate tooth crowns. These are expanded at the base, but not as abruptly as in ornithischians, have gently convex rostral and caudal edges and always terminate in a pointed tip (Attridge *et al*. 1985; Galton 1985*c*, 1986; Gow *et al*. 1990; Barrett 2000). As described by Sereno *et al*. (1993), *Eoraptor* presents 'leaf-shaped' (= lanceolate) teeth at the rostral-most part of the maxilla. This is considered here intermediate between the basal archosaur condition and that of basal sauropodomorphs, *Saturnalia* and *Silesaurus*, in which lanceolate tooth crowns occur throughout the maxilla and dentary. Interestingly, some tooth crowns described by Bonaparte (1975) in the maxilla of *Marasuchus* are somewhat 'leaf-shaped', resembling those of *Saturnalia* and basal sauropodomorphs. This suggests that the presence of some lanceolate teeth might be plesiomorphic for dinosaurs. Yet, because a complete characterisation of this morphology is not available for those basal dinosauromorphs, the outgroup is considered to lack 'leaf-shaped' tooth crowns.
27. *Tooth crowns in the central to caudocentral portions of the dentary/maxillary series of the same width as (0), or wider than (1), other tooth crowns* (modified Sereno 1986). Maximum tooth size attained in the central to caudocentral portion of the maxillary and dentary tooth rows was considered apomorphic for ornithischians by Sereno (1986). Indeed, this condition is present in most basal members of the group (Thulborn 1974; Charig & Crompton 1974; Sues 1980; Colbert 1981; Chatterjee 1984; Coombs *et al*. 1990; Sereno 1991*b*), including *Pisanosaurus*, but also in the dentary of *Silesaurus*. By contrast, in most non-dinosauromorph archosaurs (Walker 1961; Ewer 1965; Chatterjee 1978), as well as in *Saturnalia*, *Staurikosaurus* and most basal sauropodomorphs (Galton 1984*a*, 1985*c*; Attridge *et al*. 1995; Bonaparte & Plumares 1995), the maxillary and dentary teeth are not particularly wider in any portion of the tooth rows. Yet, teeth are enlarged in the central part of the *Thecodontosaurus* dentary (Yates 2003*a*). A distinct condition is seen in *Eoraptor*, *Herrerasaurus*, most basal theropods (Welles 1984; Rowe 1989; Madsen & Welles 2000), various pseudosuchians (Chatterjee 1985; Wu & Chatterjee 1993; Gower 1999) and apparently basal dinosauromorphs (Romer 1972*b*; Bonaparte 1975). These forms present higher 'caniniform teeth' in the rostrocentral portion of the maxillary tooth rows. These tooth crowns are usually also wider than those of the other teeth, but this is not comparable with the condition dealt with here.
28. *Tooth crowns on the rostral quarter of the tooth-bearing areas of the upper and lower jaws are about the same height (0) or significantly higher than more caudal teeth (1)* (modified Gauthier 1986). Gauthier (1986) used the increase in tooth height in the rostral portion of the upper jaw as an apomorphy of sauropodomorph dinosaurs more derived than *Thecodontosaurus* and *Anchisaurus*. In fact, as discussed by Gauffre (1993) and seen also in *Saturnalia*, maximum tooth height attained in the rostral quarter of both the upper and lower jaws is a common feature of most basal sauropodomorphs (Bonaparte & Vince 1979; Galton 1985*b*, *c*; Gow *et al*. 1990; Barrett 2000). By contrast, most non-dinosauromorph archosaurs (Walker 1961; Ewer 1965; Romer 1971; Barberena 1978) and apparently also basal dinosauromorphs (Romer 1972*b*), do not have particularly high teeth in the rostral portion of the jaws. This condition is retained in *Eoraptor*, *Herrerasaurus*, *Staurikosaurus*, *Pisanosaurus*, basal theropods (Gilmore 1920; Huene 1934; Rowe 1989; Sampson *et al*. 1998) and basal ornithischians (Coombs *et al*. 1990; Haubold 1991; Sereno 1991*b*; Sereno & Dong 1992). Partial exceptions to this rule are several crurotarsan archosaurs (Chatterjee 1985; Sereno 1991*a*), and some theropods (Welles 1984), which have longer tooth crowns at the rostral tip of the dentary, although this is usually not associated with longer elements in the rostral part of the upper jaw, but rather the presence of caniniform teeth.

Axial skeleton

29. *Axial intercentrum narrower to about the same width (0), or wider than (1) the centrum* (Sereno 1999). Sereno (1999) defined an axis with the intercentrum wider than the centrum as apomorphic of Herrerasauridae plus Neotheropoda. Indeed, the axial intercentrum of *Herrerasaurus* and, especially, derived theropods (Madsen 1976; Currie & Zhao 1994*a*; Madsen & Welles 2000), is much wider than the corresponding centrum, as seen also in crocodiles (Frey 1988). Other non-dinosauromorph archosaurs (Krebs 1965; Chatterjee 1978) have an axial intercentrum that approaches the width of the related centrum. This is also the case in *Plateosaurus* (SMNS 12948, 13200) and *Camarasaurus* (Madsen *et al*. 1995), the axial intercentrum of which is only slightly narrower than the centrum. A very dissimilar condition is seen in basal ornithischians, in which the highly reduced intercentrum is narrower than half the width of the centrum, so that the cranial part of the axial centrum participates in the cranial articulation for the atlas (*Scelidosaurus* – BMNH 1111).

30. *Atlantal articulation facet in axial intercentrum saddle-shaped (0) or concave, with upturned lateral borders (1)* (modified Gauthier 1986). Gauthier (1986) proposed an axial intercentrum with a deep concave fossa for the reception of the atlantal intercentrum as apomorphic for theropods. Indeed, the cranial articulation of the axial intercentrum of these dinosaurs (Madsen 1976; Bonaparte 1986; Bonaparte *et al*. 1990; Currie & Zhao 1994*a*; Madsen & Welles 2000) is composed of a deep excavation surrounded by uplifted lateral borders that expand dorsally between the odontoid process and the rib articulations of the axial centrum. A very different arrangement is seen in pseudosuchians (Chatterjee 1978; *Typothorax* – Long & Murry 1995). In these forms, the cranial articulation of the axial intercentrum is 'saddle-shaped' – concave craniocaudally and convex laterome-dially. The highly reduced axial intercentrum of ornithischians apparently also retains a concavo-convex cranial articulation (Ostrom & McIntosh 1966; Galton 1974; *Scelidosaurus* – BMNH 1111). In these forms the laterocranial corners of the axial centrum form the slightly upraised lateral borders of the atlantal articulation of the axis. In *Plateosaurus* (SMNS 12948), the cranial articulation of the axial intercentrum is not convex lateromedially, but faint lateral borders are present, as is the case in *Herrerasaurus* (Sereno & Novas 1993). Yet, neither in *Plateosaurus*, nor in *Herrerasaurus*, do the lateral borders of the axial intercentrum extend so far dorsally as in theropods.
31. *Neural arch of cranial cervical vertebrae smooth caudally (0) or with an excavation on the caudolateral surface (1)* (Fig. 6). In theropods, most cervical vertebrae have a well-developed caudal cavity surrounded by two marked laminae that extend from the transverse process to the postzygapophysis and the caudodorsal corner of the centrum (Madsen 1976; Colbert 1989, Madsen & Welles 2000; *Liliensternus* – MB R.1275). This was termed the caudal chonos by Welles (1984), probably serving for the insertion of interarticular vertebral ligaments (Frey 1988; Baumel & Raikow 1993). A similar excavation is seen in the cranial cervicovertebral elements of *Herrerasaurus*, *Staurikosaurus*, *Silesaurus* and most basal sauropodomorphs (Heerden 1979; Zhang 1988; Bonaparte 1999; *Efraasia* – SMNS 12684; *Plateosaurus* – MB R.1937; but see Yates 2003*a*). It is, however, less conspicuous and not delimited by sharp laminae. A comparable cavity is absent from the cervical vertebrae of basal ornithischians (Ostrom & McIntosh 1966; Galton 1974), most non-dinosauromorph archosaurs (Ewer 1965; Bonaparte 1972, 1999; Chatterjee 1978; Frey 1988) and *Marasuchus* (Bonaparte 1975; Sereno & Arcucci 1994), the neural arches of which have a smooth laterocaudal surface.
32. *Centra of postaxial cranial cervical vertebrae subequal to (0), or longer than (1), the axis centrum* (Gauthier 1986). Gauthier (1986) defined the extra elongation of the cervical vertebrae as an apomorphy of saurischians. Indeed, the centra of the cranial cervical vertebrae (3–5) of basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942, 1951; Galton 1976; Bonaparte & Plumares 1995; Bonaparte 1999; Yates 2003*a*) and basal theropods (Welles 1984; Colbert 1989; Currie & Zhao 1994*a*; Charig & Milner 1997; Madsen & Welles 2000) are more than 25% longer than that of the axis, a condition seen also in *Herrerasaurus* and *Eoraptor*. In ornithischians, however, the centra of these vertebrae are subequal or even shorter than that of the axis (Santa Luca 1980; Colbert 1981; Sereno 1991*b*; *Dryosaurus* MB dy I), as seen also in *Silesaurus*, *Marasuchus* and non-dinosauromorph archosaurs (Ewer 1965; Krebs 1965; Bonaparte 1972; Romer 1972*b*; Chatterjee 1978; Wu & Chatterjee 1993). Interestingly, the axial centrum of *Lewisuchus* seems to be much shorter than those of its third and fourth cervical vertebrae.
33. *Epipophyses absent (0) or present (1) in post-axial cranial cervical vertebrae* (Fig. 6; Gauthier 1986). Although present in some rauisuchians (*Batrachotomus* – SMNS various specimens), epipophyses are absent from the cervical vertebrae of most non-dinosauromorph archosaurs (Ewer 1965, Bonaparte 1972, Chatterjee 1978), as is also the case in *Marasuchus* and, apparently, *Pseudolagosuchus*. Gauthier (1986) used the presence of these structures in cranial cervical vertebrae (3–5) as a saurischian apomorphy, while Sereno & Novas (1993) considered prominent epipophyses as apomorphic for theropods (including *Herrerasaurus*). Indeed, the degree of caudal projection of cervical epipophyses varies among dinosaurs. They can occur in the form of simple unexpanded ridges on top of the postzygapophyses, as in *Staurikosaurus*, *Eoraptor*, some basal theropods (Colbert 1989; Rauhut 2003; *Liliensternus* – MB R.1275), most 'prosauropods' (Heerden 1979; Heerden & Galton 1997; Bonaparte 1999) and some ornithischians (Ostrom & McIntosh 1966; Galton 1974; Santa Luca 1980; Forster 1990; Sereno 1991*b*; *contra* Gauthier 1986), or extend caudal to the articulation facet of the postzygapophyses, as in *Herrerasaurus*, some 'prosauropods' (*Thecodontosaurus* – BMNH P24; *Efraasia* – SMNH 12684; *Plateosaurus* – SMNS F65, MB R.1937)

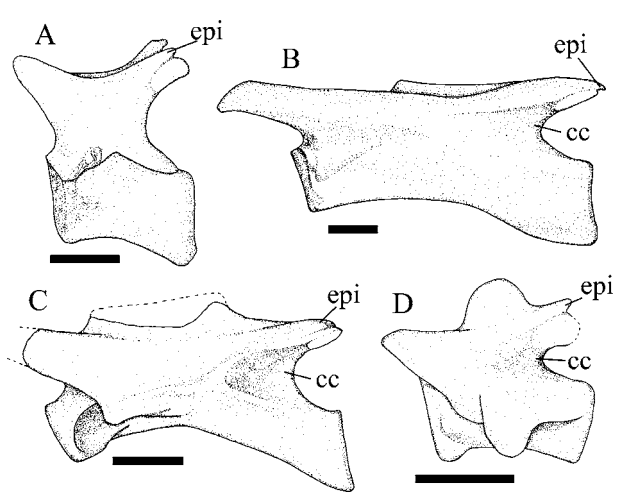

Figure 6 Lateral aspect of post-axial cranial cervical vertebrae of **A**, *Lesothosaurus diagnosticus*, third cervical vertebra based on BMNH R11004; **B**, *Plateosaurus engelhardti*, third cervical vertebra based on SMNS F65; **C**, *Liliensternus liliensterni*, third? cervical vertebra based on MB R.1275; **D**, *Staurikosaurus pricei*, fourth? cervical vertebra based on MCZ 1669. Abbreviations: **cc**, caudal chonos; **epi**, epipophysis. Scale bars: **A** = 5 mm; **B–D** = 20 mm.

and most theropods (Madsen 1976; Welles 1984; Bonaparte 1986; Currie & Zhao 1994*a*; Charig & Milner 1997; Sampson *et al*. 1998; Madsen & Welles 2000). *Silesaurus* is the only ingroup OTU that lacks cervical epipophyses, while their caudal projection seems variable among basal theropods and sauropodomorphs.

34. *Epipophyses absent (0) or present (1) in caudal cervical vertebrae (6–9)* (Sereno *et al*. 1993). Sereno *et al*. (1993) considered the presence of epipophyses in the mid-caudal cervical vertebrae as apomorphic for saurischians. Indeed, epipophyses are absent from the caudal portion of the ornithischian neck (Ostrom & McIntosh 1966; Galton 1974; Santa Luca 1980; *Dryosaurus* – MB dy I). By contrast, the caudal cervical vertebrae of *Eoraptor*, *Herrerasaurus*, *Saturnalia*, basal sauropodomorphs (Bonaparte 1999; *Thecodontosaurus* – BMNH P24; *Efraasia* – SMNS12667; *Plateosaurus* – SMNS 13200, MB R.1937) and basal theropods (Welles 1984; Bonaparte 1986; Bonaparte *et al*. 1990; Currie & Zhao 1994*a*; Charig & Milner 1997; Madsen & Welles 2000), have clear epipophyses, either as ridge-like structures or extending caudally to the postzygapophyses. As noted above, *Silesaurus*, basal dinosauromorphs and most non-dinosauromorph archosaurs, seem to lack epipophyses altogether.
35. *Centra of caudal cervical vertebrae subequal to (0) or longer than (1) those of cranial trunk vertebrae* (modified Gauthier 1986). Gauthier (1986) used the elongation of the caudal cervical vertebrae as an apomorphy of Saurischia. Indeed, an abrupt decrease in centrum length is seen in the caudal part of the neck of *Saturnalia*, basal theropods (Janensch 1925; Huene 1934; Welles 1984; Colbert 1989) and basal sauropodomorphs (Huene 1926; Young 1941*a*, 1951; Galton 1973*a*; Cooper 1981; Bonaparte & Plumares 1995; Yates 2003*a*), where the centra of cervical vertebrae 6–8 are significantly longer than those of the cranial trunk vertebrae. By contrast, *Silesaurus*, *Staurikosaurus*, *Eoraptor* and basal ornithischians (Ostrom & McIntosh 1966; Galton 1974; Santa Luca 1980; Colbert 1981; Forster 1990; *Dryosaurus* MB dy I), have caudal cervicovertebral centra that are about the same length as those of the cranial trunk elements and an abrupt decrease in centrum length is not seen. This condition is also present in *Marasuchus* (Bonaparte 1975; Sereno & Arcucci 1994) and most non-dinosauromorph archosaurs (Ewer 1965; Bonaparte 1972; Chatterjee 1978; Wu & Chatterjee 1993; Long & Murry 1995).
36. *Parapophyses do not (0) or do (1) contact the centrum in vertebrae caudal to the twelfth presacral element*. In most cervical vertebrae of ornithopods (Galton 1974; Santa Luca 1980; Norman 1986; Forster 1990) the parapophyses are placed at the neurocentral junction. An abrupt dorsal displacement of these structures is, however, seen in the neck–trunk transition and, usually, by the 13th presacral element the parapophyses are restricted to the neural arch, as apparently seen also in thyreophorans (Hennig 1924) and *Silesaurus*. A different condition occurs in basal sauropodomorphs (Young 1941*a*, 1942, 1951; Cooper 1981; Bonaparte 1999; *Efraasia* – SMNS 12354; *Riojasaurus* – PVL 3808; *Plateosaurus* – GPIT mounted skeletons) and basal theropods (Welles 1984; Bonaparte 1986; Bonaparte *et al*. 1990; Currie & Zhao 1994*a*; Charig & Milner 1997; Harris 1998; *Liliensternus* – MB R.1275). In these forms, vertebrae caudal to the 12th presacral element still have the parapophyses placed at the level of the neurocentral junction and, in various forms, the complete shift to the neural arch only occurs in the caudal portion of the trunk. The parapophyses of the 12th presacral vertebra of *Saturnalia* (MCP 3845-PV) are on the neurocentral joint, while that of the 13th presacral vertebra is enclosed in the neural arch. The condition in other members of the ingroup is more uncertain, but a similar arrangement is inferred for *Eoraptor* and *Staurikosaurus*. Similarly, in *Marasuchus*, most pseudosuchians (Walker 1961; Bonaparte 1972; Chatterjee 1978; Wu & Chatterjee 1993) and, apparently, *Lewisuchus*, the change in position of the parapophyses occurs between the 9th and 11th presacral vertebrae and the parapophyses do not contact the centrum in vertebrae caudal to the 12th presacral element.
37. *Mid-cervical ribs are short and directed caudoventrally (0) or long and sub-parallel to the neck (1)* (Sereno 1999). Sereno (1999) used mid-cervical ribs that are elongated and sub-parallel to the neck as a saurischian apomorphy. Indeed, the ribs of the cervical vertebrae of basal sauropodomorphs (Young 1941*a*; Galton 1976; He *et al*. 1988; Zhang 1988; *Plateosaurus* – GPIT mounted skeletons) and basal theropods (Gilmore 1920; Ostrom 1978; Colbert 1989; Rowe 1989; Bonaparte *et al*. 1990; Harris 1998) are parallel to the neck and usually quite elongated, often extending to the length of two cervical centra. The cervical ribs of ornithischians (Galton 1974; Santa Luca 1980; Norman 1986; Forster 1990), by contrast, are much shorter and usually form an angle of about 45° ventral to the neck. This condition is also present in most non-dinosauromorph archosaurs (Ewer 1965; Romer 1972*c*; Chatterjee 1978; Wu & Chatterjee 1993) and apparently, *Lewisuchus* (Romer 1972*b*). However, long and sub-parallel cervical ribs are inferred for *Silesaurus* (Dzik 2003), *Eoraptor* (Sereno *et al*. 1993) and *Saturnalia* (MCP 3944-PV).
38. *Hyposphene–hypantrum articulations absent (0) or present (1) in trunk vertebrae* (Gauthier 1986). Gauthier (1986) considered trunk vertebrae with hyposphene–hypantrum articulations as a saurischian apomorphy. Indeed, these structures occur in *Saturnalia*, basal theropods (Huene 1934; Welles 1984; Bonaparte 1986; Colbert 1989; Madsen & Welles 2000) and basal sauropodomorphs (Huene 1926; Bonaparte 1972; Heerden 1979; Cooper 1981; Benton *et al*. 2000). In addition, Novas (1993) showed the presence of these articulations in *Herrerasaurus*, while Bonaparte *et al*. (1999) described them for *Guaibasaurus*. Novas (1993) also argued for the presence of the hyposphene–hypantrum joint in *Staurikosaurus*, but Bittencourt (2004) considered it ambiguous. These auxiliary articulations are, however, absent in the trunk vertebrae of ornithischians (Janensch 1955; Ostrom & McIntosh 1966; Galton 1974; *Scelidosaurus* – BMNH 1111, 6704) and apparently, *Silesaurus*. Likewise, although some rauisuchians show the hyposphene–hypantrum joint (Long & Murry 1995; *Batrachotomus* — SMNS various specimens), these are absent from the trunk vertebrae of *Marasuchus* and most non-dinosauromorph archosaurs (Walker 1964; Ewer 1965; Bonaparte 1972; Chatterjee

1978). Based on Sereno *et al*. (1993) the presence of the hyposphene–hypantrum joint is inferred for *Eoraptor*.

39. *Centra and neural spines of caudal trunk vertebrae elongated (0) or axially shortened (1)* (modified Novas 1992). Novas (1992) defined the presence of caudal trunk vertebrae with axially shortened centra and caudal trunk and cranial sacral vertebrae with broad and axially shortened neural spines, as two distinct apomorphies of Herrerasauridae. These are united here into a single character, which represents the axial shortening of vertebrae in these regions. Indeed, the centra of the caudal trunk vertebrae of *Herrerasaurus* are about 70% higher than long. These are also axially compressed in the sacral area, although not as much as in the latter part of the column. The neural spines of both caudal trunk and cranial sacral vertebrae are also shortened, having a subquadratic cross-section. Basal dinosaurs in general show no axial compression of caudal trunk or cranial sacral vertebrae. Among basal sauropodomorphs, the neural spine of these elements is an axially elongated plate-like structure (Huene 1926; Galton 1973*a*; Cooper 1981). Moreover, their centra are usually longer than high (Young 1941*a*, *b*; Galton 1973*a*; Cooper 1981; Zhang 1988), as is also the case in *Saturnalia*, or less commonly about as high as long (Huene 1926; Galton 2000*b*; *Riojasaurus* – PVL 3808). The general condition for sauropodomorphs is seen also in basal theropods (Janensch 1925; Raath 1969; Welles 1984; Padian 1986; Colbert 1989; Currie & Zhao 1994*a*, Charig & Milner 1997; Madsen & Welles 2000; *Liliensternus* – MB R.1275), although some derived forms have compressed caudal trunk vertebrae (Madsen 1976). The two 'dorsosacral' vertebrae of *Silesaurus* are somewhat shortened, but the centra are still as long as high and the neural spines are plate-like. Most basal ornithischians have caudal trunk and cranial sacral centra slightly longer than high (Janensch 1955; Santa Luca 1980; Colbert 1981; *Scelidosaurus* – BMNH 6704), although the caudal trunk centra are significantly higher than long in some derived ornithopods (Norman 1986; Forster 1990). In all those forms, however, the neural spines are plate-like and not axially compressed. In *Staurikosaurus* the caudal trunk centra are about 25% higher than long, characterising an intermediate condition between those of dinosaurs in general and *Herrerasaurus*. In addition, their neural spines are also compressed and square-shaped in transverse section. Unlike *Herrerasaurus*, however, the centra of the sacral vertebrae are longer than high and the neural spines are plate-like. The latter feature is seen also in the trunk and sacral vertebrae of *Eoraptor*, the centra of which do not seem to be particularly compressed. This also represents the plesiomorphic condition for dinosaurs, since *Lagerpeton* and *Marasuchus* have caudal trunk vertebrae with centra that are longer than high, and plate-like neural spines, a condition shared with most non-dinosauromorph archosaurs (Krebs 1965; Romer 1972*c*; Long & Murry 1995).
40. *Ribs of the two primordial sacrals cover almost the entire medial surface of the iliac alae (0), or are much shorter than that surface (1)* (Fig. 7). In *Herrerasaurus* the fused transverse processes and ribs of the two sacral vertebrae are fan-shaped in dorsal aspect, expanding laterally to articulate with the almost entire medial margin of the iliac alae. This is seen also in *Staurikosaurus*, *Eoraptor* and *Saturnalia*, as well as in *Marasuchus*, *Lagerpeton* and various non-dinosauromorph archosaurs (Walker 1961; Bonaparte 1984; Long & Murry 1995). In *Scleromochlus* (Benton 1999) and pterosaurs (Wellnhofer 1975, Wild 1978), however, the transverse process-ribs of the two primordial sacrals are much reduced axially and only cover a small portion of the iliac alae. This condition is also present in most dinosaurs, in which the sacrum is composed of three vertebrae or more, as seen in basal ornithischians (Janensch 1955; Galton 1974; Santa Luca 1980; *Scelidosaurus* – BMNH 6704) and basal theropods (Gilmore 1920; Janensch 1925; Raath 1969; Welles 1984; Colbert 1989; Cuny & Galton 1993; *Liliensternus* – MB R.1275). The sacrum of 'prosauropods' is commonly composed of three vertebrae (Galton 2000*b*). Regardless of which are the two primordial elements (see discussion below), their transverse process-ribs do not occupy the entire medial margin of the iliac alae, as seen also in *Silesaurus*. The sacrum of *Pisanosaurus* is very poorly preserved, but it is possible to infer that it was composed of four or five vertebrae. Here the ribs are not fan-shaped and resemble those of typical ornithischians (Janensch 1955; *Scelidosaurus* – BMNH 6704) suggesting that those of the two primordial elements do not cover the entire medial surface of the iliac alae.

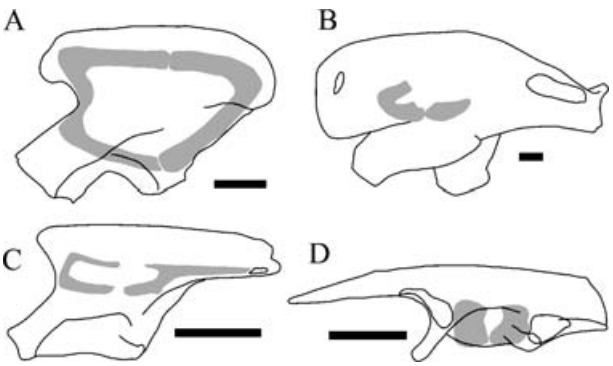

Figure 7 Lateral outlines of ilium and sacral vertebrae articulations of **A**, *Herrerasaurus ischigualastensis*, based on PVL 2566 and Novas (1993); **B**, *Dilophosaurus wetherilli*, based on Welles (1984); **C**, *Saturnalia tupiniquim*, based on MCT 3944PV; **D**, *Scelidosaurus harrisonii*, based on BMNH 6704. Primordial sacral vertebrae articulations in grey. Scale bars: A = 50 mm, **B–D** = 30 mm.

41. *Primordial trunk vertebrae are free (0) or some are incorporated into the sacrum, with their ribs/transverse processes articulating with the pelvis (1)* (Fig. 7) (Sereno *et al*. 1993).
42. *Primordial caudal vertebrae are free (0) or some are incorporated into the sacrum, with their ribs/transverse processes articulating with the pelvis* (1) (Fig. 7) (modified Galton 1976). Ever since the proposal of the name Dinosauria (Owen 1842), the increase in the number of sacral vertebrae has been used to characterise the group. More recently, two main strategies of coding characters based on this morphological transformation have been formulated. Some authors (Benton 1990; Novas 1992, 1993, 1996; Rauhut 2003; Yates 2003*a*) have adopted a topographic approach, simply taking into

consideration the number of sacral vertebrae, regardless of their homologies to caudal and/or trunk elements. Indeed, the search for such vertebral homology may be meaningless, as suggested by studies of the cervical series of modern mammals (Johnson & O'Higgins 1996). Nevertheless, Novas (1993, 1996, see also Sereno & Novas 1992) attempted to recognise whether trunk or caudal elements have been incorporated into the sacrum, a strategy applyed for character coding by Sereno *et al*. (1993), Sereno (1999), and Langer (2004). For the legitimacy of the first strategy, it is necessary to accept that 'new' (neither trunk or caudal) vertebrae have been added to the sacral series. Yet, it seems possible to identify among the vertebrae that form the dinosaur sacrum morphological traits suggesting correspondence to caudal trunk or proximal caudal vertebral elements hence the second strategy is followed here. Central to this attempt is, obviously, the identification of the two primordial sacral vertebrae in the dinosaurian sacrum.

A two-vertebra sacrum is the plesiomorphic condition for dinosaurs. It is present in most non-dinosauromorph archosaurs (Walker 1961; Ewer 1965; Romer 1972c; Chatterjee 1978; Bonaparte 1984), as well as in *Lagerpeton* and *Marasuchus*. An independent increase in the number of sacral vertebra occurred in various pseudosuchians (Walker 1964; Bonaparte 1972, 1984; Long & Murry 1995; Alcober & Parrish 1997), as well as in pterosaurs (Wild 1978; Wellnhofer 1991). Similarly, the sacrum of *Scleromochlus* is composed of more that two vertebrae (Benton 1999), which seems to include both truncosacral and caudosacral elements. By contrast, a two-vertebrae sacrum is known in *Herrerasaurus*, the last two trunk vertebra of which are not attached to the ilia, although placed between their cranial alae. *Silesaurus* shows an analogous condition, in which only the two caudal elements of a fused complex of four vertebrae in the sacral region contact the pelvic girdle. These are considered the 'true' sacral vertebrae and might represent the two primordial elements.

Among basal dinosaurs, the ribs-transverse processes of the two cranial sacral vertebrae of *Saturnalia* are the largest and articulate with the central part of the ilia. By contrast, the third sacral vertebra, with much reduced transverse processes that articulate with the caudal margins of the ilia, was presumably added from the caudal series. In *Eoraptor*, however, as suggested by Sereno *et al*. (1993), a single trunk vertebra seems to have been added to the sacrum. Bonaparte *et al*. (1999) argued that the sacrum of *Guaibasaurus* is composed of three vertebrae. These are, however, too poorly preserved to allow any further determination. For *Staurikosaurus*, no trunk vertebrae have been added to the sacrum, but it is not agreed whether the same applies for the caudal series (Colbert 1970; Galton 1977; Langer 2004; Bittencourt 2004).

The sacrum of ornithischians is highly modified and that of *Scelidosaurus* (BMNH 6704) is composed of four vertebrae. The two middle elements are those that approach more the position of the primordial sacrals of basal archosaurs, and the 'reversed-L' shape of the ribs of the third vertebra resembles that of the second primordial sacral of *Staurikosaurus*. This suggests that one caudal and one trunk vertebra were added to the sacrum of that dinosaur. Furthermore, the centra and ribs of the caudal sacral vertebrae are narrower than those in the cranial part of the sacrum, confirming the morphology also observed in the cast of the pelvis and sacrum of *Pisanosaurus*. This seems to be composed of at least four vertebrae, which are tentatively accepted as the two primordial sacrals, a truncosacral and a caudosacral. More derived ornithischians always have more than four sacral vertebrae. In the case of *Dryosaurus* (MB dy III), the cranio- and caudolateral inclination of the transverse processes of the primordial sacrals indicate their affinity. In this taxon, two trunk and two caudal vertebrae have been added to the sacrum (see Janensch 1955: fig. 23), a condition apparently shared by most basal neornithischians (Galton 1974; Maryanska & Osmólska 1974; Forster 1990), which present two caudosacral and a variable number of truncosacrals. The condition in *Lesothosaurus* is uncertain (BMNH RUB17, R11002), but at least four, and most possibly five, sacral vertebrae are present.

The basalmost condition among theropods is seen in *Liliensternus* (Cuny & Galton 1993) and *Dilophosaurus* (Welles 1984), in which the sacrum seems to be composed of four vertebrae. Based on their morphology and position (Welles 1984), these represent the two primordial sacra, plus a truncosacral and a caudosacral. Basal Tetanurae have this count increased to five. In this case it is a second truncosacral that is added, as inferred by the comparison of the four caudal sacral vertebrae of *Allosaurus* (Madsen 1976) with those of *Dilophosaurus*. This is also possibly the case in the highly modified sacrum of *Syntarsus* (Raath 1969), *Coelophysis* (Colbert 1989) and *Ceratosaurus* (Gilmore 1920), whereas in *Elaphrosaurus* (MB s/n) and abelisaurids (Bonaparte *et al*. 1990) extra trunk vertebrae are added. Various authors (Novas 1996; Galton 1999; Moser 2003; Yates 2003*b*) have recently reassessed the sacral anatomy of 'prosauropods', concluding that their usual three-vertebra sacrum has a variable addition of trunk or caudal elements. *Plateosaurus* has a caudosacral added (Galton 2000*b*; Moser 2003; Yates 2003*b*), based on the position of the two cranial-most transverse processes and the origin of the transverse process and rib of the third vertebra in the centre rather than in the cranial part of the centrum. This condition seems to be shared with *Thecodontosaurus* (Galton 1999), but is controversial if it is also present in *Efraasia* and *Anchisaurus* (Galton 1999; Moser 2003; Yates 2003*b*). By contrast, the ribs of the third vertebra of the sacrum of *Riojasaurus* (Novas 1996; PVL 3808), *Massospondylus* (Cooper 1981; Galton 1999), *Lufengosaurus* (Young 1941*a*) and *Yunanosaurus* (Young 1942), attach to the cranial part of the centrum and are believed to belong to the second primordial sacral. These forms present, therefore, a trunk vertebra added to the sacrum (Yates 2003*a*). In the sacrum of *Melanorosaurus* (*contra* Galton 1999; but see Moser 2003), a second truncosacral was added.

43. *Transverse processes of sacral vertebrae do not expand laterally (0) or expand, roofing the space between adjacent ribs (1)* (Fig. 7). The sacral vertebrae of the ornithopod *Dryosaurus* (MB dy III) bear laterally

tapering transverse processes. These are restricted to the dorsal surface of the respective ribs and do not expand craniocaudally, a condition shared by other ornithischians (Galton 1974; Maryanska & Osmólska 1974; *Scelidosaurus* – BMNH 6704). In 'prosauropods' (Young 1941*a*; Cooper 1981; Galton 2000*a*, *b*; Yates 2003*b*; *Riojasaurus* – PVL 3808), the transverse processes of the sacral vertebrae are more craniocaudally expanded and always cover a portion of the space between adjacent ribs. A similar arrangement is seen in *Herrerasaurus*, *Saturnalia* and *Eoraptor*, the two primordial sacrals of which bear transverse processes that cover part, to most, of the space between their respective ribs. Although not very expanded, the 'wing-like' transverse processes of dorsosacral 1 and sacral vertebrae of *Silesaurus* also cover part of the sacral area. For theropods, the sacral vertebrae of most basal forms have extremely expanded transverse processes, which form a complete roof in the sacral area (Gilmore 1920; Janensch 1925; Raath 1969; Colbert 1989; Bonaparte *et al*. 1990). Such dorsal covering is unknown in most non-dinosaurian archosaurs. In *Euparkeria* (Ewer 1965) and *Marasuchus* the transverse processes seem restricted to the cranial margin of the first and caudal margin of the second sacral ribs and do not expand to cover the space between them. In *Lagerpeton*, the transverse processes are broad, but do not extend laterally. The condition in various pseudosuchians is far more complex (Walker 1961; Chatterjee 1985) and derived in its own way.

44. *First primordial sacral rib plate-like (0) or dorsally expanded (1) on its cranial margin* (Fig. 7). In basal dinosauromorphs, the first sacral vertebra bears simple plate-like ribs that expand laterally to articulate with the ilium (Bonaparte 1975; Arcucci 1986; Novas 1996) and, at most, have slightly upturned cranial margins (Sereno & Arcucci 1993, 1994). A similar condition is present in other archosaurs (Ewer 1965; Romer 1972*c*; Chatterjee 1978), as well as in *Silesaurus*. The transverse processes of the latter are, however, more individualised, providing separate anchor points to the pelvis. This is seen also in *Saturnalia* and *Herrerasaurus*, the first sacral ribs of which are dorsally expanded on their cranial margin, extending until the respective transverse processes to form a 'C-shaped' pelvic junction. A dorsal expansion is seen also in the ribs of the primordial first sacral of *Staurikosaurus*, 'prosauropods' (Galton 2000*a*, *b*; Yates 2003*b*), basal theropods (Welles 1984) and ornithischians (Janensch 1955; Galton 1974; Forster 1990).
45. *Ribs of the first primordial sacral vertebra are shallower to about the same depth as (0), or deeper than (1) half the depth of the ilium* (Fig. 7; modified Novas 1992). Novas (1992) used the presence of very deep sacral ribs as an apomorphy of Herrerasauridae. Indeed, in *Herrerasaurus*, the second sacral rib is about 70% as deep as the ilium. A similar condition is seen in *Staurikosaurus*, in which this proportion is of about 60%. More typical of dinosaurs, however, are sacral ribs that are not deeper than half the iliac depth. This condition occurs in *Marasuchus*, *Lagerpeton* and most non-dinosauromorph archosaurs (Ewer 1965; Bonaparte 1972, 1984; Chatterjee 1978; Parrish 1986; Long & Murry 1995). Likewise, basal theropods (Gilmore 1920; Welles 1984; Bonaparte *et al*. 1990; Cuny & Galton 1993; Currie & Zhao 1994*a*), basal ornithischians (Galton 1974, 1981; Forster 1990; *Scelidosaurus* – BMNH 6704; *Lesothosaurus* – BMNH RUB17, R1102), *Saturnalia*, *Silesaurus* and, possibly, *Pisanosaurus*, have sacral ribs shallower than half the depth of the ilium. A similar condition is also present in basal sauropodomorphs (Galton 1973*a*, 1976; Novas, 1996; *Plateosaurus* – SMNS F65, GPIT mounted skeletons), in which the sacral ribs are about as deep as half the iliac depth.
46. *Neural spines of proximal caudal vertebrae dorsodistally (0) or dorsally directed (1)* (Novas 1992). Novas (1992) used the presence of vertical neural spines in the proximal caudal vertebrae as apomorphic for Herrerasauridae. Indeed, about five of the proximal-most caudal vertebrae of *Staurikosaurus* and *Herrerasaurus* have neural spines that extend almost vertically. This seen to represent a derived feature among dinosaurs, since distally inclined neural spines are seen in the cranial caudal vertebrae of *Marasuchus* and *Lagerpeton*, although the condition is rather variable among non-dinosauromorph archosaurs (Walker, 1961, 1964; Krebs 1965; Ewer 1965; Romer 1972*c*; Long & Murry 1995). Distally inclined neural spines are also present in the cranial caudal vertebrae of basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942, 1951; Galton 1973*a*) and basal ornithischians (Owen 1863; Galton 1974, 1981; Santa Luca 1980). This is also the case with most basal theropods (Gilmore 1920; Raath 1969; Welles 1984; Bonaparte *et al*. 1990; Madsen & Welles 2000), although the very cranial caudal vertebrae of some forms have vertical neural spines (Madsen 1976). The neural spines of the proximal caudal vertebrae of *Eoraptor* also seem to be distally inclined, as well as those of the preserved proximal caudal vertebrae of *Guaibasaurus*. The first caudal vertebra of *Silesaurus* also has a subtle distal inclination.
47. *Prezygapophyses of distal caudal vertebrae overlap about a quarter (0) or more than a quarter (1) of the adjacent centrum* (Gauthier 1986). Gauthier (1986) used the presence of a transition point in the tail as apomorphic for theropods. This arose partially from the elongation of the prezygapophyses of distal caudal vertebrae that Gauthier (1986) noted in *Staurikosaurus* and was later recognised in *Herrerasaurus* (Novas 1986, 1992). Indeed, the prezygapophyses of the distal caudal vertebrae of both *Herrerasaurus* and *Staurikosaurus* overlap more than a quarter of the preceding vertebrae. This is certainly a derived feature among dinosaurs, since much shorter prezygapophyses are seen in the distal caudal vertebrae of *Marasuchus*, non-dinosauromorph archosaurs (Walker 1961; Krebs 1965; Chatterjee 1978), basal sauropodomorphs (Huene 1926; Young 1941*a*, 1951; *Riojasaurus* – PVL 3808) and basal ornithischians (Owen 1863; Galton, 1974; Santa Luca, 1980, 1984; Colbert 1981). The primitive condition for theropods is, however, more controversial. The group in general is characterised by distal caudal vertebrae with long prezygapophyses, as seen in various basal members of the group (Janensch 1925; Raath 1969; Cuny & Galton 1993) as well as in the majority of tetanurans (Ostrom 1969; Osmólska *et al*. 1972; Madsen 1976; Currie & Zhao 1994*a*). Yet, other basal theropods have prezygapophyses of the standard dinosaur length (Welles 1984;

Madsen & Welles 2000; Rauhut 2003) and the character is coded as uncertain for the OTU 'theropods'. Some caudal vertebrae of *Silesaurus*, *Guaibasaurus*, *Eoraptor*, *Pisanosaurus*, *Saturnalia* and *Pseudolagosuchus*, are known (Casamiquela 1967; Arcucci 1987; Bonaparte *et al*. 1999; Langer *et al*. 1999) and these show the typical dinosaur condition of non-elongate prezygapophyses. Yet, none of these demonstrably belongs to the more distal portion of the tail.

Shoulder girdle and forelimb

48. *Humerus longer than or subequal to (0), or shorter than 0.6 of (1) the length of the femur* (modified Novas 1993). Novas (1993) used a humerus that is shorter than half the femoral length as a character uniting *Eoraptor*, Herrerasauridae and Neotheropoda. Indeed, the humerus of basal theropods is usually shorter than (Huene 1934; Raath 1969; Madsen & Welles 2000) or subequal to (Camp 1936; Ostrom 1978; Welles 1984; Bonaparte 1986) half the length of the femur. By contrast, the usual condition in basal dinosaurs is a humerus that corresponds to 0.6 or more of the femoral length. This is seen in *Silesaurus*, *Saturnalia*, most basal ornithischians (Owen 1863; Galton 1974; Santa Luca 1980; Colbert 1981) and basal sauropodomorphs (Huene 1926; Bonaparte 1972; Galton 1973*a*, 1976; Cooper 1981; Heerden & Galton 1997), as well as in members of the outgroup (Ewer 1965; Krebs 1965; Chatterjee 1978; Sereno & Arcucci 1994; Benton 1999). In *Herrerasaurus*, the humerus is incomplete in PVSJ 373, but its estimated length is 0.5 of that of the corresponding femur (Sereno 1993). In addition, in specimens referred to *Ischisaurus cattoi* by Reig (1963; see Novas 1993) that ratio is between 0.5 and 0.6. The humerus of the holotype of *Eoraptor* is also incomplete, but its estimated length corresponds to about 0.5 of that of the femur.
49. *Distal apex of the deltopectoral crest placed within the proximal 30% of the humeral shaft (0), or distal to that (1)* (Bakker & Galton 1974). Bakker & Galton (1974) defined the presence of an elongated deltopectoral crest as a dinosaur apomorphy. Indeed, the distal apex of the deltopectoral crest of non-dinosauromorph archosaurs is located within the proximal 30% of the bone (Walker 1961; Ewer 1965; Krebs 1965; Bonaparte 1972; Romer 1972*c*; Chatterjee 1978; Benton 1999). Moreover, it has a rounded outline and is relatively continuous to the proximal articulation of the bone. This morphology is seen also in *Silesaurus* and, apparently, in *Lewisuchus*. The deltopectoral crest of *Marasuchus* is also short, with the distal apex located within the proximal 30% of the humeral shaft. Yet, it is somewhat separated from the proximal articulation of the bone and appears to have had a subrectangular outline (Bonaparte 1975). Most basal dinosaurs retain a subrectangular deltopectoral crest, but its distal apex is placed further down the shaft (Benton 1990; Sereno 1991*a*, 1993; Fraser *et al*. 2002). In most basal ornithischians (Galton 1974, 1981; Santa Luca 1980, 1984; *Lesothosaurus* – RUB 17) and theropods (Huene 1934; Raath 1969; Colbert 1989; Welles 1984), the distal apex is placed at about 0.30 to 0.45 of the humeral length. A condition seen also in *Saturnalia* (approx. 0.45), *Eoraptor* (approx. 0.35) and *Herrerasaurus* (approx. 0.4; MACN 18.060). Sereno (1999; see also Galton 1990*a*; Benton *et al*. 2000) suggested that a deltopectoral crest that extends for more than 0.5 of the humeral length is apomorphic for 'Prosauropoda'. Indeed, most basal sauropodomorphs (Huene 1926; Young 1941*a*, 1951; Bonaparte 1972; Galton 1973*a*; Cooper 1981; Yates & Kitching 2003) have an extended deltopectoral crest. The reverse condition is, however, seen in other members of the group (Galton 1976; Heerden 1979; Cooper 1984; Zhang 1988; Benton *et al*. 2000).
50. *Humeral distal end is narrower than or equal to (0), or wider than (1) 0.3 of the total length of the bone*. In most basal dinosaurs, the distal end of the humerus accounts for about 0.25 of the maximum length of the bone, as seen in basal ornithischians (Thulborn 1972; Galton 1974, 1981; Colbert 1981) and basal theropods (Huene 1934; Raath 1969; Welles 1984). A similar condition is present in *Silesaurus*, *Eoraptor* and *Herrerasaurus* (MACN 18.060), in which the distal width of the humerus is about 0.3 of the length of the bone. In *Saturnalia* and basal sauropodomorphs (Huene 1926; Bonaparte 1972; Galton 1973*a*, 1976; Heerden 1979; Cooper 1981), however, the distal width of the humerus is greater than 0.3 of its maximal length. The general dinosaur condition is also present in basal dinosauromorphs (Romer 1972*b*; Bonaparte 1975), *Scleromochlus* (Benton 1999) and various non-dinosauromorph archosaurs (Ewer 1965; Krebs 1965; Bonaparte 1972; Wu & Chatterjee 1993).
51. *Radius longer (0) or shorter (1) than 0.8 of the length of the humerus*. In non-dinosauromorph archosaurs (Walker 1964; Ewer 1965; Krebs 1965), including *Scleromochlus* (Benton 1999), the radius is usually longer than 0.8 of the humeral length. This condition has also been reported for *Marasuchus* (Bonaparte 1975; Sereno & Arcucci 1994), although a shorter radius is present in the holotype of *Lagosuchus talampayensis* (Sereno & Arcucci 1994). Similarly, a radius that is longer than 0.8 of the humerus length has been reported for *Eoraptor* and *Herrerasaurus*. *Silesaurus* is unique among putative basal dinosaurs because its radius is longer than the humerus. However, most dinosaurs have a much shorter radius. That bone is about 0.6 to 0.7 of the humeral length in *Saturnalia*, basal theropods (Raath 1969; Ostrom 1978; Welles 1984; Colbert 1989; Charig & Milner 1997), basal ornithischians (Thulborn 1972; Galton 1974, 1981; Santa Luca 1980; but see Peng 1992) and basal sauropodomorphs (Huene 1926; Bonaparte 1972; Galton 1973*a*, 1976; Cooper 1981).
52. *Manual length (measured as the average length of digits I–III) accounts for less than 0.3 (0), more than 0.3 but less than 0.4 (1), or more than 0.4 (2) of the total length of humerus plus radius* [ordered] (modified Gauthier 1986). Gauthier (1986) used a manus that is longer than 45% of the humerus plus radius length as apomorphic for Saurischia. Sereno *et al*. (1993; but see Novas 1993), however, suggested that a manus longer than 50% of those elements is an apomorphy shared by *Eoraptor*, Herrerasauridae and Neotheropoda. Indeed, as noted by Gauthier (1986), the length of the manus in pseudosuchians is usually less than 30% that of the humerus plus radius (Romer 1956; Krebs 1965; Long & Murry 1995). Among dinosaurs, this condition seems to be retained

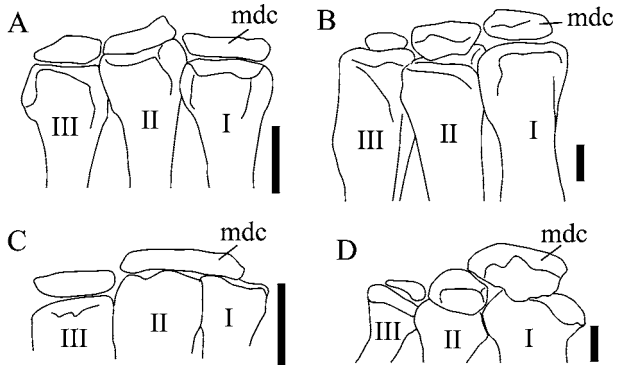

Figure 8 Extensor aspect of the proximal portion of metacarpals I–III and 'correspondent' distal carpals of **A**, *Heterodontosaurus tucki*, right manus based on Santa Luca (1980); **B**, *Herrerasaurus ischigualstensis*, left (reversed) manus based on Sereno (1994); **C**, *Coelophysis bauri*, left (reversed) manus based on Colbert (1989); **D**, *Plateosaurus engelhardti*, right manus based on SMNS '*Pachysaurus ajax*'. Abbreviations: **I–III**, Metacarpals I–III; **mdc**, medial-most distal carpal. Scale bars = 5 mm.

by ornithischians in general, as seen in thyreophorans (Ostrom & McIntosh 1966), basal euornithopods (Galton 1974) and marginocephalians (Sereno 1990; Dodson & Currie 1990), although *Heterodontosaurus* has a derived long manus (Santa Luca 1984). The manus of basal sauropodomorphs is more elongated, usually corresponding to 30–40% of the humerus plus radius length (Huene 1926; Galton 1973*a*, 1976; Cooper 1981; Benton *et al*. 2000). Theropods have an even longer hand, which is always longer than 40% of the length of the humerus plus radius (Gilmore 1920; Raath 1969; Welles 1984; Colbert 1989). *Herrerasaurus* and *Eoraptor* share with theropods such an elongated manus, which is about 50% the humerus plus radius length (Novas 1993; Sereno *et al*. 1993).

53. *Medialmost distal carpal subequal (0) or significantly larger than (1) other distal carpals* (Fig. 8; Gauthier (1986). Gauthier (1986) used the presence of a distal carpal I that overlaps the base of metacarpals I and II as a theropod apomorphy. Indeed, among basal dinosaurs, only in theropods does the medial-most distal carpal cap, at least partially, metacarpal II (Gilmore 1920; Ostrom 1969; Raath 1969; Barsbold 1983; Colbert 1989; Russell & Dong 1994; Currie & Carpenter 2000). Accordingly, this element is usually about twice the size of the other distal carpals and Gauthier (1986) suggested that it may correspond to the fusion of the original distal carpals I and II. A larger medial-most distal carpal is seen also in basal sauropodomorphs (Huene 1926; Young 1941*a*, *b*; Cooper 1981; Benton *et al*. 2000). Yet, in these forms, it does not cap metacarpal II. Instead, its lateral portion overlaps the laterally adjacent distal carpal, which is the element that caps metacarpal II (Cooper 1981; *Plateosaurus* – GPIT mounted skeletons, SMNS '*Pachysaurus*'). This arrangement suggests that the fusion of distal carpals I and II may not have been the mechanism responsible for the enlargement of the medial-most distal carpal seen in these forms. In *Herrerasaurus* and basal ornithischians the medial-most distal carpal is not significantly larger than the others and only caps metacarpal I (Santa Luca 1980). This condition is also present in basal archosauromorphs (Gregory 1945; Gow 1975) and might represent the plesiomorphic condition for dinosaurs.
54. *Distal carpal V present (0) or absent (1)* (Sereno 1999). Sereno (1999, but see Novas 1993) used the absence of the fifth distal carpal as an apomorphy of Saurischia. Indeed, *Heterodontosaurus* has five distal carpals (Santa Luca 1980), as is apparently the case in basal archosauromorphs (Gregory 1945). *Herrerasaurus*, however, has only four distal carpals and the fifth element seems to have been lost, or incorporated into the fourth. In basal theropods, a maximum number of three distal individual bones are present in the carpus (Raath 1969; Colbert 1989), which might correspond to the fused distal carpals I and II and distal carpals III and IV. In various members of the group, however, the number of distal carpal elements is even more restricted (Gilmore 1920; Ostrom 1969; Barsbold 1983; Russell & Dong 1994). Basal sauropodomorphs usually possess three large distal carpals (Young 1941*a*, *b*; Galton & Cluver 1976; Cooper 1981), but a small lateral element is present in some forms (Broom 1911; Huene 1932; Young 1941*a*), which might correspond to the fourth distal carpal. However, the presence of a fifth distal element has never been claimed.
55. *Extensor pits in metacarpals I–III absent, or shallow and symmetrical (0) or deep and asymmetrical* (1) (modified Sereno *et al*. 1993). Sereno *et al*. (1993) proposed the presence of deep extensor pits in metacarpals I–III as an apomorphy shared by *Eoraptor*, Herrerasauridae and Neotheropoda. Indeed, deep excavations for the attachment of the extensor ligaments are seen in the dorsal surface of the main metacarpals of most theropods (Gilmore 1920; Galton & Jensen 1979; Raath 1990; Currie & Zhao 1994*a*). Similar structures were reported for *Heterodontosaurus* (Santa Luca 1980) and *Scutellosaurus* (Colbert 1981), but the metacarpals of most basal ornithischians seem to lack marked extensor pits (Galton 1974; Forster 1990; Sereno 1991*b*). The metacarpals of basal sauropodomorphs bear extensor pits (Broom 1911; Huene 1926, 1932; Bonaparte 1972; Galton 1976; Cooper 1981), but these are generally not as well-developed as those of theropods, as is the case for non-dinosauromorph archosaurs (Walker 1961; Bonaparte 1972; Wu & Chatterjee 1993; Long & Murry 1995). Extensor pits are also present in the metacarpals of *Eoraptor* and *Herrerasaurus*. Whether their depth approaches more that of theropods or of other dinosaurs is, however, difficult to determine. Sereno (1999) used their asymmetry as indicative of the close resemblance of the extensor pits of *Eoraptor*, herrerasaurids and theropods, and this is tentatively accepted here.
56. *Width of metacarpal I at the middle of the shaft accounts for less (0) or more than (1) 0.35 of the total length of the bone* (modified Bakker & Galton 1974).
57. *Digit I with metacarpal longer than (0) or subequal to shorter than (1) the ungual* (Sereno 1999). Bakker & Galton (1974) used a short, stout metacarpal I as a characteristic feature of saurischians. Accordingly, several authors (Gauthier 1986; Benton 1990, 1999; Sereno *et al*. 1993; Novas 1993; Sereno 1999) defined the 'saurischian pollex' as unusually robust, bearing a stout

metacarpal, which is shorter than the phalanges of the digit and less than half the length of metacarpal II. The picture is, in fact, more complex. Basal sauropodomorphs (Broom 1911; Huene 1926; Young 1941*a*; Bonaparte 1972; Galton 1976; Cooper 1981; He *et al*. 1988; Zhang 1988; Benton *et al*. 2000), for example, bear a huge pollex. It is much wider than other manual digits and metacarpal I is never longer than its ungual, although it is longer than phalanx I in some forms. In addition, metacarpal I is always wider than 35% of its length. Accordingly, an extra enlargement of the pollex is often defined as an apomorphy of sauropodomorphs (Gauthier 1986; Benton 1990; Benton *et al*. 2000), while theropods present a slightly dissimilar condition. Their metacarpal I is also shorter than both phalanges of the digit, and wider than 35% of its length (Gilmore 1920; Raath 1969; Welles 1984; Sereno & Wild 1992; Currie & Carpenter 2000), but its digit I is not much wider than the others. In basal ornithischians, however, metacarpal I is always longer than both phalanges of digit I, while its robustness is quite variable (Galton 1974; Santa Luca 1980; Forster 1990; Sereno 1991*b*). In both *Herrerasaurus* and *Eoraptor* metacarpal I is slightly longer than the ungual, but not longer than the first phalanx of the digit. Yet, metacarpal I of *Herrerasaurus* is slender (its width is about 22% of its length), while that of *Eoraptor* is stout (width about 38% of the length). In pseudosuchians, metacarpal I is significantly longer than the two phalanges of the digit and not wider than 35% of its length (Walker 1961, 1964; Krebs 1965; Bonaparte 1972; Chatterjee 1978; Wu & Chatterjee 1993; Long & Murry 1995).

58. *Distal condyles of metacarpal I are approximately aligned (0) or the lateral condyle is more distally expanded (1)* (modified Bakker & Galton 1974). Bakker & Galton (1974) mentioned that a thumb articulation that forces the claw to diverge and point inwards during extension is characteristic of saurischians. Part of this unusual articulation is given by the asymmetrical distal ginglymus of metacarpal I, the lateral condyle of which extends further distally that the medial (Galton 1971; Cooper 1981; Gauthier 1986). This is clearly seen in basal sauropodomorphs (Broom 1911; Huene 1926; Young 1941*b*; Bonaparte 1972; Cooper 1981; He *et al*. 1988) and basal theropods (Gilmore 1920; Raath 1969; Welles 1984; Colbert 1989), as well as in *Eoraptor*. In *Herrerasaurus*, however, although the lateral condyle of the distal ginglymus of metacarpal I extends further distally than the medial, their asymmetry is not comparable to that of basal theropods or sauropodomorphs. Instead, it approaches more that of some basal ornithischians, in which the lateral condyle also extends slightly further distally that the medial (Santa Luca 1980; Forster 1990; Sereno 1991*b*). Among non-dinosauriform archosaurs, the distal ginglymus of metacarpal I is either symmetrical (Walker 1961; Krebs 1965; Chatterjee 1978; Wu & Chatterjee 1993) or slightly asymmetrical (Ewer 1965; Bonaparte 1972).
59. *First phalanx of manual digit I is not (0) or is (1) the longest non-ungual phalanx of the manus* (Gauthier 1986). In his definition of the 'saurischian pollex', Gauthier (1986) noted that the first phalanx of the pollex is the longest non-ungual phalanx of the manus. Indeed, this is the case in *Herrerasaurus*, basal sauropodomorphs (Broom 1911; Huene 1926; Young 1941*b*; Bonaparte 1972; Galton 1976; Cooper 1981; Benton *et al*. 2000) and basal theropods (Raath 1969; Colbert 1989; Currie & Carpenter 2000). In ornithischians, however, the first phalanges of digits II and III are as long as, or often longer, than the first phalanx of digit I (Galton 1974; Santa Luca 1980; Forster 1990; Sereno 1991*b*). Similarly, in most pseudosuchians (Romer 1956; Wu & Chatterjee 1993), the first phalanx of digit I is not significantly longer than other non-ungual phalanges of the manus.
60. *Twisted first phalanx absent (0) or present (1) in manual digit I* (Benton *et al*. 2000). Benton *et al*. (2000) used the presence of a twisted first phalanx of digit I as an apomorphy of a monophyletic 'Prosauropoda'. Indeed, in all 'prosauropods' (Broom 1911; Huene 1926; Cooper 1981) the first phalanx of the pollex is twisted, so that the transverse axes of proximal and distal articulations form an angle of about 45° to one another. This is, however, not an unique feature of these dinosaurs, but part of the peculiar morphology of the 'saurischian pollex' (Cooper 1981; Gauthier 1986). In fact, the first phalanx of digit I is also twisted in *Herrerasaurus* and theropods (Madsen 1976; Currie & Carpenter 2000; *Liliensternus* – MB R.1275) and even in the highly modified sauropod manus, the first phalanx of digit I shows a certain degree of twisting (Gilmore 1936; Ostrom & McIntosh 1966; Yates & Kitching 2003). In ornithischians, however, the transverse axes of the proximal and distal articulations of the first phalanx of digit I are aligned in the same plane (Galton 1974; Santa Luca 1980; Forster 1990; Dodson & Currie 1990; Sereno 1991*b*), a condition also present in most pseudosuchians (Walker 1961; Krebs 1965; Wu & Chatterjee 1993; Long & Murry 1995).
61. *Metacarpal II shorter (0) or subequal to longer (1) than metacarpal III* (modified Gauthier 1986). Gauthier (1986; see also Benton 1990; Dingus & Rowe 1998) suggested that saurischians are characterised by an asymmetrical manus, in which digit II is the longest. Indeed, in both basal sauropodomorphs (Huene 1926; Young 1941*a*; Bonaparte 1972; Galton 1976; Cooper 1981; Zhang 1988; Benton *et al*. 2000) and basal theropods (Gilmore 1920; Raath 1969; Osmólska *et al*. 1972; Welles 1984; Colbert 1989; Currie & Carpenter 2000) metacarpal II is never significantly shorter than metacarpal III, as is digit II in relation to digit III. In *Herrerasaurus* and *Eoraptor*, however, both metacarpal and digit III are the longest in the manus, which is also the usual condition for ornithischians (Ostrom & McIntosh 1966; Thulborn 1972; Galton 1974; Sereno 1990; Dodson & Currie 1990; but see Santa Luca 1980; Forster 1990) and pseudosuchians (Walker 1961; Krebs 1965; Chatterjee 1978; Wu & Chatterjee 1993).
62. *Manual digit II with second phalanx shorter (0) or longer than (1) first phalanx* (modified Gauthier 1986). Gauthier (1986) used the presence of elongated penultimate phalanges in digits I–III as a theropod apomorphy. Later, various authors (Novas 1993; Sereno *et al*. 1993; Sereno 1999) suggested the same character in support of the monopoly of Neotheropoda plus Herrerasauridae. This transformation is represented here by the length relation between the phalanges of digit II. Accordingly, in various theropods (Osborn 1916; Gilmore 1920; Raath

1969), the penultimate phalanges of the functional digits are significantly longer than more proximal elements. A less marked length difference is seen in *Herrerasaurus*, as well as in other theropods (Welles 1984; Colbert 1989). Among ornithischians, only *Heterodontosaurus* (Santa Luca 1980) presents a similar morphology, which was probably acquired as a convergence. In other members of the group (Galton 1974; Forster 1990; Sereno 1991*b*), however, as well as in basal sauropodomorphs (Huene 1926; Bonaparte 1972; Galton 1976; Cooper 1981; Benton *et al*. 2000) and, apparently, *Eoraptor*, the penultimate phalanges of the functional digits are not significantly longer than more proximal elements, a condition also present in most pseudosuchians (Romer 1956; Walker 1961; Wu & Chatterjee 1993).

63. *Unguals of manual digits II and III are slightly (0) or strongly (1) curved* (Gauthier 1986). Gauthier (1986) used strongly curved, laterally compressed and pointed manual unguals as an apomorphy of theropods. He suggested the comparison between *Massospondylus* and *Deinonychus* as indicative of the higher curvature in theropods. In fact, if this comparison is performed between more basal theropods (Camp 1936; Raath 1969; Ostrom 1978; Welles 1984; Colbert 1989) and forms such as *Thecodontosaurus* (Benton *et al*. 2000; Yates 2003*a*) the distinction between theropods and sauropodomorphs is not so clear. In fact, a strongly curved ungual forms the manual digit I of various non-theropod dinosaurs (Galton & Cluver 1976; Santa Luca 1980) and the discussion is here centred on those of digits II and III. In *Herrerasaurus*, the curvature of these unguals is certainly more marked than in basal sauropodomorphs and approaches that seen in a variety of theropods (Huene 1934; Madsen 1976; Galton & Jensen 1979; Currie & Zhao 1994*a*). However, the manual unguals of *Eoraptor*, most basal ornithischians (Galton 1974; Santa Luca 1980), basal sauropodomorphs (Huene 1926; Cooper 1981) and most pseudosuchians (Krebs 1965; Chatterjee 1978), are not as curved as those of derived theropods.
64. *Shaft of metacarpal IV about the same width as (0), or significantly narrower than (1) that of metacarpals I–III* (modified Sereno *et al*. 1993).
65. *Manual digit IV with two or more (0) or fewer than two (1) phalanges* (modified Bakker & Galton 1974). As noted by several authors (Bakker & Galton 1974; Gauthier & Padian 1985), dinosaurs show a marked trend towards the reduction of the two outer manual digits. The condition for archosaurs in general is a manual digit IV with at least four phalanges, as seen in basal archosauromorphs (Gregory 1945; Gow 1975) and pseudosuchians (Romer 1956). Moreover, metacarpal IV of most pseudosuchians is not significantly narrower than the inner metacarpals (Walker 1961; Krebs 1965; Chatterjee 1978; Wu & Chatterjee 1993; but see Walker 1964). By contrast, virtually all dinosaurs have fewer than four phalanges in manual digit IV and none of them is an ungual. For ornithischians, the primitive condition regarding the number of phalanges in that digit is difficult to assess. Among bipedal neornithischians, *Psittacosaurus* has a single phalanx (Sereno 1990), whereas ornithopods seem to show a basic count of three (Romer 1956; Galton 1974; Santa Luca 1980; Norman 1986). The two-phalanges fourth finger of *Stegosaurus* (Ostrom & MacIntosh 1966; Galton 1990*b*) is too modified to infer the condition in thyreophorans, whereas *Lesothosaurus* may possess two or three phalanges (Sereno 1991*b*). Furthermore, metacarpal IV of ornithischians is not significantly narrower than the inner metacarpals. This is also the case for sauropodomorphs, the basal members of which also seem to have two phalanges in manual digit IV (Galton 1973*a*; Benton *et al*. 2000). Yet, a trend toward an increase in this number seems to occur among more derived members of the group (Huene 1926; Young 1941*a*; Galton & Cluver 1976; Cooper 1981), which usually have three, or even four (*Plateosaurus* – '*Pachysaurus ajax*': Huene 1932), phalanges in that digit.

The extra reduction of the fourth manual digit is regarded as typical of theropods (Benton 1990; Novas 1993; Sereno *et al*. 1993). Indeed, various members of the group lack that digit altogether (Osborn 1916; Gilmore 1920). It is, however, present in more basal forms, in which it usually bears a single phalanx (Raath 1969; Galton 1971; Colbert 1989), but a second element has also been reported (Gilmore 1920; Welles 1984; Rowe 1989). In all these forms, metacarpal IV is significantly narrower than the inner metacarpals. This is also the case in *Herrerasaurus* and *Eoraptor*, both of which have a single phalanx in manual digit IV. Novas (1993) has proposed the reduction in length of both metacarpal and digit IV as apomorphic for *Herrerasaurus*, *Eoraptor* and Neotheropoda. This transformation is represented here by the reduction in width of metacarpal IV.

66. *Proximal portions of metacarpals IV and V set lateral to (0) or at the palmar surfaces of (1) metacarpals III and IV, respectively* (Gauthier 1986). Gauthier (1986) proposed that metacarpals/digits IV and V lying, respectively, on the palmar surfaces of metacarpals III and IV, represents a saurischian apomorphy. This is related to the reduction of the outer manual digits in the asymmetrical 'saurischian hand'. Indeed, it is exactly in the forms in which digits IV and V are very reduced – i.e. *Herrerasaurus* and theropods (Osborn 1916; Raath 1969; Welles 1984) – that their position on the palmar surface of the hand is clear. This is seen also in non-dinosaurian archosaurs with reduced outer digits (Walker 1964), casting doubt upon the independence of these characters. In most pseudosuchians, however, the metacarpals are aligned in an almost straight to sub-circular fashion. In addition, because the lateral elements are not reduced, their overlap by more medial metacarpals is minimal (Walker 1961; *Pseudopalatus*: Long & Murry 1995). This condition is seen also in ornithischians (Galton 1974; Santa Luca 1980; Forster 1990; Sereno 1991*b*), as well as in some basal sauropodomorphs (*Plateosaurus* – '*Pachysaurus ajax*': Huene 1932), in which the metacarpals are arranged in a semicircle.

As pointed out by Gauthier (1986), some basal sauropodomorphs show an inwards displacement of the two outer manual digits, disrupting the usually uniform semicircle formed by them (Broom 1911; Young 1941*a*, 1942; Huene 1932: pl. 37; Cooper 1981). This condition is considered homologous to the palmar position of these digits in *Herrerasaurus* and theropods. Yet, the suggestion that digits IV and V also lie on the palmar surface of the sauropod hand is rejected here. In fact,

in these forms (Janensch 1922; Gilmore 1936; Bonnan 2003), the metacarpals form a pillar, standing vertically in a circle, as seen also in *Stegosaurus* (Galton 1990*b*). In *Eoraptor*, although a certain overlap between the metacarpals is present, metacarpals IV and V are set mainly laterally to metacarpals III and IV.

67. *Manual digit V possesses (0) or lacks (1) phalanges* (modified Bakker & Galton 1974). As discussed before, the two outer digits of the manus are markedly reduced in dinosaurs in general and theropods in particular. As for digit V, this includes a reduction in the length and width of the metacarpal and the loss of phalanges or the entire digit (Gauthier 1986; Novas 1993; Sereno 1999). The condition for the dinosaur outgroup seems to be a manual digit V bearing three phalanges (Gregory 1945; Romer 1956; Gow 1975; Long & Murry 1995). However, almost no basal dinosaur has more than two phalanges in this digit, the metacarpal of which is also always reduced in length. This trend is clearly seen in basal theropods, where the only vestige of manual digit V is a nubbin of bone reported by Colbert (1989) for *Coelophysis*.

    Manual digit V is present in all other basal dinosaurs. In most ornithischians metacarpal V is relatively robust and bears at least one (Galton 1974; Forster 1990; Sereno 1991*b*; *Abrictosaurus* – BMNH RUB-54), but often more than one phalanx (Gilmore 1915; Maryanska 1977; Santa Luca 1980; Galton 1981; Norman 1986; but see Sereno 1990). In sauropodomorphs the situation is similar. Metacarpal V is robust and typical 'prosauropods' have three (Huene 1926; Young 1941*a*) or more often two (Broom 1911; Huene 1932; Young 1941*b*, Galton 1973*a*; Cooper 1981; Zhang 1988) phalanges. Yet, it seems that digit V of the basalmost 'prosauropod', *Thecodontosaurus*, lacks phalanges altogether (Benton *et al*. 2000). Similarly, *Herrerasaurus* is distinctive among non-theropod basal dinosaurs because its metacarpal V is reduced to a very thin spur of bone that lacks phalanges. Metacarpal V of *Eoraptor* is more robust but phalanges are also absent.

Pelvic girdle and hind limb

68. *Preacetabular ala short (0) or elongated, extending cranially to the pubic peduncle (1)* (Figs 7 & 9; modified Galton 1976). Galton (1976) listed a short and pointed preacetabular ala as a characteristic feature of the 'prosauropod' ilium. Indeed, contrary to most basal theropods (Gilmore 1920; Raath 1969; Welles 1984; Padian 1986; Colbert 1989) and ornithischians (Charig 1972; Galton 1972; Thulborn 1974; Santa Luca 1980, 1984), in which the preacetabular iliac ala extends cranial to the pubic peduncle, most basal sauropodomorphs (Young 1941*a*, 1942; Bonaparte 1972; Galton 1973*a*, 1984*b*, 2000*b*; Heerden 1979; Benton *et al*. 2000) have a much shorter ala, which usually does not extend cranially to the pubic peduncle. Cooper (1981) suggested that 'prosauropods' had a cartilaginous extension of the preacetabular ala that extended further cranially. Its occasional ossification would explain the elongated ala seen in a few members of the group (Galton 1976; Yates 2003*a*). By contrast, an unexpanded preacetabular ala is seen in *Silesaurus*, *Saturnalia*, *Staurikosaurus*, *Herrerasaurus*, *Eoraptor*, *Marasuchus*, *Lagerpeton* and non-dinosauromorph archosaurs (Walker 1961; Ewer 1965; Krebs 1965; Bonaparte 1972; Romer 1972*a*; Chatterjee 1978).

69. *Ventral margin of iliac acetabulum convex (0), straight (1), or concave (2)* [ordered] (Figs 7 & 9; modified Bakker & Galton 1974). Since the suggestion of a monophyletic Dinosauria, the open acetabulum has been used to diagnose the group (Bakker & Galton 1974; Bonaparte 1975). More recently, the term semiperforate acetabulum has been introduced to define the plesiomorphic condition for the group, given that various authors (Gauthier & Padian 1985; Novas 1996; Benton 1999; Benton *et al*. 2000; Carrano 2000; Fraser *et al*. 2002) noted that some basal dinosaurs lack a fully opened acetabulum. Accordingly, Gauthier (1986) has proposed that the full opening of the acetabulum occurred independently several times in dinosaur evolution. Indeed, in *Silesaurus*, most basal dinosauriforms (Sereno & Arcucci 1993; Novas 1996) and non-dinosauriform archosaurs (Walker 1961; Ewer 1965; Krebs 1965; Romer 1972*a*; Chatterjee 1978), the iliac medial acetabular wall is ventrally convex and shows extensive ventral contact with the other pelvic bones. Exceptions to this pattern among pseudosuchians include poposaurids (Galton 1985*d*; Long & Murry 1995) and ornithosuchids (Walker 1964; Bonaparte 1972), the ventral margin of the iliac acetabular wall of which is straight to slightly concave.

    Most basal dinosaurs have a ventrally concave iliac margin, defining an acetabulum that is at least semiperforated. This condition is seen in *Staurikosaurus*, *Herrerasaurus*, as well as some basal ornithischians (Santa Luca 1984; Sereno 1991*b*) and basal sauropodomorphs (Galton 1973*a*; Benton *et al*. 2000; Yates 2003*a*, *b*), in which the perforated portion of the acetabulum is significantly smaller than the entire articulation surface. However, an almost completely open acetabulum is seen in most ornithopods (Janensch 1955; Santa Luca 1980; Forster 1990), theropods (Gilmore 1920; Huene 1934; Raath 1969; Welles 1984; Padian 1986) and derived sauropodomorphs (Young 1942; Galton 1976; Cooper 1981, 1984; Zhang 1988). A transitional condition is seen in *Saturnalia*, *Guaibasaurus* and *Scelidosaurus* (BMNH 6704), where the ventral iliac margin is straight. This allows a very restricted acetabular aperture, which is not sufficient for the passage of the femoral head. In *Eoraptor* the acetabulum is certainly not fully open, but a certain degree of aperture is present. Similarly, the internal cast of the pelvic girdle of *Pisanosaurus* shows that the acetabulum was perforated, but the degree of aperture is unclear.

70. *Postacetabular ala of the ilium shorter (0), shorter than 40% (1), or longer than the space between the preacetabular and postacetabular embayment of the bone (2)* [unordered] (Figs 7 & 9; modified Forster 1999). Forster (1999) used a postacetabular ala of the ilium that is longer than the acetabulum as an apomorphy of theropods. Indeed, the postacetabular ala of theropods is always longer than the space between the preacetabular and postacetabular embayments of the ilium (Gilmore 1920; Janensch 1925; Huene 1934; Raath 1969; Bonaparte 1986; Welles 1984; Padian 1986). This condition is, however, also present in *Silesaurus*, *Saturnalia*

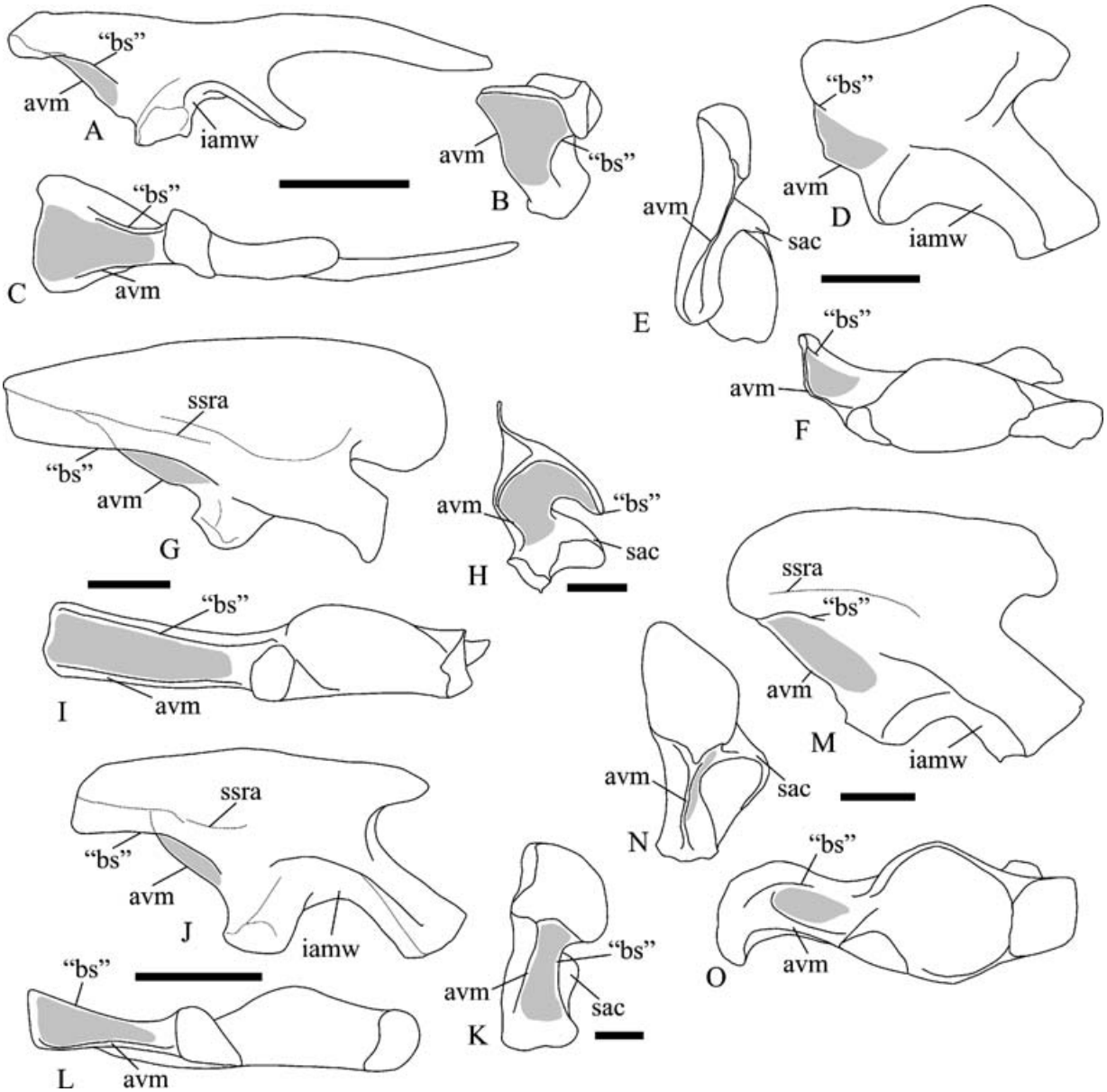

Figure 9 Ilium of **A–C**, *Dryosaurus lettowvorbekki*, based on MB dy II and III and Galton (1981); **D–F**, *Staurikosaurus pricei*, based on MCZ 1669; **G–I**, theropods, based on *Liliensternus liliensterni* (MB R.1275) (**G** and **I**) and *Elaphrosaurus bambergi* (MB 'mounted skeleton' and Janensch, 1925) (**H**); **J–L**, 'Prosauropods', based on *Efraasia diagnostica* (SMNS 12684, 12667, and Galton 1973) (**J and L**), and *Plateosaurus engelhardti* (SMNS 13200) (**K**); **M–O** *Herrerasaurus ischigualastensis*, based on PVL 2566 and Novas (1993). Lateral (**A, D, G, J, M**), caudal (**B, E, H, K, N**) and ventral (**C, F, I, L, O**) aspects. Abbreviations: **avm**, ventral margin of caudal ala; **'bs'** 'brevis shelf'; **iamw**, medial wall of iliac acetabulum; **sac**, supraacetabular crest; **ssra**, dorsal margin of second sacral rib articulation; **'shading'**, hypothesised origin area of *M. caudofemoralis brevis*. Scale bars = 50 mm.

and *Guaibasaurus*. A distinct condition is seen in *Eoraptor* and Staurikosaurus, in which the postacetabular ala is extremely reduced and no longer than 40% of the space between the embayments of the ilium. Yet, the general condition within the dinosaur lineage is a postacetabular ala of intermediate length, as seen in *Lagerpeton*, *Marasuchus*, *Herrerasaurus*, basal sauropodomorphs (Huene 1926; Bonaparte 1972; Galton 1973*a*, 1976; Cooper 1981; Yates 2003*b*) and basal ornithischians (Janensch 1955; Galton 1974; Santa Luca 1980, 1984; Sereno 1991*b*).

71. *Ventral portion of the postacetabular ala does not bear (0) or bears (1) a deep fossa in its caudal portion for the origin of* M. caudofemoralis brevis (Fig. 9; modified Gauthier & Padian 1985). Gauthier & Padian (1985) noted that the origin area of the *M. caudofemoralis* brevis is usually more developed in dinosaurs than in other archosaurs, forming a fossa in the ventral portion of the iliac postacetabular ala. Indeed, that muscle originated on the slightly laterally facing ventral surface of the cranial part of the ala of *Marasuchus* (PVL 3871; Fraser *et al.* 2002: fig. 5c 'n'). This is bound medially by the

medioventral margin of the bone, just lateral to the articulation to the second sacral vertebra and laterodorsally by a faint shelf. Some non-dinosaur archosaurs share a similarly narrow muscle origin (Hutchinson 2001*a*: table 3) while others possess a larger fossa (see Long & Murry 1995: fig. 150a–b). In *Staurikosaurus* and *Herrerasaurus*, the origin of the *M. caudofemoralis brevis* extends over the mainly vertically orientated lateroventral surface of the iliac postacetabular ala. This is bounded dorsally by the 'brevis shelf' of Novas (1996, dorsal to the 'furrow' in Novas 1993: fig. 5a) and ventrally by the ventral margin of the ala (Fig. 9: avm), which extends from the caudal surface of the ischiadic peduncle to the laterocaudal corner of the ilium, forming a wall that articulates medially to the deep ribs of the second sacral vertebra (see Novas 1996: fig. 7e). In other basal dinosaurs, however, that muscle originated from a ventrally facing and more deeply excavated area (the 'brevis fossa') enclosed by enlarged laminae, i.e. the 'median shelf' and 'iliac blade' of Hutchinson (2001*a*).

In basal sauropodomorphs (Young 1941*a*; Cooper 1981; Yates 2003*b*; *Efraasia* – SMNS 12667; *cf. Riojasaurus* – PVL 3805; *Plateosaurus* – SMNS F65, 12398) the origin of the *M. caudofemoralis brevis* is represented by a concave and craniocaudally elongated 'brevis fossa', bounded medially by the medioventral margin of the postacetabular ala (Fig. 9: avm) and laterally by a marked ridge (Fig. 9: "bs"). The latter corresponds to the 'brevis shelf' of *Herrerasaurus*, but its caudal portion expands ventrally to laterally overhang other parts of the ala, while the former is divided in two parts. The caudal part is equivalent to the corresponding portion of the 'second medial ridge' of Hutchinson (2001*a*: fig. 6). However, the cranial part forms the caudoventral margin of the last sacral rib articulation, whereas the cranial part of 'mr2' (Hutchinson 2001*a*: fig. 6) forms the dorsal margin of that same structure. Accordingly, only the laterally free caudal part of 'mr2' forms the medial margin of the 'brevis fossa'. Its cranial portion enters the medial surface of the ilium and marks the dorsal edge of the sacral rib articulations instead of the margin of the 'brevis fossa' as indicated by Hutchinson (2001*a*: fig. 6a) for *Massospondylus*. Likewise, the medial iliac ridge of *Thecodontosaurus* (Benton *et al*. 2000: fig. 15d) is not the 'brevis shelf', but the 'second medial ridge' (Hutchinson 2001*a*), as seen also in other archosaurs (Ewer 1965; Galton 1985*d*) and 'prosauropods' (Young 1942; Galton 2000*b*). A prosauropod-like 'brevis fossa' is shared by *Saturnalia*, *Silesaurus* (ZPAL AbIII 404/1), *Eoraptor* and *Guaibasaurus*, while an analogous condition occurs in certain rauisuchians (*sensu* Gower 2000), in which the articulation area of the last sacral rib is bounded dorsally by a ridge and ventrally by the ventral margin of the postacetabular ala (Galton 1985*d*: fig. 4c; Long & Murry 1995: fig. 137c; Galton & Walker 1996: fig. 1h).

The 'brevis fossa' (channel of the caudofemoralis: Welles 1984) of theropods is slightly distinctive (Gilmore 1920; Madsen 1976; Galton & Jensen 1979; Padian 1986; Currie & Zhao 1994*a*). The 'medial blade' of Currie & Zhao (1994*a*; Hutchinson 2001*a*: fig. 6 'mr2') represents the ventromedial margin of the postacetabular ala, whereas the 'spine' of Welles (1984) corresponds to the 'brevis shelf' of 'prosauropods' and *Herrerasaurus*. We concur with Hutchinson (2001*a*) that the 'spine' is not neomorphic for dinosaurs, but only more expanded than in most archosaurs. Yet, while the 'brevis shelf' of 'prosauropods' is directed ventrolaterally, the 'spine' of most basal theropods is more expanded and laterally directed (but see Hutchinson 2001*a*), forming a broader fossa (Janensch 1925; Raath 1990; Britt 1991; *Liliensternus* – MB R.1275). In basal ornithischians (*Scelidosaurus* – BMNH 1111, 6704; *Lesothosaurus* – BMNH R11008, RUB 17), the 'brevis shelf' is not laterally expanded, but directed ventrally. Yet, the ventral margin of the ala slopes dorsomedially to form a broad flat to concave horizontal area for the origin of *M. caudofemoralis brevis* (Maryanska & Osmólska 1974; Galton 1974, 1981; Norman 1986; Forster 1990; *Dryosaurus*, MB – mounted skeleton) that corresponds to the brevis fossa.

72. *Supraacetabular crest absent to weakly developed (0) or well-developed, accounting for more than 0.3 of the iliac acetabulum depth (1)* (Fig. 9; Gauthier & Padian 1985). Gauthier & Padian (1985; see also Gauthier 1986) used the presence of a prominent supraacetabular crest as an apomorphy of dinosaurs. Indeed, *Eoraptor*, *Herrerasaurus*, *Staurikosaurus*, *Saturnalia*, *Silesaurus*, *Guaibasaurus*, basal theropods (Gilmore 1920; Huene 1934; Raath 1990) and sauropodomorphs (Young 1941*a*; Galton 1973*a*, 1976, 1984*b*; Yates 2003*a*) have a supraacetabular crest that is more developed than that of *Lagerpeton*, *Marasuchus* and non-dinosauromorph archosaurs (Walker 1961; Romer 1972*c*; Parrish 1986), although a strong supraacetabular crest is known in a variety of pseudosuchians (Bonaparte 1984; Parrish 1986; Long & Murry 1995). Ornithischians are an exception to this rule, given that their supraacetabular crest is usually not very well-developed (Maryanska & Osmólska 1974; Galton 1974, 1981; Santa Luca 1980; Norman 1986; Forster 1990; *Lesothosaurus* – BMNH R11008, RUB 17; *Scelidosaurus* – BMNH 1111, 6704).
73. *'Brevis shelf' diminishes cranially (0) or merges to the supraacetabular crest (1)* (Fig. 9). As previously discussed (character 71), the postacetabular ala of dinosaurs has a lateral ridge or shelf that lateromedially bounds the origin area of the *M. caudofemoralis brevis* (the 'brevis fossa'). In *Saturnalia*, *Herrerasaurus*, *Staurikosaurus*, *Silesaurus*, *Guaibasaurus*, basal sauropodomorphs (Yates 2003*a*; *Plateosaurus* – SMNS F65) and basal ornithischians (*Dryosaurus*, MB – mounted skeleton; *Scelidosaurus* – BMNH 1111, 6704), this shelf extends through most of the ala, but diminishes cranially, disappearing at a point caudoventral to the caudal margin of the supraacetabular crest. In theropods, however, the 'brevis shelf' ('spine' in Welles 1984) is more cranially extended, merging to the supraacetabular crest (Gilmore 1920; Janensch 1925; Raath 1969; Welles 1984; Britt 1991; *Liliensternus* – MB R.1275), as seen also in *Eoraptor*. *Marasuchus* (PVL 3871) exhibits a homologue but very restricted lateral ledge (Fraser *et al*. 2002).
74. *Ischiadic peduncle of the ilium mainly vertical in lateral aspect (0) or well expanded caudally to the cranial margin of the postacetabular embayment (1)* (Fig. 9). In

Lagerpeton, *Marasuchus* and most non-dinosauromorph archosaurs (Ewer 1965; Krebs 1965; Romer 1972*c*; Crush 1984; Leptosuchus – Long & Murry 1995), the ischiadic peduncle of the ilium is mainly vertically orientated. It marks the maximum cranial extension of the postacetabular embayment and its articulation to the ischium is mainly on a horizontal plane. A similar condition is seen in *Staurikosaurus*, *Saturnalia*, *Guaibasaurus*, *Silesaurus*, *Herrerasaurus*, basal ornithischians (Maryanska & Osmólska 1974; Galton 1974, 1981; Santa Luca 1980, 1984), and a variety of basal sauropodomorphs (Young 1941*a*; Galton 1973*a*, 1976, 1984*b*; Yates 2003*a*, *b*). Among these, the ischiadic peduncle of *Herrerasaurus* bulges somewhat at the contact with the ischium, extending the postacetabular embayment slightly cranial to the ischiadic peduncle. This probably arises from the robustness of the pelvis, as also seen in other robust dinosaurs (Huene 1926; Bonaparte 1972; Heerden 1979; Cooper 1981; Norman 1986; Forster 1990; Galton 2000*b*), but is not comparable to the condition in *Eoraptor* and most basal theropods (Gilmore 1920; Janensch 1925; Huene 1934; Bonaparte 1986; Padian 1986; Britt 1991; Currie & Zhao 1994*a*). In these forms, the ischiadic peduncle is directed caudoventrally, rather than ventrally and most of its articulation to the ischium forms an angle of about 45° to the horizontal plane. Accordingly, the ischiadic peduncle is significantly extended caudal to the cranial margin of the postacetabular embayment of the ilium, forming its ventral border.

75. *Pelvis propubic (0) or opisthopubic (1)*. The distinction between saurischians and ornithischians based on the form of the pelvis (Seeley 1888) is probably the best known dinosaur morphological trait. Yet, in a phylogenetic context, only the opisthopubic pelvis of ornithischians is of significance (Dingus & Rowe 1998), whereas the saurischian propubic pelvis represents the retention of a plesiomorphic feature widespread among archosaurs in general (Ewer 1965; Cruickshank 1972; Charig 1972; Arcucci 1987; Sereno & Arcucci 1993, 1994). Indeed, all known ornithischians have a markedly opisthopubic pelvis, in which the pubis is completely retroverted, so that it lies subparallel to the ischium (Ostrom & McIntosh 1966; Charig 1972; Santa Luca 1980; Norman 1986; Sereno 1991*b*). Otherwise, only therizinosaurs (Barsbold 1979; Barsbold & Maryanska 1990), dromaeosaurs (Perle 1985; Xu *et al*. 1999), advanced alvarezsaurids (Hutchinson & Chiappe 1998) and birds (Baumel & Witmer 1993), have a similarly retroverted pubis. Yet, a more subtle retroversion, in which the pubis is vertically orientated, is seen in other theropods (Ostrom 1976; Novas & Puerta 1997) as well as in *Herrerasaurus*. By contrast, a typical propubic pubis is present in *Silesaurus*, *Eoraptor*, basal theropods (Gilmore 1920; Raath 1969; Ostrom 1978; Colbert 1989) and most basal sauropodomorphs (Huene 1926; Galton 1976; Cooper 1981; Yates 2003*a*). Among these, the pubis of *Staurikosaurus*, *Guaibasaurus*, *Saturnalia* and some basal sauropodomorphs (Galton 1984*b*), seems to be more vertically orientated than usual. This is, however, not comparable to the condition in ornithischians and *Herrerasaurus*. Bonaparte (1976) claimed that a 'caudal pubic process' is seen in the holotypic internal pelvic cast of *Pisanosaurus*. So far as may be determined in this poorly preserved specimen, however, we agree with Sereno (1991*b*) who rejected the presence of such a process and suggested that a primitive propubic pelvis was more likely for *Pisanosaurus*.

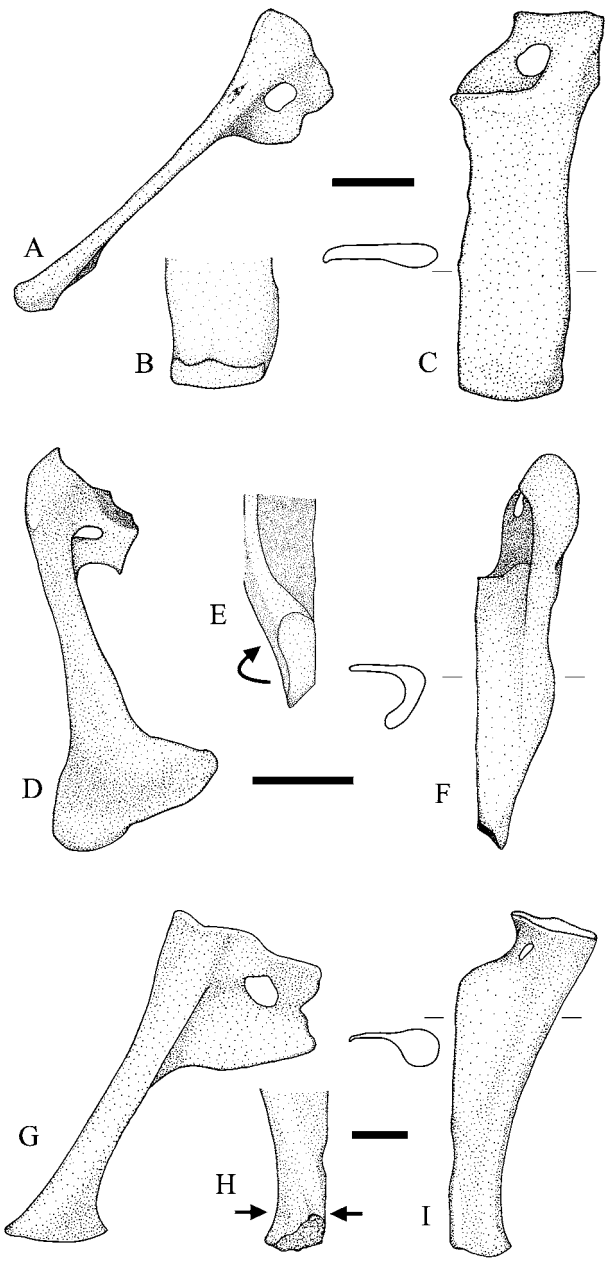

Figure 10 Pubis of **A–C**, *Plateosaurus engelhardti*, left pubis based on GPIT 'skelett 2' and Yates (2003*b*); **D–F**, *Herrerasaurus ischigualastensis*, right (reversed) pubis, based on PVL 2566 and Novas (1993); **G–I**, *Torvosaurus tanneri*, right (reversed) pubis, based on Galton & Jensen (1979). Lateral (**A, D, G**) and cranial, with outline of transverse section (**C, F, I**), aspects of the pubis and distal pubis in caudal aspect (**B, E, H**). Arrows approximately indicate the change required for the distal pubis of *Plateosaurus* to acquire a shape like that of *Herrerasaurus* and *Torvosaurus*. Scale bars = 100 mm.

76. *Distal pubis craniocaudally bulging (0) or unexpanded (1)* (Fig. 10; modified Sereno & Novas 1992).

77. *Lateral margin of the pubis level with its medial part (0) or caudally folded at its distal portion, with the pubic pair showing a U-shaped transverse section (1)* (Fig. 10). The presence of a well-developed 'pubic-boot' has often been used as an apomorphy supporting a close relationship between theropods and herrerasaurids (Sereno & Novas 1992; Novas 1993; Sereno 1999). This is surprising, given that no basal theropod (Huene 1934; Welles 1984; Padian 1986; Raath 1990; Carpenter 1997; Sullivan & Lucas 1999) has a well-developed 'pubic-boot'. In fact, the distal expansion of the pubis in these forms is much less extensive than that apparently seen in *Herrerasaurus* and approaches more the distal bulging of basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942; Bonaparte 1972; Galton 1976; Jain *et al.* 1979; Cooper 1981, 1984; Novas 1992). This condition is also present in *Eoraptor* and *Saturnalia*, as well as in *Pseudolagosuchus* and most pseudosuchians (Walker 1961, 1964; Chatterjee 1978). However, the distal pubis does not apparently bulge in *Marasuchus*, *Silesaurus*, *Guaibasaurus*, or basal ornithischians (Ostrom & McIntosh 1966; Santa Luca 1980; Forster 1990; *Lesothosaurus* – BMNH RUB17, R11001; *Scelidosaurus* – BMNH 1111).

    In none of the above-mentioned forms is the distal pubis as expanded as in theropods that have a fully developed 'pubic boot' (Madsen 1976; Bonaparte 1986; Currie & Zhao 1994*a*; Brochu 2003). Among basal dinosaurs, a similar condition is only attained by *Herrerasaurus*. Yet, contrary to that of advanced theropods, the boot-shaped morphology of the pubis of *Herrerasaurus* does not reflect the craniocaudal expansion of the distal end of the bone. Instead, it arises from the caudoventral folding of the lateral margin of its lateromedially expanded distal portion, which also confers a more marked U-shaped cross-section on that part of the bone, if compared to those of basal theropods (Huene 1926; Padian 1986; Galton & Jensen 1979). This folding also accounts for the distal reduction in the lateromedial breadth of the pubic blade, defined as a theropod apomorphy by Sereno (1999). A less marked version of this folding is seen in *Marasuchus* and *Staurikosaurus*, but not in *Pseudolagosuchus*, nor in other non-dinosaurian archosaurs or basal dinosaurs. In these forms, the entire dorsal surface of the distal pubes is roughly in the same plane as the rest of the dorsal surface of the pair. This is also seen in *Eoraptor*, *Guaibasaurus*, *Saturnalia*, basal theropods (Galton & Jensen 1979; Welles 1984; Padian 1986) and basal sauropodomorphs (Huene 1926; Galton 1973*a*). In addition, despite their distinctive shapes, the distal pubic margins in both *Herrerasaurus* and *Staurikosaurus* also bulge slightly.

78. *Distal pubis nearly as broad as (0) or significantly narrower than proximal part of the blade (1) and lateromedially compressed and not broader than deep* (2) [ordered] (Fig. 10; modified Galton 1976; Sereno 1999). Galton (1976) defined the distal end of the pubis forming a broad 'apron' as typical of 'prosauropods'. Indeed, the distal pubis of various basal sauropodomorphs is lateromedially expanded (Huene 1926; Galton 1973*a*, 1976, 1984*b*; Yates 2003*b*; Yates & Kitching 2003). The distal outline is subrectangular and equally deep throughout its breadth. By contrast, in other basal sauropodomorphs (Young 1941*a*, 1942; Galton 1976), as well as in *Saturnalia*, the distal end of the pubis is shallower medially and does not form an 'apron'. Although not subrectangular, but usually elliptical to subtriangular, the distal outline of their pubis is broader than deep. Furthermore, it is also as broad as the proximal part of the pubic blade, measured just distal to the 'pubic tubercle' (*sensu* Hutchinson 2001*a*). Likewise, *Lagerpeton*, *Marasuchus* and most non-dinosauromorph archosaurs (Walker 1961, 1964; Ewer 1965; Romer 1972*c*; Bonaparte 1972; Crush 1984; *Leptosuchus* – Long & Murry 1995), have a lateromedially elongated distal pubis. Obviously, the highly modified ornithischian pubis does not fit into this pattern. The pair is much narrower distally than proximally (Ostrom & McIntosh 1966) and each bone bears a rod-like shaft, the distal end of which is subcircular in outline and not lateromedially expanded (*Lesothosaurus* – BMNH RUB17, R11001, *Scelidosaurus* – BMNH 1111). Similarly, the distal pubis of basal theropods (Galton & Jensen 1979; Welles 1984; Padian 1986; *Liliensternus* – MB R.1275; *Gogirasaurus* – MB 1985.G.1-3) is deeper than broad and usually subtriangular. Indeed, Sereno (1999) defined a distal narrowing in the pubic pair as apomorphic for the group. This condition is seen also in *Guaibasaurus* and *Silesaurus*, but not in *Eoraptor*, the distal pubis of which is broader than deep, as also seems to be the case of *Silesaurus*. Despite the modifications discussed in the previous character, it is clear that the distal pubis of *Staurikosaurus* and *Herrerasaurus* is lateromedially expanded. In fact, they resemble those of 'prosauropods', the lateral part of which has been ventrally bent.

79. *Ischiadic medioventral lamina extends for more than half of the bone length (0) or is restricted to its proximal third (1)* (Fig. 11; modified Novas 1992). Novas (1992, 1996) suggested that the ventral keel of the ischium is apomorphically reduced in dinosaurs (see 'Ingroup apomorphies,' above). Indeed, the ischiadic shaft in basal theropods (Gilmore 1920; Janensch 1925; Huene 1934; Raath 1969; Galton & Jensen 1979; Bonaparte 1986; Welles 1984) and basal sauropodomorphs (Huene 1926; Young 1941*a*, *b*; Bonaparte 1972; Heerden 1979; Cooper 1981, 1984; Galton 1984*b*) is mainly rod-like and the medioventral lamina is restricted to the cranial quarter of the bone, forming the obturator plate. An equivalent condition is present in *Staurikosaurus*, *Herrerasaurus*, *Guaibasaurus*, *Saturnalia* and *Eoraptor*. Furthermore, Novas (1996) noticed similarities between the ischium of *Lesothosaurus* and that of basal dinosauromorphs. In fact, like other basal dinosaurs, the ischium of *Lesothosaurus* (BMNH BUB17) has the distal margin of its obturator plate marked by a constriction of the medioventral lamina. This is not present in basal dinosauromorphs, in which the medioventral lamina is continuous with the obturator plate. Yet, the ischium of *Lesothosaurus* is primitive in relation to that of non-ornithischian basal dinosaurs, because it is not rod-like distal to the aforementioned constriction. Instead, it retains a subtle medioventral lamina. Remains of both the obturator plate and the medial lamina are seen also in *Heterodontosaurus* (Santa Luca 1980), the proximal part of the latter forming the 'obturator process' of more derived

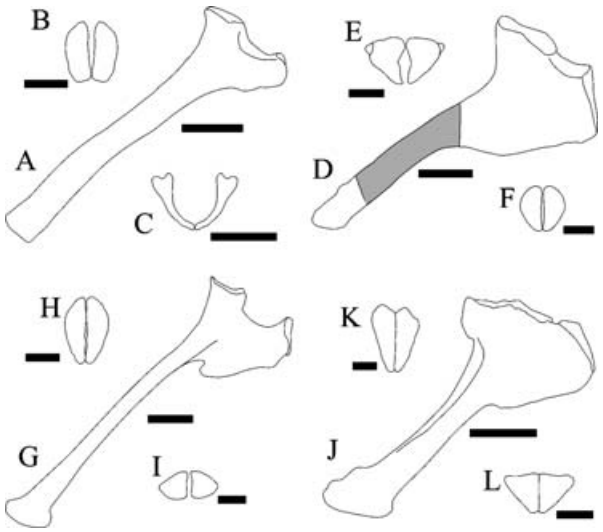

Figure 11 Ischium of **A**, *Scelidosaurus harrisonii*, based on BMNH 6704; **B**, cf. *Lesothosaurus diagnosticus*, based on BNHM R 11001; **C**, *Lesothosaurus diagnosticus*, based on Thulborn (1972); **D, E**, *Herrerasaurus ischigualastensis*, based on Novas (1993; shading represents unpreserved portion); **F**, *Staurikosaurus pricei*, based on MCZ 1669; **G–I**, *Syntarsus rhodesiensis*, based on Raath (1969, 1990); **H**, *Coelophysis* sp., based on Padian (1986); **J–K**, *Plateosaurus engelhardti*, based on Huene (1926) and Yates (2003*b*); **L**, *Massospondylus carinatus*, based on Cooper (1981). Lateral (**A, D, G, J**) and distal (**B, E,H, K**) aspects, with outlines of mid-shaft cross-section (**C, F, I, L**). Scale bars: **A, E, G, H, L** = 20 mm; **B, C, F, I** = 10 mm; **D, K** = 50 mm; **J** = 100 mm.

ornithopods (Galton 1981; Norman 1986; Forster 1990; see also 'ob' in Thulborn 1972: fig. 9). This condition is distinct in thyreophorans (Ostrom & McIntosh 1966; *Scelidosaurus* – BMNH 6704), the obturator plate of which is very reduced and the medial lamina is modified into a broader medial symphyseal area. The condition in *Silesaurus* is ambiguous based on the literature data.

80. *Distal end of ischium is the same width as the rest of the shaft (0) or dorsoventrally expanded (1)* (Fig. 11; modified Smith & Galton 1990). Smith & Galton (1990) defined the presence of a well-expanded distal end of the ischium as a characteristic feature of some ornithomimosaurs (i.e. *Archaeornithomimus*) and *Elaphrosaurus*. Later, Novas (1993) suggested that this feature evolved independently in Theropoda and Sauropodomorpha, while Forster (1999) and Sereno (1999) used the distally expanded ischium as a diagnostic for Neotheropoda. Indeed, the ischium of all basal theropods (Huene 1934; Galton & Jensen 1979; Bonaparte 1986; Welles 1984; Padian 1986; Bonaparte *et al*. 1990; Raath 1990) shows some degree of distal expansion. However, the ischium of *Herrerasaurus* and *Eoraptor* maintains the same depth throughout its shaft and no indication of distal bulging is present. Likewise, the ischium of most basal ornithischians (Ostrom & McIntosh 1966; Santa Luca 1980; *Scelidosaurus* – BMNH 6704; ?*Lesothosaurus* – BMNH R11001) lacks a distal bulge, as seen also in *Silesaurus*, *Lagerpeton*, *Marasuchus* and most non-dinosauromorph archosaurs (Walker 1961; Romer 1972*c*; *Leptosuchus* – Long & Murry 1995). Yet, similarly to theropods, the distal ischium of *Guaibasaurus*, *Saturnalia* and basal sauropodomorphs (Huene 1926; Young 1942; Bonaparte 1972; Heerden 1979; Jain *et al*. 1975; Yates 2003*a*, *b*), is markedly expanded craniocaudally.

81. *Distal outline of ischium is roughly semicircular (0) or sub-triangular (1)* (Fig. 11; Sereno 1999). Sereno (1999) used an ischium with a sub-triangular distal outline as an apomorphy of 'prosauropods'. Indeed, in various sauropodomorphs (Young 1941*a*, 1942; Heerden 1979; Buffetaut *et al*. 1995; *Efraasia* – SMNS 12354), including some sauropods (Janensch 1961; Cooper 1984), the distal ischium has a very broad and flat dorsal margin and a sub-triangular distal outline. The distal ischium of other 'prosauropods' (Huene 1926; Galton 1976; ?*Massospondylus* – BPI 4693), however, is not so dorsally flat. Yet, the distal outline is still subtriangular, because the ridge extending through the lateral surface of the shaft reaches the distal end of the bone near its dorsal portion and the medial margin of the distal end does not rise dorsally. A similar arrangement is seen also in *Herrerasaurus*, *Saturnalia* and *Guaibasaurus*. By contrast, the distal ischium of basal theropods (Gilmore 1920; Padian 1986; *Lilienstern* – MB R.1275) and basal ornithischians (*Scelidosaurus* – BMNH 6704; ?*Lesothosaurus* – BMNH R11001), is roughly semicircular, as also appear to be those of *Staurikosaurus* and *Eoraptor*. In these forms, the aforementioned lateral ridge reaches the distal end of the ischium at mid-height, so that its medial margin is dorsally raised and the dorsal surface laterally inclined. This character is inapplicable to the laminated ischiadic shaft of basal dinosauromorphs and non-dinosauromorph archosaurs.

82. *Proximal portion of the* M. iliofemoralis cranialis *insertion merges into the femoral shaft at a low-angle inclination (0) or forms a steep margin (1), which is separated from the shaft by a marked cleft (2)* [ordered] (Fig. 12; modified Bakker & Galton 1974). Bakker & Galton (1974) noted that basal dinosaurs show a 'spike-like ridge' on the lateroproximal surface of the femur, whereas in other archosaurs this area is smoother. That 'ridge', usually termed 'anterior' or 'lesser trochanter', is proposed to correspond to the femoral insertion of the *M. iliofemoralis cranialis* (sensu Rowe 1986; *M. iliotrochantericus caudalis* of Hutchinson 2001*b*). The presence of this structure was considered apomorphic for Dinosauriformes (Novas 1992, 1996; Sereno & Arcucci 1994), whereas its enlargement was regarded as a dinosaurian apomorphy (Gauthier & Padian 1985; Gauthier 1986; Novas 1996). Indeed, the iliofemoral musculature of crocodiles inserts on a broad area on the lateral surface of the femur, where no clearly defined scar is seen (Romer 1923). This condition was probably shared by most pseudosuchians (Walker 1977; Charig 1972), which lack marked attachment points for this muscle (Walker 1961; Long & Murry 1995). An exception is the well-developed scar of ornithosuchids (Walker 1964; Bonaparte 1972), the proximal position of which indicates a shift in the insertion of the muscle. Likewise, the *M. iliofemoralis cranialis* of basal dinosauromorphs inserted on the lateroproximal surface of the femur (Novas 1996; Hutchinson 2001*b*), defining a rugose area that does not project to form a trochanter.

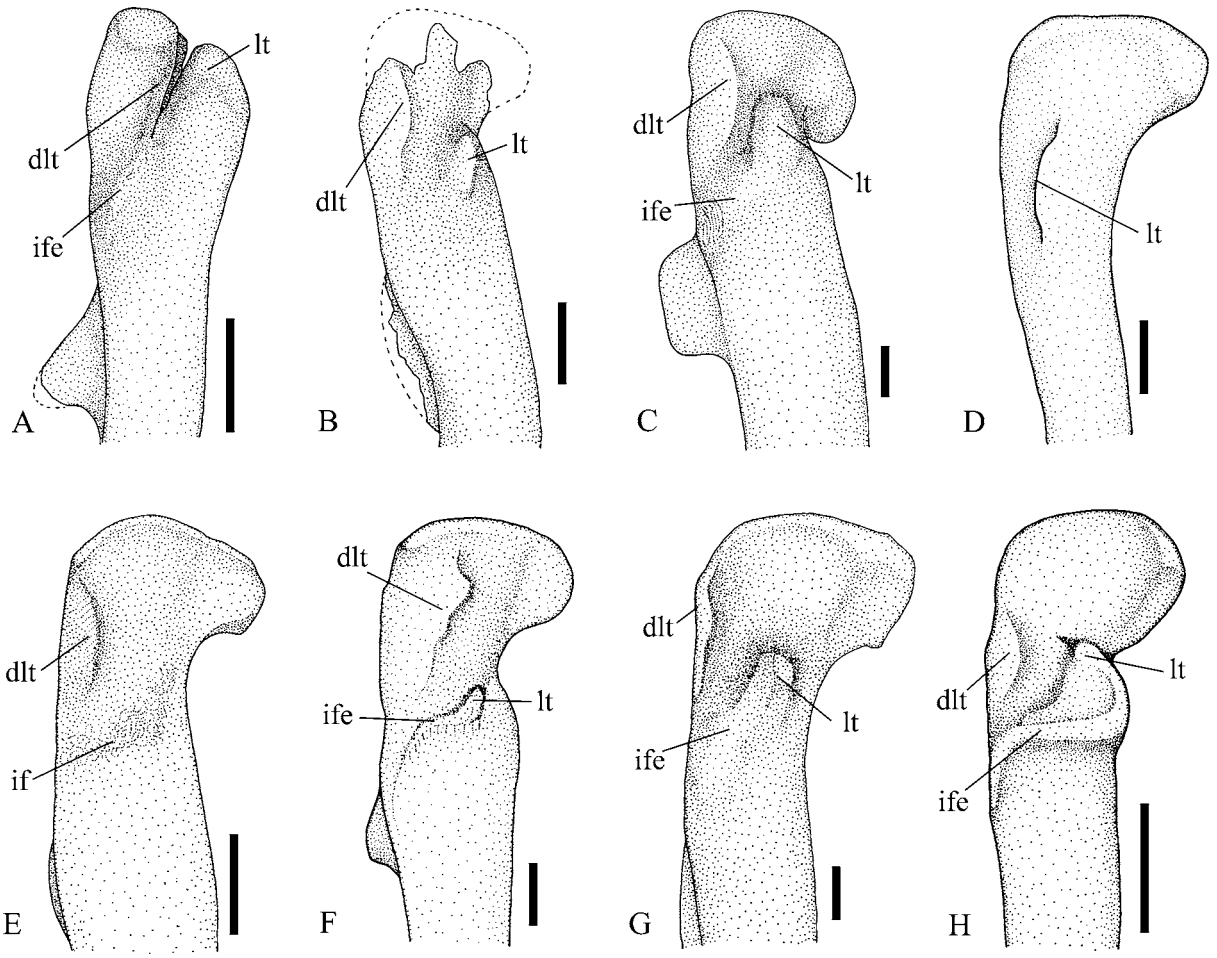

Figure 12 Lateral aspect of proximal femur of **A**, *Lesothosaurus diagnosticus*, right femur based on BMNH RUB17; **B**, *Guaibasaurus candelariensis*, right femur based on MCN-PV 2355; **C**, *Efraasia diagnostica*, right femur based on SMNS 12684; **D**, cf. *Massospondylus carinatus*, left (reversed) femur based on BPI 5006; **E**, *Staurikosaurus pricei*, left (reversed) femur based on MCZ 1669; **F**, *Herrerasaurus ischigualastensis*, right femur based on PVSJ 373; **G**, *Lilienstenus liliensterni*, left (reversed) femur based on MB R.1275; **H**, *Syntarsus rhodesiensis*, left (reversed) femur based on QVM QG 174; Abbreviations: **dlt**, 'dorsolateral trochanter'; **if**, insertion of *M. iliofemorale*; **ife**, insertion of *M. iliofemoralis extermus*; **lt**, 'lesser trochanter'. Scale bars: **A** = 10 mm, **B–H** = 20 mm.

In basal dinosaurs, the insertion area of the *M. iliofemoralis cranialis* is more conspicuous and a raised trochanter (i.e. 'lesser trochanter') is seen. This is surely related to the greater significance of that muscle in hindlimb function, which seems to have increased in the early evolution of the group. Because the stress of the *M. iliofemoralis cranialis* is orientated proximally and sub-parallel to the femoral axis, the higher its biomechanical importance, the more proximally projected its insertion point is expected to be. Indeed, the degree of proximal projection of the 'lesser trochanter' is not constant among dinosaurs, but shows substantial variations. In basal sauropodomorphs it is usually regarded as ridge-like (Galton & Upchurch 2004). Indeed, the insertion area of their *M. iliofemoralis cranialis* is more proximodistally elongated than that of most other dinosaurs, but only in some forms does the proximal margin form a low angle to the femoral shaft (Seeley 1898; Young 1941*b*; Bonaparte 1972; Galton 1976, 1984*b*; Cooper 1984; Gauffre 1993; Moser 2003). In other 'prosauropods' (Huene 1926; Cooper 1981; *Efraasia* – SMNS 12684; *Thecodontosaurus* – BRSUG various specimen) its proximal margin forms a steeper angle to the shaft. A similar condition is seen in *Eoraptor*, *Silesaurus*, *Guaibasaurus*, *Saturnalia*, *Herrerasaurus* and some basal theropods (Padian 1986; Rowe 1989; Madsen & Welles 2000; robust *Syntarsus rhodesiensis* – Raath 1990), in which the 'lesser trochanter' is a knob-like structure. Yet, in most theropods (Andrews 1921; Janensch 1925; Welles 1984; Bonaparte 1986; Currie & Zhao 1994*a*; Rauhut & Hungerbühler 2000; gracile *Syntarsus rhodesiensis* – QVM QG 169, 715; *Liliensternus* – MB R.1275), the 'lesser trochanter' projects proximally from the lateral margin of the femur and is separated from the shaft by a marked cleft, as is also typical of ornithischians (Thulborn 1972; Galton 1974, 1981; Colbert 1981; Santa Luca 1984).

The lateroproximal surface of the femur of *Staurikosaurus* bears an S-shaped area with distinctive texture. This is surely related to the insertion of the *M. iliofemorale* and is interpreted here as an inconspicuous homologue of the 'lesser trochanter' and 'trochanteric shelf'.

The ridge identified by Galton (1977, 2000*a*) as the 'lesser trochanter' is, in fact, homologous to the 'dorsolateral trochanter' of *Guaibasaurus* (Bonaparte *et al*. 1999), which takes part in the composition of the 'greater trochanter' of other dinosaurs (Sereno 1991*b*: fig. 8e; Thulborn 1992: fig. 3).

83. *'Trochanteric shelf' present (0) or absent (1) on the lateral surface of the proximal femur* (Fig. 12; Rowe & Gauthier 1990). Rowe & Gauthier (1990) proposed the presence of a 'trochanteric shelf' on the femur of robust individuals as an apomorphy of 'ceratosaurs'. Indeed, as seen in various members of this group (Andrews 1921; Padian 1986; Rowe 1989; Raath 1990; Madsen & Welles 2000; Rauhut & Hungerbühler 2000), the lateroproximal surface of the femur has a protruding sigmoid scar for the insertion of the *M. iliofemorale*. This is composed of a knob-like 'lesser trochanter' and the 'trochanteric shelf', the latter probably representing the insertion area of the *M. iliofemoralis externus* (*sensu* Rowe 1986, see also Hutchinson 2001*b*). The 'shelf' extends caudally from the trochanter, through the lateral surface of the femur, turning distally and merging into the shaft, at the caudolateral corner of the bone. This peculiar structure is, however, not present in all 'ceratosaurs' (Welles 1984; Rauhut & Hungerbühler 2000; *Liliensternus* – MB R.1275) and is also absent from the gracile forms of *Syntarsus* (Raath 1990). Moreover, as first recognised by Novas (1992), the 'trochanteric shelf' is not an unique feature of these theropods, but also occurs in basal dinosauromorphs, *Silesaurus*, *Herrerasaurus* and *Saturnalia* (Novas 1993; Sereno & Arcucci 1994; Hutchinson 2001*b*; Langer 2003; Dzik 2003).

Basal dinosaurs that lack a protruding transverse insertion for the iliofemoral musculature usually have a transverse muscle scar extending through the lateroproximal surface of the femur (*Eoraptor* – PVSJ 512; *Lesothosaurus* – BMNH RUB17, R11001; *Heterodontosaurus* – (Novas 1996); *Efraasia* – SMNS 12684; *Thecodontosaurus* – BRSUG various specimens; *Liliensternus* – MB R.1275; *Elaphrosaurus* – MB mounted skeleton). This is equivalent to the 'trochanteric shelf' and frequently connects the 'lesser trochanter' to a muscle insertion area located caudoventrally to it, at the caudolateral corner of the femur (Thulborn 1972; Carrano *et al*. 2002), that most probably also accommodated a branch of the *M. iliofemoralis externus*. *Guaibasaurus*, however, shows an unique condition among the members of the ingroup: no muscle scar is seen caudal to its 'lesser trochanter', which is the single osteological trace of the *M. iliofemorale insertion*.

84. *Fourth trochanter symmetrical, with distal and proximal margins forming similar low-angle slopes to the shaft (0), asymmetrical, with distal margin forming a steeper angle to the shaft (1)*. In most non-dinosauriform archosaurs (Ewer 1965; Romer 1972*c*; Chatterjee 1978; *Stagonolepis* – Long & Murry 1995) the fourth trochanter forms a small ridge on the caudomedial corner of the femur, whereas in rauisuchians (Sill 1974) it is mound-like. *Scleromochlus* and pterosaurs apparently lost the fourth trochanter (Sereno 1991*a*; Bennett 1996), but the structure is retained in basal dinosauromorphs (Sereno & Arcucci 1993, 1994; *Pseudolagosuchus* – PVL 4629) in the form of a prominent sharp ridge. Among dinosaurs, the fourth trochanter of ornithischians is apparently unique because of its 'pendent' shape (Dollo 1888; Romer 1927; but see Cooper 1981), which is already present in all basal members of the group (Thulborn 1972; Santa Luca 1980, 1984; Colbert 1981). This peculiar morphology surely reflects a distally orientated muscular stress, which Galton (1969) interpreted as derived from a head of the *M. gastrocnemius* extending on to the caudal surface of the proximal fibula – the main muscle inserting in the fourth trochanter is the *M. caudifemoralis longus* (Gatesy 1990). As in basal dinosauromorphs, the fourth trochanter of *Silesaurus*, *Staurikosaurus*, *Guaibasaurus* and basal theropods (Huene 1934; Raath 1969; Welles 1984; Currie & Zhao 1994*a*; Madsen & Welles 2000) shows no osteological indications of a distally-orientated muscular stress and its proximal and distal margins form nearly equal low angles to the femoral shaft. However, in *Herrerasaurus*, *Saturnalia*, *Eoraptor* and most basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942; Bonaparte 1972; Galton 1973*a*; Cooper 1981, 1984; Yates & Kitching 2003; *Thecodontosaurus* – BRSUG various specimens), the distal border of the fourth trochanter forms a much steeper angle with the femoral shaft. This condition is termed here 'semi-pendent', and indicates that the trochanter supported some degree of distal muscular stress, although probably not as much as in ornithischians.

85. *Lateral condyle of tibia set at the centre of the lateroproximal corner of the bone (0) or level with the medial condyle at its caudal border (1)*. The position of the lateral condyle of the tibia varies among basal dinosauromorphs. In *Lagerpeton* it is placed right at the laterocaudal corner of the proximal surface, whereas in *Marasuchus* and *Pseudolagosuchus* the condyle is displaced cranially and is set at the centre of the lateral surface of the proximal tibia. This condition is shared by *Saturnalia* as well as by most basal sauropodomorphs (Young 1941*a*; Bonaparte 1972; Galton 1976; Heerden 1979; Cooper 1984; Benton *et al*. 2000) and ornithischians (Thulborn 1972; Galton 1974, 1981; Santa Luca 1980; *Scelidosaurus* – BMNH 1111). However, as in *Lagerpeton*, the lateral condyle of the tibia of *Silesaurus*, *Pisanosaurus*, *Herrerasaurus*, *Staurikosaurus*, *Eoraptor* and most basal theropods (Gilmore 1920; Janensch 1925; Huene 1934; Welles 1984; Padian 1986; Currie & Zhao 1994*a*; Carpenter 1997; *Syntarsus rhodesiensis* – QVM QG 691, 792), is level with the medial condyle at the caudal border of the bone.

86. *Distal tibia sub-quadrangular to sub-circular (0) or transversely elongated (1)* (Fig. 13; Gauthier & Padian 1985). Gauthier & Padian (1985; see also Gauthier 1986) used a lateromedially broadened distal tibia as a dinosaur apomorphy. Indeed, Novas (1992, 1996) has shown that a sub-quadrangular distal tibia is a plesiomorphic feature for dinosaurs, given that it is present in *Marasuchus* and *Pseudolagosuchus*. Yet, as discussed by Brinkman & Sues (1987; see also Benton 1999) various basal dinosaurs retain a sub-quadrangular distal tibia and its lateromedial expansion may define less inclusive groups within Dinosauria. Accordingly, *Pisanosaurus*, *Saturnalia, Staurikosaurus*, *Herrerasaurus* (PVSJ 373, PVL 2566, but see Novas 1992) and *Thecodontosaurus*

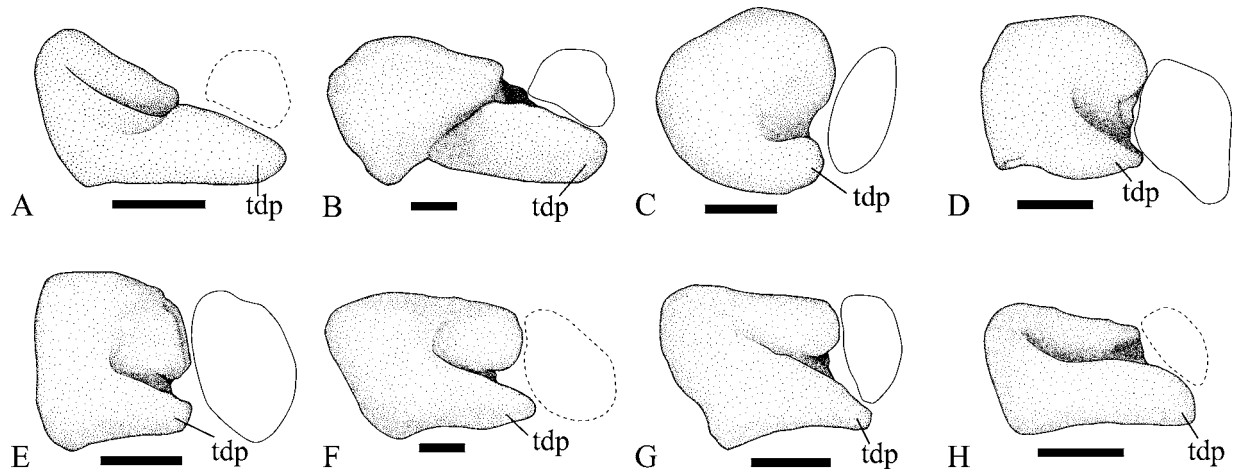

Figure 13 Distal tibia and outline of distal fibula of **A**, cf. *Lesothosaurus diagnosticus*, right tibia (reversed) based on BMNH R11001; **B**, *Scelidosaurus harrisonii*, right (reversed) tibia and fibula based on BMNH 1111; **C**, *Staurikosaurus pricei*, left tibia and fibula based on MCZ 1669; **D**, *Herrerasarus ischigualastensis*, left tibia and fibula based on PVSJ 373; **E**, *Saturnalia tupiniquim*, right (reversed) tibia and fibula based on MCT 3944PV; **F**, cf. *Riojasaurus incertus*, right (reversed) tibia based on PVL 3525; **G**, *Liliensternus liliensterni*, left tibia and fibula based on MB R.1275; **H**, *Syntarsus rhodesiensis*, left tibia based on QVM QG 792. Abbreviations: **tdp**, descending process of tibia. Scale bars: **A, C, E, H** = 10 mm; **B, D, F, G** = 20 mm.

(Benton *et al*. 2000; BMNH P24) have a distal tibia that is as broad as, or narrower than, craniocaudally long. By contrast, most basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942; Novas 1989; Galton 1976; Cooper 1981; Moser 2003), as well as some basal theropods (Welles 1984; Padian 1986; Carpenter 1997), have a distal tibia that is slightly broader than craniocaudally long, a condition seen also in *Silesaurus*, *Eoraptor* and *Guaibasaurus*. In other theropods (Madsen 1976; Britt 1991; Currie & Zhao 1994*a*; *Syntarsus rhodesiensis* – QVM QG 691, 792) and basal ornithischians (Thulborn 1972; Galton 1974, 1981, 1982; *Scelidosaurus* – BMNH 1111) the distal tibia is markedly compressed craniocaudally and much broader than craniocaudally long.

87. *Mediocranial corner of distal tibia forms a rounded oblique to right (0) or an acute angle (1)* (Fig. 13). As discussed under the previous character, the distal tibia of *Marasuchus* and *Pseudolagosuchus* is sub-quadrangular and the mediocranial corner forms a right to slightly low angle. This condition is retained in *Eoraptor*, *Staurikosaurus*, *Herrerasaurus* and *Saturnalia*. However, in *Silesaurus*, *Guaibasaurus*, *Pisanosaurus*, basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942; Cooper 1981; Novas 1989; Benton *et al*. 2000; Moser 2003; *Thecodontosaurus* – BRSUG 23623), theropods (Madsen 1976; Welles 1984; Padian 1986; Britt 1991; Currie & Zhao 1994*a*; Carpenter 1997; *Liliensternus* – MB R.1275; *Syntarsus rhodesiensis* – QVM QG 691, 792) and ornithischians (Thulborn 1972; Galton 1974, 1981, 1982; *Scelidosaurus* – BMNH 1111), the cranial and medial margins of the distal tibia form an acute angle.
88. *Depression in distal tibia for the astragalar ascending process wider (0) or narrower (1) than the tibial descending process* (Fig. 13). As discussed by Novas (1989, 1996), dinosaurs are characterised by the presence of a marked caudolateral descending process of the distal tibia. Although not so well-developed, an homologous flange is seen also in *Marasuchus* and *Pseudolagosuchus*. In these forms, the flange is rather thin and represents about one-third of the distal craniocaudal breadth of the bone. Dinosaurs are derived in relation to other dinosauriforms because their tibial descending process fits caudally into the ascending process of the astragalus. As a result, cranial to the descending process, their distal tibia bears a flat depressed surface for the articulation of the astragalar ascending process. In most basal members of the group, this surface is rather large and broader than the descending process, which remains almost as thin as its osteological correlate in basal dinosauriforms. This condition is shared by *Silesaurus*, *Eoraptor*, *Herrerasaurus*, *Staurikosaurus*, *Guaibasaurus*, *Pisanosaurus*, *Saturnalia* and basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942; Novas 1989; Moser 2003; *Thecodontosaurus* – BRSUG 23623; ?*Massospondylus* – PBI 4693, 5238). By contrast, in basal theropods (Madsen 1976; Welles 1984; Padian 1986; Britt 1991; Currie & Zhao 1994*a*; Carpenter 1997; *Liliensternus* – MB R.1275; *Syntarsus rhodesiensis* – QVM QG 691, 792) and basal ornithischians (Galton 1981; *Lesothosaurus* – BMNH RUB 17; *Scelidosaurus* – BMNH 1111) the descending process of the tibia is the same breadth or more often broader than the articular surface for the ascending process of the astragalus.
89. *Medial margin of distal tibia subequal to (0) or broader than (1) the lateral* (Fig. 13). The sub-quadrangular distal tibia of basal dinosauriforms has lateral and medial margins subequal in breadth. This feature is retained in *Herrerasaurus*, *Silesaurus* and *Eoraptor*. However, the lateral portion of the distal tibia is craniocaudally compressed in basal theropods (Welles 1984; Padian 1986; Britt 1991; Currie & Zhao 1994*a*; Carpenter 1997; *Liliensternus* – MB R.1275; *Syntarsus rhodesiensis* – QVM QG 691, 792) and significantly narrower than the lateral. This is seen also in *Guaibasaurus*, *Saturnalia*, *Pisanosaurus*, basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942; Cooper

1981; Novas 1989; Benton *et al*. 2000; Moser 2003) and basal ornithischians (Thulborn 1972; Galton 1974, 1981; *Scelidosaurus* – BMNH 1111). The character is inapplicable to the sub-circular distal tibia of *Staurikosaurus*.

90. *Caudolateral flange of distal tibia short and does not project (0) or projects caudal to the fibula (1)* (Fig. 13; modified Novas 1989). As stated above, dinosauriforms are characterised by the presence of a descending tibial process. Among dinosaurs, the further lateral extension of this process, forming the 'postfibular-wing' (= outer malleolus), has been suggested to characterise ornithischians (Novas 1989; Sereno 1999) and theropods (Novas 1989). Indeed, in basal ornithischians (Ostrom & McIntosh 1966; Thulborn 1972; Galton 1974, 1981; Colbert 1981; Norman 1986; Forster 1990; *Scelidosaurus* – BMNH 1111) and in various theropods (Gilmore 1920; Bonaparte 1986; Raath 1990; Britt 1991; Currie & Zhao 1994*a*; *Elaphrosaurus* – MB mounted skeleton) the descending process of the tibia is markedly extended laterally, covering most of the caudal margin of the fibula. In some basal theropods, however, this lateral expansion is not so well marked (Welles 1984; Padian 1986; Carpenter 1997; *Liliensternus* – MB R.1275). In these forms, as well as in *Pisanosaurus*, *Guaibasaurus*, *Eoraptor* and, apparently, *Silesaurus*, although expanded laterally, the 'postfibular wing' does not cover half of the caudal margin of the fibula. A similar condition is also present in some basal sauropodomorphs (Novas 1989; Cooper 1981; Galton 1984*b*; *Plateosaurus* – SMNS F65), in which the distal-most part of the descending process of the tibia partially overlaps the fibula caudally. In other members of the group (Young 1942; Galton 1976; Moser 2003; *Thecodontosaurus* – BRSUG 23623, 23624; ?*Massospondylus* – PBI 4693, 5238), the descending process does not project further laterally than the craniolateral corner of the tibia. These forms are defined as lacking a 'postfibular wing' altogether, as is also the case in *Staurikosaurus*, *Herrerasaurus* and *Saturnalia*.
91. *Fibula wider than (0) or subequal to narrower than (1) half the width of the tibia at the middle of their shafts* (modified Gauthier 1986). Gauthier (1986; see also Bennett 1996; Benton 1999) used a thin fibula that tapers distally as an apomorphy of Ornithodira, while other authors defined the reduction of this bone as diagnostic for Dinosauria (Benton & Clark 1988; Benton 1990), or of less inclusive groups within it (Sereno *et al*. 1993; Sereno 1999). Indeed, the fibula is a rather robust bone in pseudosuchians (Walker 1961; Krebs 1965; Bonaparte 1972; Chatterjee 1978, 1985) and the width of its shaft approaches that of the tibia. In *Scleromochlus* (Benton 1999), *Marasuchus* and *Pseudolagosuchus*, the fibula is much thinner, but its lateromedial breadth still represents more than half that of the tibia. This condition is retained in *Herrerasaurus*, *Staurikosaurus*, *Silesaurus*, *Saturnalia*, *Guaibasaurus*, *Eoraptor* and basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942; Bonaparte 1972; Galton 1973*a*, 1976, 1984*b*; Cooper 1984; Zhang 1988; *Thecodontosaurus* – BMNH P24). By contrast, in *Pisanosaurus*, basal theropods (Gilmore 1920; Camp 1936; Welles 1984; Padian 1986; Raath 1990; Currie & Zhao 1994*a*; *Liliensternus* – MB R.1275) and basal ornithischians (Thulborn 1972; Galton 1981; Colbert 1981; Norman 1986), the fibular shaft is more lateromedially compressed and represents at most half the width of the tibia.
92. *Proximal surface of the astragalus lacks (0) or possesses a marked elliptical slot for the descending process of the tibia (1)* (Fig. 14). As discussed by various authors (Novas 1989, 1992, 1993, 1996; Sereno *et al*. 1993; Sereno 1999) the proximal astragalar articulation of dinosaurs is characterised by the presence of a marked craniolateral ascending process, a fainter version of which is seen also in basal dinosauromorphs (Novas 1989, 1996; Sereno & Arcucci 1993, 1994). Novas (1989) used the presence of an elliptical depression behind this process for the articulation of the tibial descending process as a dinosaurian apomorphy. Indeed, as previously discussed, only dinosaurs have a tibial descending process that articulates caudal to the ascending process of the astragalus. In most forms this articulation is rather flat and nearly continuous with that on the medial part of the bone. This is the case in *Guaibasaurus*, basal theropods (Gilmore 1920; Young 1951; Welles 1984; Britt 1991; *Liliensternus* – MB R.2175; *Syntarsus rhodesiensis* – QVM QG-174, 786, 792), basal ornithischians (Galton 1974, 1981; Colbert 1981; Norman 1986; *Scelidosaurus* – BMNH 1111), sauropods (Cooper 1984) and apparently *Silesaurus*. By contrast, as discussed by Galton (1976) and Benton *et al*. (2000), 'prosauropods' are distinct from other dinosaurs because of a more developed interlocking articulation between tibia and astragalus, where a proximal elliptical basin caudal to the ascending process of the astragalus ('dorsal basin' in Novas 1989) is clearly separated from the more medial articulation area of the bone and into which the descending process of the tibia slots. Although typical of 'prosauropods' (Cruickshank 1980; Cooper 1981; Novas 1989; Heerden & Galton 1997; Galton & Heerden 1998), this arrangement is seen also in *Herrerasaurus* and *Saturnalia*.
93. *Astragalus lacks (0) or possesses (1) a platform cranial to the ascending process* (Fig. 14). The caudal margin of the astragalar ascending process of basal dinosaurs always bears a concavity for the articulation of the descending process of the tibia, but its cranial margin presents different morphologies. In most basal forms, the cranial surface of the process is continuous with the rest of the bone, as seen in ornithischians (Galton 1974, 1981; Colbert 1981; *Scelidosaurus* – BMNH 1111; but see Norman 1986) and sauropods (Cooper 1984), as well as in *Pisanosaurus* and *Silesaurus*. However, in *Saturnalia*, basal theropods (Huene 1934; Welles & Long 1974; Madsen 1976; Raath 1990; Britt 1991; Currie & Zhao 1994*a*; Madsen & Welles 2000) and 'prosauropods' (Huene 1926; Young 1942; Cruickshank 1980; Novas 1989; Galton & Heerden 1998), the astragalar ascending process is delimited cranially by a platform, which separates it from the main cranial margin of the bone. This platform is not present on the astragalus of *Guaibasaurus*, but a small rounded concavity is seen on the cranial surface of its ascending process. Yet, this is not considered homologous to the platform itself, but to similar concavities known in various other dinosaurs, whether combined with the platform (Welles & Long

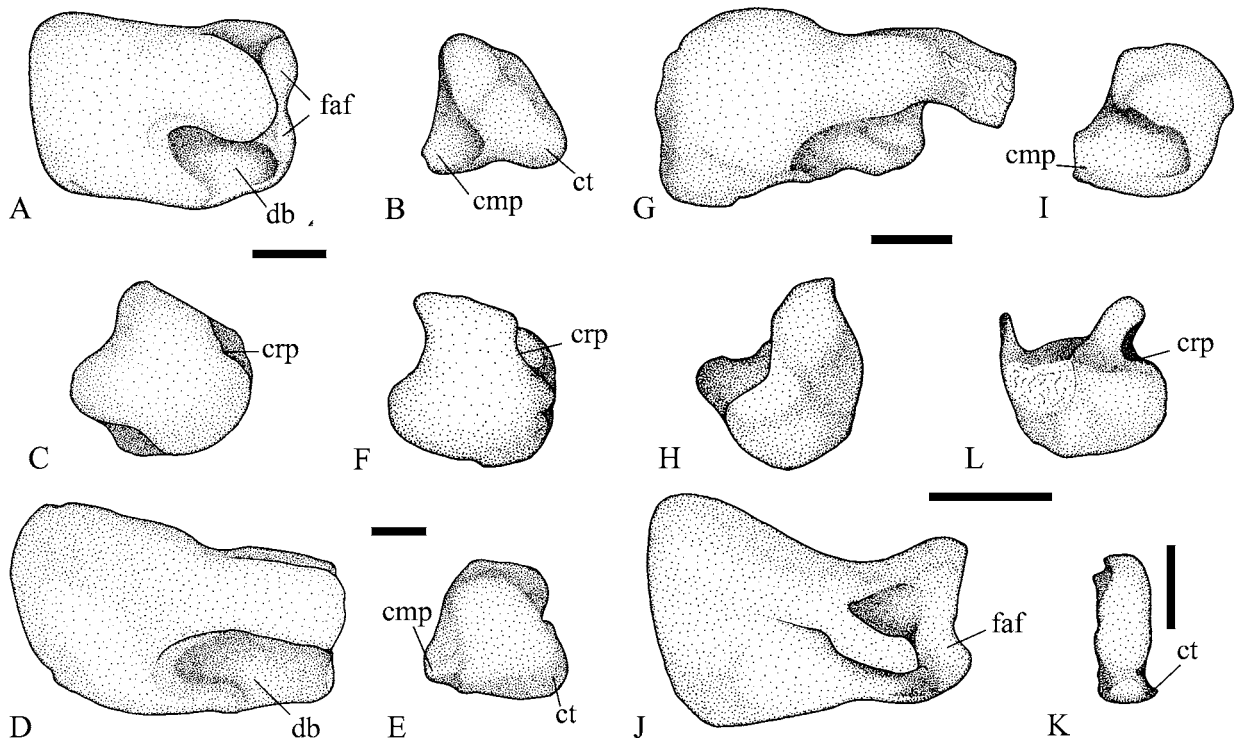

Figure 14 Tarsal bones of **A–C**, *Herrerasarus ischigualastensis*, left astragalus (reversed) and right calcaneum based on PVL 2566; **D–F**, *Plateosaurus engelhardti*, left (reversed) tarsus based on GPIT 'skelett 2'; **G–I**, *Scelidosaurus harrisonii*, right tarsus based on BMNH 1111; **J–L**, *Syntarsus rhodesiensis*, right astragalus based on QVM QG-CT-6 and left calcaneum (reversed) based on QVM unnumbered. Proximal (**A, B, D, E, G, I, J, K**) and lateral (**C, F, H, L**) aspects. Abbreviations: **cmp**, calcaneal medial process; **crp**, astragalar cranial platform; **ct**, calcaneal tuber; **db**, astragalar dorsal basin; **faf**, fibular articulation facet on astragalus. Scale bars: **A–I** = 20 mm; **J–L** = 10 mm.

1974; Novas 1989; Currie & Zhao 1994*a*; *Liliensternus* – MB R.2175) or not (Galton 1981; *Scelidosaurus* – BMNH 1111). The condition in *Herrerasaurus* seems variable. A platform is present in the holotype of the taxon, as well as in that of *Ischisaurus*, but not in PVSJ 373 (Novas 1993), in which a small cavity similar to that of *Guaibasaurus* is seen. The condition in the dinosaur outgroup is also somewhat equivocal. Sereno & Arcucci (1994) described a 'cranial hollow' in the astragalus of *Marasuchus*, but its homology to the dinosaur cranial platform (Cruikshank 1980), the 'hollow' of more basal archosaurs (Sereno 1991*a*), or the concavity of *Guaibasaurus*, is unclear. Yet, no traces of a cranial platform are seen in *Pseudolagosuchus* or *Lagerpeton* and its absence is defined as the outgroup condition.

94. *Articular facet for fibula occupies more (0) or less that (1) 0.3 of the transverse width of the astragalus* (Fig. 14; modified Sereno 1999). Sereno (1999) considered a laterally facing fibular articulation on the astragalus as apomorphic for sauropodomorphs. Indeed, this articulation occupies a minimal portion of the astragalar transverse width in these dinosaurs (Huene 1926; Young 1942; Cruickshank 1980; Cooper 1981, 1984; Novas 1989; Heerden & Galton 1997; Galton & Heerden 1998), although it seems to face dorsolaterally in some forms (Benton *et al.* 2000). An equally restricted fibula–astragalus contact is seen in ornithischians (Galton 1974, 1981; Forster 1990; *Scelidosaurus* – BMNH 1111). In these forms, the fibula merely touches the lateroproximal surface of the astragalar ascending process and no proper articulation facet is seen. Note that the large lateral facet on the proximal surface of the astragalus of *Scutellosaurus* (Novas 1996: fig. 5d 'f') represents the articulation of the 'outer malleolus' of the tibia. A reverse condition is seen in *Silesaurus*, basal dinosauromorphs and other archosaurs (Cruickshank 1979; Sereno & Arcucci 1991; Sereno 1991*a*). The fibular articulation on their astragalus is extensive, occupying more than 0.3 of the transverse width of the bone. *Herrerasaurus*, *Saturnalia*, *Eoraptor*, *Guaibasaurus*, *Pisanosaurus* and basal theropods (Welles & Long 1974; Novas 1989; Raath 1990; *Liliensternus* – MB R.2175) present an intermediate condition. As in basal dinosauromorphs, the fibular articulation on the astragalus faces dorsolaterally, but it is less extensive than in those forms.

95. *Calcaneum proximodistally compressed with calcaneal tuber and medial process (0) or transversely compressed, with the reduction of these projections (1)* (Fig. 14; modified Novas 1989). The calcaneum of basal dinosauromorphs is a proximodistally flattened triradiate bone. It bears a marked caudal tuber and a medial process that articulates ventrally to the astragalus (respectively 'tb' and 'pv' in Novas 1989), which are also conspicuous in non-dinosauromorph archosaurs (respectively 't' and 'va' in Sereno 1991*a*). This condition is retained in *Herrerasaurus*, *Saturnalia* and, apparently, *Silesaurus*, in which the calcaneum bears well-defined medial and caudal projections. Basal sauropodomorphs also have a flat and triradiate calcaneum, although the medial and caudal projections are less prominent in most

forms (Huene 1926; Young 1942; Cooper 1981; Novas 1989). By contrast, the calcaneum of basal ornithischians (Galton 1974; Norman 1986; *Scelidosaurus* – BMNH 1111; *Dryosaurus* – HNN mounted skeleton) and basal theropods (Gilmore 1920; Welles 1984; Currie & Zhao 1994*a*; Sereno *et al*. 1996; *Liliensternus* – MB R.2175; *Syntarsus rhodesiensis* – QVM QG174), is completely modified. The bone is strongly compressed lateromedially and usually deeper than broad. Moreover, the 'calcaneal tuber' and medial projection are vestigial (Madsen 1976: plate 52, figs A, E; *Scelidosaurus* – BMNH 1111) and the astragalo—calcaneal articulation is mainly flat. An intermediate condition is present in *Pisanosaurus* and *Guaibasaurus*. Their calcaneum still retains a defined tuber and lateral processes, but they are also lateromedially compressed. This is especially patent in *Pisanosaurus*, the calcaneum of which is twice as long craniocaudally as broad lateromedially. In *Guaibasaurus*, however, the calcaneum is still broader than long, as is also the case in *Eoraptor*.

96. *Caudomedial prong of lateral distal tarsal is blunt (0) or pointed (1)* (modified Novas 1993). Novas (1993, see also Novas 1996) used the presence of a sub-triangular lateral distal tarsal as an apomorphy of dinosaurs. By contrast, the lateral distal tarsal of basal dinosauromorphs is '8-shaped' (Novas 1996), bearing a strong caudal projection. This projection is seen also in various dinosaurs in the form of a mediocaudal prong, which caudally overlaps the medial distal tarsal (Padian 1986). As in basal dinosauromorphs, this projection is blunt in theropods (Raath 1990; Currie & Zhao 1994*a*) and ornithischians (Galton 1974; Forster 1990), in which the medial margin of the bone is flat to rounded. However, in *Herrerasaurus*, *Saturnalia* and basal sauropodomorphs (Huene 1926; Young 1941*a*; Cooper 1981), the prong tapers medially to a pointed end, giving the lateral distal tarsal its 'typical' sub-triangular shape.
97. *Proximal metatarsal IV lacks (0) or possesses (1) an elongated lateral expansion cranial to metatarsal V* (modified Sereno 1999). Sereno (1999) suggested a proximal articulation of metatarsal IV that is three times broader than deep as an apomorphy of 'prosauropods'. In fact, this reflects the presence, in basal sauropodomorphs (Huene 1926; Young 1941*a*, 1942; Cooper 1981, 1984; *cf. Riojasaurus* – PVL n6; *Thecodontosaurus* – BRSUG 23628) of a marked tapering lateral expansion in the proximal portion of that bone, which overlaps the cranial surface of metatarsal V. Yet, such an expansion is not unique to sauropodomorphs, but also occurs in *Saturnalia* and *Herrerasaurus*. Similarly to those forms, metatarsal V of basal theropods also fits on to the laterocaudal surface of the sub-triangular proximal articulation of metatarsal IV (Gilmore 1920; Huene 1934; Welles 1984; Currie & Zhao 1994*a*), which lacks a pointed lateral extension. A similar condition is seen in *Pisanosaurus* and basal ornithischians (Galton & Jensen 1973; Galton 1974; Forster 1990; *Lesothosaurus* – BMNH RUB17; *Scelidosaurus* – BMNH 1111), in which the proximal outline of metatarsal IV is sub-triangular and lacks an expanded lateral projection. Such a lateral projection is also absent from the proximal metatarsal IV of *Silesaurus* and basal dinosauromorphs (Novas 1996).
98. *Distal articulation surface of metatarsal IV broader than deep to as broad as deep (0), or deeper than broad (1)* (Sereno 1999). In non-dinosauromorph archosaurs, metatarsal IV has a distal articulation in which both condyles are about the same depth, which is usually less than its maximum breadth (Bonaparte 1972, Long & Murry 1995). In dinosaurs, because of their trend towards a tridactyl posture, metatarsal IV tends to bear an asymmetrical distal articulation, in which the medial portion is higher than the lateral. In most basal members of the group the maximum breadth of the entire articulation is larger than or subequal to the depth of its medial portion, as seen in *Herrerasaurus*, *Eoraptor*, basal ornithischians (Ostrom & McIntosh 1966; *Lesothosaurus* – BMNH RUB17; *Scelidosaurus* – BMNH 1111), most basal sauropodomorphs (Huene 1926; Young 1941*a*; Cooper 1981, 1984; *Thecodontosaurus* – BRSUG 23628; *cf. Riojasaurus* – PVL n6) and apparently also *Guaibasaurus*. By contrast, the distal articulation of metatarsal IV of theropods (Gilmore 1920; Huene 1934; Welles 1984; Padian 1986; Britt 1991; Currie & Zhao 1994*a*) is lateromedially compressed and significantly deeper than broad. Accordingly, Sereno (1999) suggested this feature as apomorphic for the group. A similarly deep distal metatarsal IV is, however, seen also in *Saturnalia*, *Pisanosaurus* and basal ornithopods (Galton 1974, 1981).

ANALYSIS AND RESULTS

The software MacClade 3.07 (Maddison & Maddison 1997) was used to score the 98 morphological characters defined above for the hypothetical outgroup and the ingroup OTUs into a character-taxon data matrix (see Appendix). The character states of the hypothetical outgroup were scored as '0', while other character states were coded as '1', in the case of binary characters and '1' or '2', in the case of multistate characters. Inapplicable characters, as well as those regarded as missing data (unknown or uncertain characters states) for single taxon OTUs, have been coded as a question mark (?). Multiple values, e.g. 0&1, 1&2, were applied for variable characters of single taxon OTUs and when the definition of the character states for the outgroup or composite ingroup OTUs was ambiguous.

The data matrix was analysed using PAUP version 4.0b4a (Swofford 2000). The search was rooted in the outgroup and the ingroup made monophyletic. Missing data and inapplicable character states were treated as 'uncertainty' and multiple states as 'polymorphism'. All characters were equally weighted and all multistate characters were ordered, except character 70. The 'branch-and-bound' search option was employed and a single Most Parsimonious Tree (MPT) of 203 steps (Consistency Index (CI) = 0.6059; Homoplasy Index (HI) = 0.4828; Retention Index (RI) = 0.5556; Rescaled CI = 0.3366) was found (Fig. 15). Robustness was assessed by bootstrapping (Felsenstein 1985) and decay indices (Bremer 1988, 1994). Bootstrap values were calculated using the bootstrap search option in PAUP with 100,000 replicates of 'branch-and-bound' searches. Bremer-support values were defined by promoting 'branch-and-bound' searches in PAUP for trees successively longer than the MPT, which were summarised by both strict and 50% majority rule consensus.

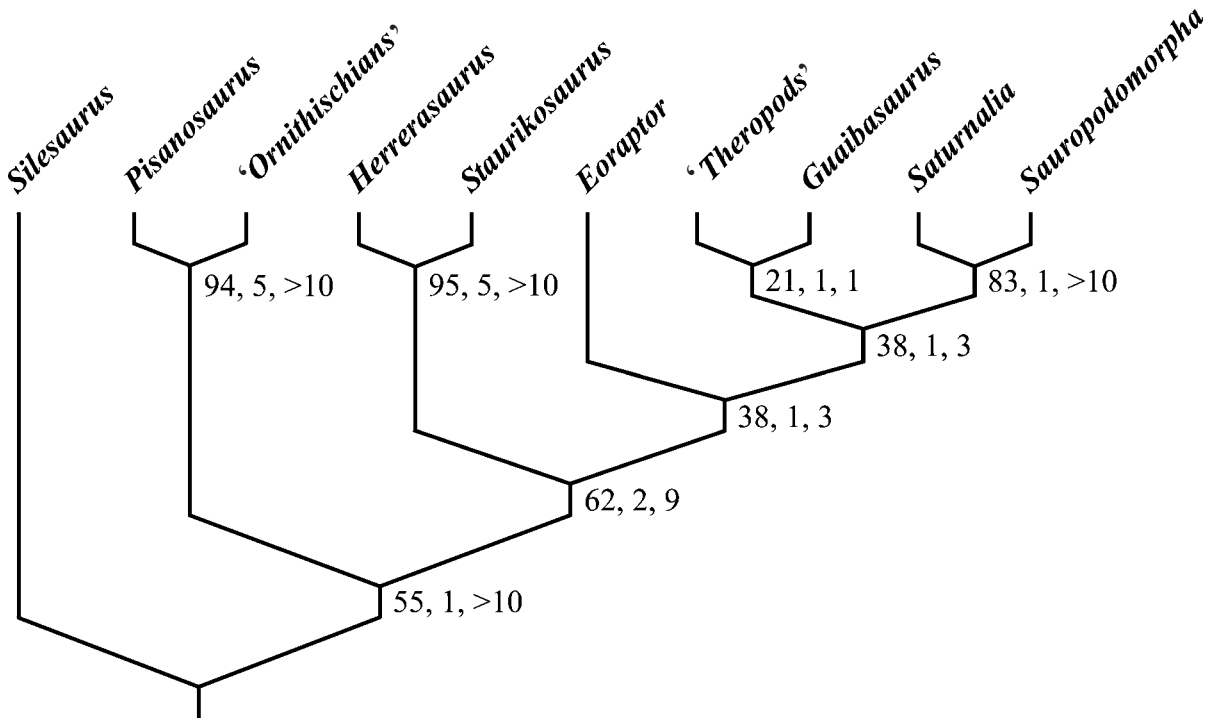

Figure 15 Single 'most parsimonious tree' (MPT) of 203 steps found in the analysis of the data-matrix given in the Appendix. Clade statistics are, respectively, bootstrap value, 'strict' and 'majority rule' values of Bremer support.

In an attempt to explore fully the potential of the data matrix, additional analyses were performed. First, the complete data set was analysed using the command 'Emulate PeeWee' in PAUP, based on the implied weighting strategies developed by Goloboff (1993). This resulted in four MPTs (Goloboff fit = −776.9; CI = 0.6029; HI = 0.4853; RI = 0.5500; Rescaled CI = 0.3316), the majority rule consensus of which is shown in Figure 16A. The trees differ only in the position of *Guaibasaurus* and otherwise are congruent with the MPT derived from the unweighted analysis (Fig. 15). In addition, given its amount of missing data (70%) and unstable position in the latter analysis, the OTU *Guaibasaurus* was excluded from a second analysis performed with implied weighting. A single MPT (Goloboff fit = −783.7; CI = 0.6162; HI = 0.4697; RI = 0.5581; Rescaled CI = 0.3439) was recovered (Fig. 16B), which is also congruent with the MPT (Fig. 15) resulting from the analysis of the complete data set. Bootstrap values are also given in the topologies of Fig. 16 and were calculated based on the same data sets and search criteria applied to generate them.

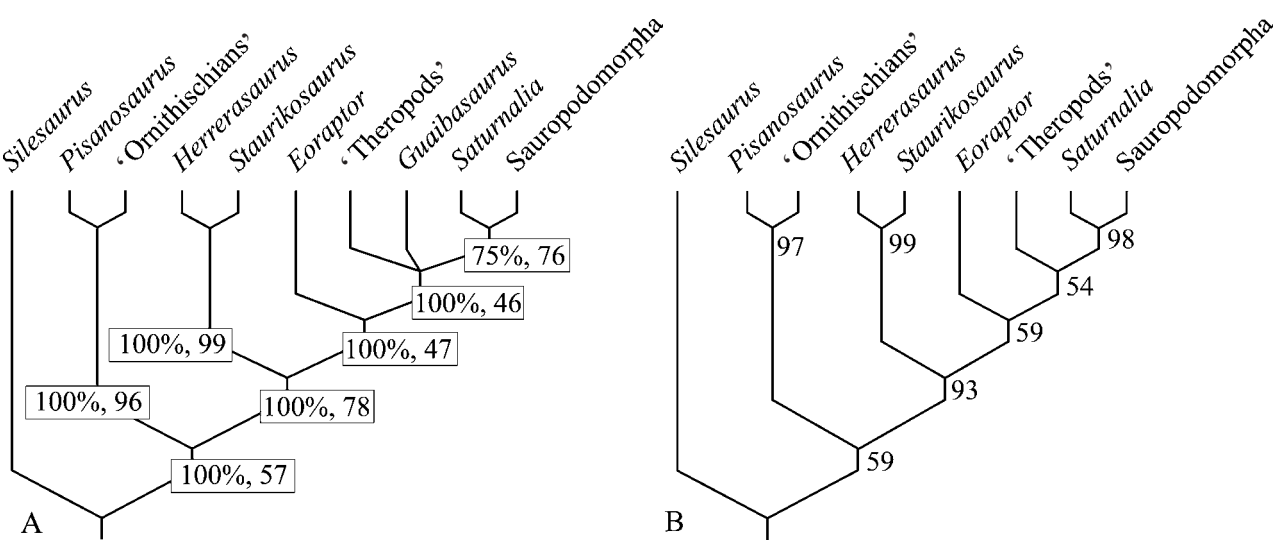

Figure 16 **A**, 'Majority rule' consensus of four most parsimonious trees (MPTs) found in the analysis of the data-matrix given in the Appendix applying the 'Emulate PeeWee' command of PAUP. **B**, Single MPT found in analyses of the data-matrix given in the Appendix, with the exclusion of *Guaibasaurus*. Clade statistics: percentage of MPTs in which the clade occurs (only in **A**) and bootstrap values.

Discussion: hypotheses of early dinosaur relationships

Silesaurus and dinosaur origins

In the original description of *Silesaurus opolensis*, Dzik (2003: 573) proposed three possible phylogenetic positions for the taxon. The suggestion that it belongs to a lineage leading to sauropodomorphs and ornithischians is rejected here, given that full support is provided for a saurischian clade including sauropodomorphs and theropods exclusive of ornithischians (see below). For the remaining two hypotheses, the present numerical analysis favoured the location of *Silesaurus* outside Dinosauria, rather than on the ornithischian lineage. Yet, the support for a dinosaur clade to the exclusion of *Silesaurus* is not compelling (Figs 15 & 16), because there is morphological evidence suggesting its ornithischian affinity. Indeed, *Silesaurus* shares with ornithischians apomorphic dental features such as maxillary/dentary tooth crowns that bear a marked low eminence and attain maximum craniocaudal breadth in the middle of the dental series. In addition, these forms share with *Saturnalia* and sauropodomorphs tooth crowns that are straight and expanded at the base. Moreover, certain postcranial characters not unique to *Silesaurus* and ornithischians may also support their affinity under certain topological constraints. These include sacral vertebrae with transverse processes not craniocaudally expanded, distal pubis not bulging and significantly narrower than the proximal part of the blade and a distal tibia with an acute-angled mediocranial corner.

If *Silesaurus* belongs to the ornithischian lineage, it represents a true dinosaur (Padian & May 1993) and the characters listed in the 'ingroup apomorphies' section, above are apomorphic for the whole group. Alternatively, if it is defined as the sister-taxon to Dinosauria, the characters that support the Saurischia–Ornithischia clade, exclusive of *Silesaurus*, represent the 'true' dinosaur apomorphies. Some of these are shared by all ingroup OTUs except *Silesaurus*, namely: (1) foramen-sized post-temporal opening; (2) epipophyses on cervical vertebrae; (3) dorsally expanded cranial margin of first primordial sacral rib; (4) distal apex of deltopectoral crest placed distal to the proximal 30% of the humeral shaft; (5) ventral margin of iliac acetabulum straight to concave; (6) articulation facet for fibula occupying less that 0.3 of the transverse width of the astragalus. Some characters not shared by all basal members of the ingroup may also represent dinosaur apomorphies under ACCTRAN: (1) tapering rostral ramus of jugal (reversed in *Herrerasaurus* and some basal theropods); (2) loss of trochanteric shelf (reversed in *Herrerasaurus*, *Saturnalia* and some basal theropods); (3) asymmetrical fourth trochanter (reversed in *Staurikosaurus*, *Guaibasaurus* and basal theropods); (4) trunk vertebrae incorporated into the sacrum (reversed in *Herrerasaurus*, *Staurikosaurus*, *Saturnalia* and some basal sauropodomorphs); (5) tail vertebrae incorporated into the sacrum (reversed in *Herrerasaurus*, *Eoraptor* and some basal sauropodomorphs).

Either as a basal ornithischian or the sister taxon to Dinosauria, an animal such as *Silesaurus* was unexpected at the base of the dinosaur phylogenetic tree. It has been described as a probable herbivore, but true herbivory seems less common in basal dinosaurs than usually admitted and the dentition of *Silesaurus* matches a general pattern that does not necessarily indicate that diet (Barrett 2000). Indeed, dinosaurs are part of an archosaur radiation that primitively preyed upon small animals or were adapted to an omnivorous diet (Arcucci 1997; Benton 1999; Barrett 2000). These are small to medium-sized bipeds (Bonaparte 1975; Padian 1984; Sereno 1991*b*), whereas quadrupedalism reappeared in some dinosaur groups along with their increase in size. Curiously, its long arms indicates that the gracile *Silesaurus* was a quadruped, hinting that the diversity of the early radiation of dinosaurs is still under-represented in the fossil record and that basal members of the group probably exploited far more niches than previously thought (see also Haubold & Klein 2002).

The early radiation of saurischian dinosaurs

The monophyly of a saurischian clade including *Eoraptor*, *Guaibasaurus*, *Herrerasaurus*, *Saturnalia*, *Staurikosaurus*, theropods and sauropodomorphs, to the exclusion of *Silesaurus* and ornithischians is one of the better supported results of the present analysis (Figs 15 & 16). Numerous morphological characters unambiguously suggest this hypothesis of relationship (characters 2, 11, 30, 32, 34, 38, 52, 54, 59, 60, 67 and 79), but some of the previously proposed saurischian apomorphies present some problems and were questioned by Langer (2004). These include a jugal that overlaps the ventral margin of the lacrimal and possesses a forked caudal ramus – also seen in *Lesothosaurus* (BMNH RUB17, R8501) and *Scelidosaurus* (BMNH R1111) – axial epipophyses and overlapping proximal portions of metatarsals II–IV. In addition, Novas (1993) resurrected a character first proposed by Gauthier (1986), suggesting that saurischians are characterised by the presence of axial postzygapophyses that are set entirely lateral to the prezygapophyses. Yet, in various basal saurischians (Welles 1984; Madsen & Welles 2000; *Plateosaurus* – SMNS F65, GPIT mounted skeletons), there is a clear overlap between the axial pre- and postzygapophyses, in a fashion very similar to that of basal ornithischians (*Scelidosaurus* – BMNH 1111). Moreover, the elongation of the first phalanx of manual digit I in relation to its respective metacarpal (Sereno *et al*. 1993) seems to reflect the combination of two different transformations: the shortening of the metacarpal, which is apomorphic for Eusaurischia (character 57) and the elongation of the first phalanx (character 59) which is, indeed, apomorphic for saurischians as a whole.

A monophyletic Dinosauria exclusive of *Herrerasaurus* or herrerasaurids has been advocated by Brinkman & Sues (1987), Benton (1990), Novas (1992) and Fraser *et al*. (2002). Yet, most features used to support the basal condition of herrerasaurids among dinosaurs are seen in basal members of most major dinosaur groups (characters 41, 42, 69, 82, 83 and 86) and do not clearly indicate that hypothesis of relationship. This is the case for trunk and tail vertebrae not incorporated into the sacrum (Benton 1990; Novas 1992; Fraser *et al*. 2002), the well-developed medial wall of the acetabulum (Brinkman & Sues 1987), the not proximally expanded 'lesser trochanter' (Novas 1992), the well-developed 'trochanteric shelf' (Novas 1992) and the non-transversely elongated distal end of the tibia (Benton 1990).

One of the few herrerasaurid features that indicates their basal position among dinosaurs is the absence of a well-developed fossa for the insertion of the caudofemoral musculature (Novas 1992; Fraser *et al*. 2002). Alternatively,

there is evidence (see character 71) that the 'brevis fossae' of saurischians and ornithischians are not primarily homologous. In this case, ornithischians and non-herrerasaurid saurischians could have independently developed superficially similar structures and the herrerasaurid condition represents the retention of a dinosaur plesiomorphy. Another character that might support the basal position of *Herrerasaurus* is the fifth pedal digit (Brinkman & Sues 1987) that represents about 75% of the length of the third metatarsal and bears a small first phalanx. However, that digit is shorter and lacks phalanges in *Lagerpeton*, *Marasuchus*, *Guaibasaurus*, *Saturnalia*, *Thecodontosaurus* (Yates 2003*a*), ornithischians (Owen 1863; Forster 1990) and basal theropods (Raath 1969; Welles 1984; Colbert 1989; Rowe 1989). In this case, unless *Herrerasaurus* is basal to Dinosauromorpha, its longer pedal digit V has to be interpreted as a reversal, which is also reported among sauropodomorphs.

The monophyly of Herrerasauridae

The close affinity between *Herrerasaurus* and *Staurikosaurus* within a monophyletic Herrerasauridae was proposed by Benedetto (1973; see also Galton 1985*d*; Novas 1986) and supported by cladistic studies (Novas 1992; Sereno 1999; Rauhut 2003; Langer 2004). This is corroborated in the present analysis (Figs 15 & 16), based mainly on morphological transformations (characters 39, 45, 46 and 77) first proposed by Novas (1992). In addition, under the topological constraints of Fig. 15, some homoplastic features can also be considered to characterise the group (characters 20, 41, 47, 71 and 90). Yet, the scapular features used by Novas (1992) to support a monophyletic Herrerasauridae are ambiguous, given that the acromion is not preserved in the type specimen of *Staurikosaurus* (Bittencourt 2004) and the scapular blade does not seem to be strap-shaped (Galton 2000*a*). Likewise, Sereno (1999) used a crested laterocranial margin of the proximal femoral shaft as apomorphic for Herrerasauridae. If this stands for the 'keel' reported in *Herrerasaurus* (Novas 1993: fig. 7), it is not apomorphic for the group, given that it occurs in *Saturnalia* and is not clearly seen in *Staurikosaurus* (Novas 1993).

Most studies supporting a paraphyletic Herrerasauridae defined *Herrerasaurus* as more closely related to other dinosaurs (Brinkman & Sues 1987; Benton 1990), but this arrangement is not supported by the available morphological evidence. *Contra* Benton (1990), it is not clear that the neck of *Herrerasaurus* is more elongated than that of *Staurikosaurus* and the pubo-ischiadic contact does not seem to differ significantly in both forms; *contra* Brinkman & Sues (1987), the distal tibia of *Herrerasaurus* is not more transversely expanded than that of *Staurikosaurus* (character 86). In fact, the only character that could suggest this hypothesis is the absence of a protruding insertion for the iliofemoral musculature on the femur of *Staurikosaurus* (characters 82 and 83).

Herrerasaurids and Eoraptor *as basal theropods*

Most recent cladistic studies advocate the nesting of *Eoraptor* and Herrerasauridae within Theropoda (Sereno & Novas 1992, 1993; Sereno *et al*. 1993; Novas 1993, 1996; Sereno 1999; Rauhut 2003). Indeed, *Eoraptor* and/or herrerasaurids share various theropod features. These were included in the present analysis (characters 13, 24, 25, 29, 48, 52, 55 and 64), but their signal was not enough to enforce that hypothesis of relationship. By contrast, other previously proposed apomorphies of that clade do not seem to support this arrangement unambiguously (characters 16, 33, 65, 67, 78 and 83). Moreover, Sereno (1999) suggested various doubtful postcranial features as apomorphies of Theropoda (encompassing herrerasaurids and *Eoraptor*). These include intermetacarpal articular facets on metacarpals I–III, which are seen also in other basal dinosaurs (Broom 1911; Huene 1932: pl. 11; Santa Luca 1980), as well as the presence of an 'arched' brevis fossa and an ischiadic obturator process. By our understanding of this anatomical term, an obturator process is clearly present in the ischium of basal sauropodomorphs (Huene 1926; Cooper 1981), as well as in ornithischians – *Lesothosaurus* (BMNH RUB17) – although it is not as ventrally expanded in these forms as in most saurischians (character 79). In addition, herrerasaurids possess an area for the insertion of the *m. caudifemoralis brevis* similar to that of *Marasuchus* and less lateromedially and dorsoventrally expanded than that of theropods (character 71). Moreover, *contra* Sereno *et al*. (1993; Sereno 1999), no significant difference was recognised in the expansion of the medullary cavity of the long bones of basal saurischians.

Previous assessments of the phylogenetic position of herrerasaurids defined them as more derived than *Eoraptor* and the sister group to 'Neotheropoda' (Sereno *et al*. 1993; Novas 1993, 1996; Sereno 1999; Rauhut 2003), but some of the characters employed by those authors fail to support this arrangement (characters 47 and 76). This is also the case for a dorsally constricted lower temporal fenestra (Sereno & Novas 1993), which is seen in various basal sauropodomorphs (Young 1941*a*, 1942; Bonaparte & Vince 1979; Gow *et al*. 1990; Bonaparte & Plumares 1995) and a strap-shaped scapular blade (Sereno *et al*. 1993; Sereno 1999). In fact, although the scapular blade of some derived theropods (Gauthier 1986; Bonaparte *et al*. 1990; Currie & Zhao 1994*a*; Currie & Carpenter 2000; Madsen & Welles 2000) approaches the shape seen in *Herrerasaurus*, that of most basal members of the group (Huene 1934; Welles 1984; Rowe 1989; Colbert 1989; Raath 1990; Carpenter 1997) expands dorsally as in other basal dinosaurs (Owen 1863; Huene 1926; Thulborn 1972; Bonaparte 1972; Galton 1973*a*; Santa Luca 1980; Cooper 1981).

Another postulated herrerasaurid–theropod apomorphy is a cranial depression on the distal femur (Sereno 1999) interpreted here as the cranioproximal extension of the sulcus intercondylaris seen in most derived dinosaurs (Galton 1976; Forster 1990; Currie & Zhao 1994*a*). This is, however, absent from the cranial surface of the distal femur of *Herrerasaurus*, *Staurikosaurus* and several other basal dinosaurs such as *Saturnalia*, *Lilliensternus* (MB R.2175) and *Lesothosaurus* (BMNH RUB17). Sereno *et al*. (1993) also considered herrerasaurids and theropods to be more derived than *Eoraptor* because of the transversally wider proximal end of their fibula. In fact, the proximal end of the fibula of *Eoraptor* is particularly compressed lateromedially. If this is not the result of taphonomic deformation, it is a potential autapomorphy of the taxon. In contrast, the proximal fibula of all other dinosaurs is rather similar in its transverse width (Huene 1926; Thulborn 1972; Welles 1984; Padian 1986; *Pisanosaurus*–PVL 2577; *Saturnalia*–MCP 3845-PV) and that of *Herrerasaurus* and theropods is believed simply to retain the plesiomorphic condition.

In fact, the only characters that clearly support a close relationship between *Herrerasaurus* and theropods, to the exclusion of *Eoraptor*, are typical predatory features. These include the cranio-mandibular and intramandibular joints, the long penultimate manual phalanges and the trenchant unguals (characters 20, 22, 62 and 63). Rauhut (2003) points out the uncertainly in these characters, which are unknown in immediate dinosaur outgroups, and suggests that they are either plesiomorphies lost in the more omnivorous/herbivorous ornithischians and sauropodomorphs or theropod (including herrerasaurid) apomorphies. Alternatively, under the constraints of our phylogenetic hypothesis (Fig. 15), these are interpreted as convergences that appeared independently in herrerasaurids and theropods, possibly as adaptations to their carnivorous diet. Indeed, herrerasaurids may have represented a basal lineage of saurischians that briefly occupied the niche of medium- to large-sized terrestrial predators in the Late Triassic, before this role was taken over by theropods.

The present study also indicates that herrerasaurids are more basal in the dinosaur tree than *Eoraptor* (Fig. 15). Indeed, various characters that *Eoraptor* shares with sauropodomorphs and theropods are absent in *Herrerasaurus* (characters 6, 8, 9, 10, 12, 56 and 58). In addition, *Eoraptor* has a horizontal ridge on the lateral surface of the maxilla, which is unknown in *Herrerasaurus* and basal ornithischians (Weishampel & Witmer 1990; Coombs *et al.* 1990; Sereno 1991*b*; Haubold 1991), but characterises coelophysids (Rowe & Gauthier 1990). Indeed, a fainter version of this ridge is also present in *Thecodontosaurus* (BMNH P24) and it might represent a condition of saurischians more derived than *Herrerasaurus* that has been lost in more derived theropods (Welles 1984; Madsen & Welles 2000) and sauropodomorphs (Huene 1926; Galton 1984*a*; Bonaparte & Plumares 1995). Moreover, *Eoraptor* has some features that are unknown in any non-theropod basal dinosaur (characters 3, 73 and 74), as well as some that suggest a sauropodomorph affinity. The latter include the presence of lanceolate teeth that are somewhat longer in the cranial-most part of the upper jaw, and a larger external naris, if compared to those of *Herrerasaurus* and basal theropods (Welles 1984; Madsen & Welles 2000).

The monophyly of Eusaurischia

In the past few years, the notion that herrerasaurids and/or *Eoraptor* represent basal theropods has been challenged by independent studies (Padian & May 1993; Holtz 1995; Bonaparte & Plumares 1995; Langer *et al.* 1999, Langer 2001*a*, *b*, 2004, Fraser *et al.* 2002; Yates 2003*a*). As advocated here (Fig. 15), some of these proposals consider those dinosaurs as saurischians basal to the theropod–sauropodomorph dichotomy. Obviously, central to this hypothesis is the assumption of a monophyletic Eusaurischia, as defined by Padian *et al.* (1999). Indeed, several characters unambiguously indicate the close relationship between theropods and sauropodomorphs, to the exclusion of herrerasaurids and *Eoraptor* (characters 5, 35, 57, 61 and 80). In addition, some homoplastic features (characters 51 and 89) also suggest this arrangement, while the larger size of the medial-most distal carpal in theropods and sauropodomorphs (character 53) implies a derived condition relative to *Herrerasaurus*. By contrast, the theropod affinity of *Guaibasaurus* within Eusaurischia, as proposed by Langer (2004), is very poorly constrained (Fig. 15 & 16). Not surprisingly, only two homoplastic features sustain this arrangement (characters 78 and 84).

In conclusion, the phylogenetic hypothesis advocated here excludes herrerasaurids and *Eoraptor* from Theropoda. Yet, the eusaurischian clade, as well as that composed of *Eoraptor* plus Eusaurischia, are not supported by high bootstrap and Bremer-support values (Fig. 15). Accordingly, the major conclusion that may be drawn from the present study is that, partially due to the poor knowledge of basal dinosauromorphs, the available morphological data are simply not enough to explain early saurischian evolution comprehensively. Indeed, a strong case in favour of any particular hypothesis regarding the position of herrerasaurids and *Eoraptor* is still out of reach.

Saturnalia tupiniquim *and early sauropodomorph evolution*

Saturnalia has been considered the basal-most member of the sauropodomorph lineage (Langer *et al.* 1999; Langer 2002; Yates 2003*a*, Yates & Kitching 2003) and the present cladistic analysis confirms that it is closer to sauropodomorphs than to any other basal dinosaur or major dinosaur group. The *Saturnalia*–Sauropodomorpha clade (Fig. 15) is supported by four apomorphies unknown in any other ingroup OTU, namely: (1) short head; (2) long and narrow ventral ramus of the squamosal; (3) high tooth crowns on the rostral quarter of the tooth-bearing areas; (4) broad distal humerus. Moreover, based on the chosen topology, *Saturnalia* and sauropodomorphs are also characterised by some homoplastic dental features (characters 24, 25 and 26). These are shared with ornithischians and/or *Silesaurus* and represent adaptations towards a more herbivorous diet. Furthermore, *Saturnalia* and sauropodomorphs share with *Herrerasaurus* some tarsal–pedal features (characters 92, 96 and 97). Yet, it is ambiguous whether these are convergently apomorphic, or represent saurischian plesiomorphic traits reversed in Theropoda.

The hypothesis that *Saturnalia* is basal to all sauropodomorphs has not been tested by the present phylogenetic analysis. Instead, it was assumed *a priori,* based on several morphological features that indicate its primitiveness within the sauropodomorph lineage. Indeed, unlike most sauropodomorphs (Galton 1976; Bonaparte & Vince 1979; He *et al.* 1988; Gauffre 1993; Bonaparte & Plumares 1995; Benton *et al.* 2000; Yates 2003*a*, *b*), the dentary of *Saturnalia* does not have a downturned cranial margin, but is straight as in other basal saurischians (Colbert 1989; Sereno & Novas 1992). Furthermore, as in those dinosaurs, the tooth serrations of *Saturnalia* are finer, forming right angles to the margin of the teeth. By contrast, those of 'prosauropods' are coarser and oblique to the tooth margin (Galton 1986; Attridge *et al.* 1985; Gauffre 1993; Yates 2003*a*). In addition, among the characters discussed in the present phylogenetic study, the incisure that separates the distal margins of the pubic pair and the 'trochanteric shelf' also suggest a basal condition for *Saturnalia*. These traits are unknown in sauropodomorphs, which have a broad distal 'pubic apron' and lack a 'trochanteric shelf'.

Other primitive features of *Saturnalia* reflect its higher cursoriality relative to sauropodomorphs. These include a

femur that is not longer than the tibia and bears the fourth trochanter placed proximally on the shaft. Sauropodomorphs, by contrast, have a shorter tibia (Galton 1990*a*; Yates 2003*b*) and a fourth trochanter placed within the distal 70% of the femur (Bakker & Galton 1974; Galton 1973*a*, 1976; Cooper 1984; Buffetaut *et al*. 2000; Yates & Kitching 2003; *Thecodontosaurus* – BRSUG 236/4). Likewise, *Saturnalia* has a well-defined scar on the lateral tibia for the articulation of the fibula. This is homologous to the fibular flange of theropods (Huene 1934; Welles 1984; Padian 1986) and suggests that those bones were closely appressed. By contrast, the tibia and fibula of sauropodomorphs are usually more separated from one another (Bonaparte 1972; Galton 1976; Cooper 1981, 1984).

Sauropodomorphs are also characterised by an increase in robustness of the lateral pedal digits, while *Saturnalia* lacks some of the typical features related to this transformation. These include a metatarsal II with a medially concave proximal articulation that is broader than half that of metatarsal III and a distal articulation that is subequal to, or wider than, that of metatarsal III, as well as a transversely flared proximal metatarsal V. These are typical of sauropodomorphs (Broom 1911; Young 1941*a*; Galton 1976, 1984*b*; Bonaparte & Vince 1979; Casamiquela 1980; Cooper 1984; Galton & Heerden 1985; Zhang 1988; Yates & Kitching 2003; *Thecodontosaurus* – BMNH P24), but unknown in other basal dinosaurs (Owen 1863; Huene 1934; Raath 1969; Sereno 1991*b*; Novas 1993).

Sereno (1999) diagnosed Sauropodomorpha based on a laterally orientated fibular articulation on the astragalus and a long ungual phalanx in pedal digit I. Indeed, these features are seen in most basal members of the group (Huene 1926; Galton 1976; Cruickshank 1980; Cooper 1981, 1984; Galton & Heerden 1985, 1998; Zhang 1988; Novas 1989), but not in *Thecodontosaurus* (Benton *et al*. 2000; BMNH P24) or *Saturnalia*. Accordingly, these are perhaps apomorphic for sauropodomorphs more derived than those two taxa. Similarly, *Saturnalia* and apparently *Thecodontosaurus* (Yates 2003*a*) lack phalanges in the fifth pedal digit. This seems to represent the retention of a dinosaurian plesiomorphy (see discussion in Yates 2003*a*), given that a similar condition is present in basal dinosauromorphs (Sereno & Arcucci 1993, 1994) and most basal dinosaurs (Owen 1863; Colbert 1989; Rowe 1989; Forster 1990), except for *Herrerasaurus*. By contrast, at least one phalanx is present in pedal digit V of most basal sauropodomorphs (Huene 1926; Young 1941*a*; Galton 1976; Galton & Cluver 1976; Cooper 1981, 1984; Zhang 1988; Yates & Kitching 2003).

Conclusions

The origin of dinosaurs can be traced back to the Late Triassic, based on skeletal remains found in Carnian strata of various parts of the world, including South and North America, Europe, Africa and India. Of these, only the Ischigualastian beds of South America have preserved a relatively rich dinosaur fauna, in which various taxa were recognised, some of them represented by complete specimens. This is the case for *Staurikosaurus pricei* and *Saturnalia tupiniquim* from the Santa Maria Formation, southern Brazil, as well as *Herrerasaurus ischigualastensis* and *Eoraptor lunensis* from the Ischigualasto Formation, northwestern Argentina. Despite this relatively adequate anatomical knowledge, previous phylogenetic studies of the early radiation of dinosaurs disagree in most details, especially regarding the position of these basal members of the group. A detailed reassessment of those studies, with information from new basal dinosaur specimens and a close re-study of other materials have allowed us to evaluate the different hypotheses of early dinosaur relationships, defining their strength in the light of currently available information.

Dinosaurs are part of a bipedal radiation of small gracile archosaurs that flourished during the Mid- to Late Triassic, also including *Scleromochlus*, and basal dinosauromorphs such as *Lagerpeton* and *Marasuchus*. Most other archosaurs were quadrupeds and adaptations towards an active bipedal locomotion certainly played an important role in the early evolution of the group. An exception is the quadruped *Silesaurus opolensis* from the Late Triassic of Poland, which has shown that the diversity of early dinosauromorphs was underestimated in terms of ecological adaptations. The phylogenetic hypothesis favoured here has *Silesaurus* as sister-taxon to a monophyletic Dinosauria, as defined by a series of apomorphies of Saurischia plus Ornithischia that are unknown in that taxon. Alternatively, there is also limited evidence (based mainly on the sharing of some dental features) for the nesting of *Silesaurus* within ornithischians, hence within Dinosauria.

The clade Dinosauria is composed of the classical Saurischia–Ornithischia dichotomy, the major clade that rose to dominate the land for some 160 million years of the Mesozoic and, in the form of birds, still plays an important role in modern ecosystems. The general view that *Pisanosaurus mertii* from the Late Triassic of Argentina represents the basalmost ornithischian is upheld here, although doubt is cast on many of the supposed ornithischian features of the rather poorly preserved sole specimen. Nevertheless, *Pisanosaurus* is the only relatively well-known Carnian ornithischian and the group continues to be recognised mainly from incomplete remains through the rest of the Triassic, only achieving higher diversity and abundance in the Early Jurassic.

Based on the most parsimonious phylogenetic hypothesis presented here, the majority of Triassic dinosaurs (including *Herrerasaurus*, *Staurikosaurus* and *Eoraptor*) are assigned to the saurischian lineage and previous hypotheses that place these forms outside Dinosauria are not supported. In addition, Saurischia is composed of two major monophyletic groups: Herrerasauridae (including *Herrerasaurus* and *Staurikosaurus*) and Eusaurischia (including the theropod and sauropodomorph lineages). Herrerasaurids, therefore, represent an unique radiation of medium to large-sized carnivorous saurischians, restricted to the Late Triassic. An alternative widely accepted view, that these dinosaurs are basal members of Theropoda, is not endorsed here. Instead, the characters shared by these dinosaurs are regarded as convergences that have arisen independently, possibly as adaptations to their predatory habits.

Much more successful than herrerasaurids was their sister group, which includes the sauropodomorph and theropod lineages. Unlike herrerasaurids, the early evolution of these dinosaurs was not accompanied by a significant increase in size, nor by marked diet-related adaptations and basal members such as *Eoraptor* and *Saturnalia* were small forms that in various respects resemble basal dinosauromorphs and early

ornithischians. The phylogenetic position of *Eoraptor* is controversial. It is considered here as the sister taxon to Eusaurischia, but there is morphological evidence for a closer affinity to theropods. *Saturnalia*, however, is consensually admitted as a stem-taxon to Sauropodomorpha, whereas *Guaibasaurus candelariensis*, from the latest Triassic of south Brazil, might be a basal theropod, although this hypothesis is not strongly supported.

From that basal saurischian stock, two main and fundamentally distinct groups of dinosaurs evolved. Sauropodomorphs became large-sized, quadrupedal plant-eaters. They include the first important pulse of dinosaurian diversification, with 'prosauropods' as one of the most abundant groups of terrestrial tetrapods in the Late Triassic. Theropods, by contrast, occupied the niche of bipedal hunters. They were not very abundant during the Triassic, but in the Jurassic they established themselves as the dominant top predators of most terrestrial ecosystems.

Uncertainties about the placement of many of the basal dinosaurs result from their rarity, the incompleteness of some specimens and poor knowledge of many immediate outgroups. In addition, synapomorphies of the key dinosaurian clades that are clear in derived forms from the later Triassic and Jurassic are often not present in their basal members. These share several plesiomorphies and are rather similar to each other. Some excellent new basal dinosaurs have come to light in the last few years and more complete material of known taxa such as *Saturnalia*, *Guaibasaurus*, *Eoraptor* and *Silesaurus*, as well as new taxa, such as putative ornithischians and theropods from the Carnian of Brazil, will surely help to clarify the phylogeny further.

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Appendix: Character-taxon data matrix

(a = 0/1; b = 1/2).

	10	20	30	40	50
	/	/	/	/	/
Outgroup	0000000a00	0000000000	0000000000	0000000000	0000000000
Silesaurus	0000001???	?0????000?	??111210??	1000001001	001000?000
Pisanosaurus	0?????????	???????110	?1111010??	??????????1	11??0?????
Ornithischians	0000000000	0100002110	0111101000	0010000001	1101000010
Herrerasaurus	010?000000	10101?1001	?000000011	1111???110	0011111110
Staurikosaurus	0?????????	???????001	?00000????	1?1?00??10	0??1111???
Eoraptor	0111011111	111?01?0?0	?1000100??	?111001100	101??0?110
Guaibasaurus	??????????	??????????	??????????	???????1??	?????0????
Theropods	0111111111	1a10a1200a	1000000011	1111111101	111100a110
Saturnalia	1????????1	1??1???00?	??011201??	???1101100	011100?011
Sauropodomorpha	1101111111	11011a1000	110112a101	1111111101	0a11000011

	60	70	80	90	
	/	/	/	/	
Outgroup	0000000000	0000000000	0000000000	?000000000	00000000
Silesaurus	0?????????	???????002	11000101?0	?100111001	00000?0?
Pisanosaurus	??????????	????????2?	??????????	????101011	1?011?01
Ornithischians	10000a0000	0000000120	1000110200	0211011111	10011000
Herrerasaurus	0201100011	0111111020	0100101010	1101100000	01a10110
Staurikosaurus	??????????	???????021	010000101?	00101000?0	0???????
Eoraptor	02??1101??	0001101021	1111000010	0111110001	0??10??0
Guaibasaurus	??????????	????????12	1100010a11	1110?11011	00010??0
Theropods	1211111111	1111a11122	1111000211	0ba0111111	10111001
Saturnalia	1?????????	???????012	1100000011	1101000010	01110111
Sauropodomorpha	1111011111	100001a020	1100000011	1a110a101a	01110110