

Basal Saurischia

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The name Saurischia was coined by Seeley in lectures given in 1887, published in 1888, to designate those dinosaurs possessing a propubic pelvis. This plesiomorphic feature distinguishes them from ornithischians, which have an opisthopubic pelvis. Despite its general acceptance as a taxonomic unit since the proposal of the name (Huene 1932; Romer 1956; Colbert 1964a; Steel 1970), the monophyly of Saurischia was heavily questioned in the 1960s and 1970s (Charig et al. 1965; Charig 1976b; Reig 1970; Romer 1972c; Thulborn 1975; Cruickshank 1979). Its status as a natural group was, however, fixed by Bakker and Galton (1974), Bonaparte (1975b) and, more importantly, Gauthier (1986), who formally established the monophyly of the group.

The taxa discussed in this chapter (table 2.1) are usually considered to be among the oldest known dinosaurs. They include the most basal saurischians, as well as various forms of uncertain affinity once assigned to the group. The most important of these records come from the South American beds of Ischigualastian age (Bonaparte 1982b), usually dated as Carnian (Rogers et al. 1993; Lucas 1998). These comprise the Ischigualasto Formation in northwestern Argentina, which has yielded *Herrerasaurus ischigualastensis* (Reig 1963) and *Eoraptor lunensis* (Sereno et al. 1993), and the Upper Santa Maria Formation, in southern Brazil, which yielded *Staurikosaurus pricei* (Colbert 1970). In addition, putative Triassic basal dinosaurs from other South American strata (Huene 1942; Bonaparte et al. 1999) and other parts of the world (Benton and Walker 1985; Galton 1985a; Chatterjee 1987; Long and Murry 1995; Fraser et al. 2002) are also considered.

The dating of the tetrapod-bearing Late Triassic continental deposits is poorly constrained (for tentative global correlation see Anderson and Cruickshank 1978; Ochev and Shishkin 1989; and Lucas 1998). Contrary to the claims of some (Hunt et al. 1998; Heckert and Lucas 1999; Flynn et al. 1999b), there is not a strong basis for the correlation of most Carnian strata worldwide, and the question which is the oldest known dinosaur is still to be answered. Here, several reputed dinosaur-bearing Carnian beds are tentatively correlated with the Ischigualastian. These include the Lossiemouth Sandstone Formation in Scotland (Benton and Walker 1985), the Lower Maleri Formation in India (Kutty and Sengupta 1989), the Argana Formation in Morocco (Jalil 1996), the Pebbly Arkose Formation in Zimbabwe (Raath 1996), and the Makay Formation in Madagascar (Flynn

et al. 1999b; Langer et al. 2000), as well as various strata in the western United States and on the Atlantic Coast of both the United States and Canada (Olsen et al. 1989; Long and Murry 1995; Hunt et al. 1998; Lucas 1998).

Interestingly, while saurischian dinosaurs are abundant in Carnian strata and became the dominant component of various Norian faunas, ornithischians are barely represented through this time interval. *Pisanosaurus mertii*, from the Ischigualasto Formation, is the sole reasonably well known Triassic member of the group, which only achieved higher abundance and diversity during Early Jurassic times (Weishampel and Norman 1989).

Definition and Diagnosis

Saurischia is here defined as a stem-based taxon including all dinosaurs that share a more recent common ancestor with *Allosaurus* than with *Stegosaurus*. Accordingly, this clade can be diagnosed by the following synapomorphies: narial fossa expanded in the rostroventral corner of the naris; subnarial foramen; lacrimal folds over the caudal and/or dorsocaudal part of the antorbital fenestra; articular facet for the atlas in axial intercentrum concave, with upturned lateral borders; neural arch of cranial cervical vertebra with a marked concavity between the postzygapophyses and the caudodorsal corner of the centrum (chonoa); centra of postaxial cranial cervical vertebrae (3–5) longer than that of the axis; epipophyses on the caudal cervical vertebrae (6–9); hyposphene-hypantrum articulation in dorsal vertebrae; expanded transverse processes of sacral vertebrae roofing the space between adjacent ribs; distal carpal 5 absent; first phalanx of manual digit I twisted and the longest nonungual phalanx of the manus; well-developed supracetabular crest, accounting for more than 0.3 of the iliac acetabulum depth; and the medioventral lamina of the ischium restricted to the proximal third of the bone.

Anatomy

Most basal saurischians are known from incomplete postcranial remains. Exceptions are *Herrerasaurus ischigualastensis* and

TABLE 2.1
Basal Saurischia

	<i>Occurrence</i>	<i>Age</i>	<i>Material</i>
Dinosauria Owen, 1842			
Saurischia Seeley, 1888			
Herrerasauridae			
Herrerasaurus Reig, 1963 (= <i>Ischisaurus</i> Reig, 1963; <i>Freguellisaurus</i> Novas, 1986)			
H. ischigualastensis Reig, 1963 (including <i>Ischisaurus cattoi</i> Reig, 1963; <i>Freguellisaurus ischigualastensis</i> Novas, 1986)	Ischigualasto Formation (San Juan), Argentina	Carnian	Various partial skeletons, including a complete skull and mandible
Staurikosaurus Colbert, 1970			
S. pricei Colbert, 1970	Upper Santa Maria Formation (Rio Grande do Sul), Brazil	?late Ladinian or early Carnian	Partial postcranial skeleton with mandible
Unnamed clade			
Eoraptor Sereno, Forster, Rogers, et Monetta, 1993			
E. lunensis Sereno, Forster, Rogers, et Monetta, 1993	Ischigualasto Formation (San Juan), Argentina	Carnian	2 nearly complete skeletons
Eusaurischia Padian, Hutchinson, et Holtz, 1999			
Guaibasaurus Bonaparte, Ferigolo, et Ribeiro, 1999			
G. candelariensis Bonaparte, Ferigolo, et Ribeiro, 1999	Caturrita Formation (Rio Grande do Sul), Brazil	late Carnian	Partial postcranial skeleton and a fragmentary hindlimb
Saurischia incertae sedis			
Alwalkeria Chatterjee et Creisler, 1994 (= <i>Walkeria</i> Chatterjee, 1986)			
A. maleriensis (Chatterjee, 1986) (= <i>Walkeria maleriensis</i> Chatterjee, 1986)	Lower Maleri Formation (Andhra Pradesh), India	Carnian–Norian	Partial skull and postcranial remains
Chindesaurus Long et Murry, 1995 (including <i>Caseosaurus</i> Hunt, Lucas, Heckert, Sullivan, et Lockley, 1998)			
C. bryansmalli Long et Murry, 1995 (including <i>Caseosaurus crosbyensis</i> Hunt, Lucas, Heckert, Sullivan, et Lockley, 1998)	Petrified Forest Formation (Arizona); Bull Canyon Formation (New Mexico); Tecovas Formation (Texas), United States	late Carnian–early Norian	Partial postcranial skeleton and various isolated bones
Dinosauria incertae sedis			
Aliwalia Galton, 1985f			
A. rex Galton, 1985f	Lower Elliot Formation (Cape Province), South Africa	late Carnian or early Norian	Partial femur and ?maxilla
Unnamed dinosaur (= Herrerasauria incertae sedis Galton, 1985a)	Middle Stubensandstein (Baden-Württemberg), Germany	middle Norian	Proximal femur
Possible Dinosauria			
Saltopus Huene, 1910			
S. elginensis Huene, 1910	Lossiemouth Sandstone Formation (Grampian), Scotland	late Carnian	Partial postcranial skeleton
Spondylosoma Huene, 1942			
S. absconditum Huene, 1942	Upper Santa Maria Formation (Rio Grande do Sul), Brazil	?late Ladinian or early Carnian	Various postcranial remains
Nomina dubia		Material	
<i>Agnosphitys cromhallensis</i> Fraser, Padian, Walkden, et Davis, 2002		Isolated maxilla, ilium, humerus, and astragali	
<i>Teyuwasu barberenai</i> Kischlat, 1999		Right femur and tibia	
<i>Thecospondylus horneri</i> Seeley, 1882		Internal mold of sacrum	

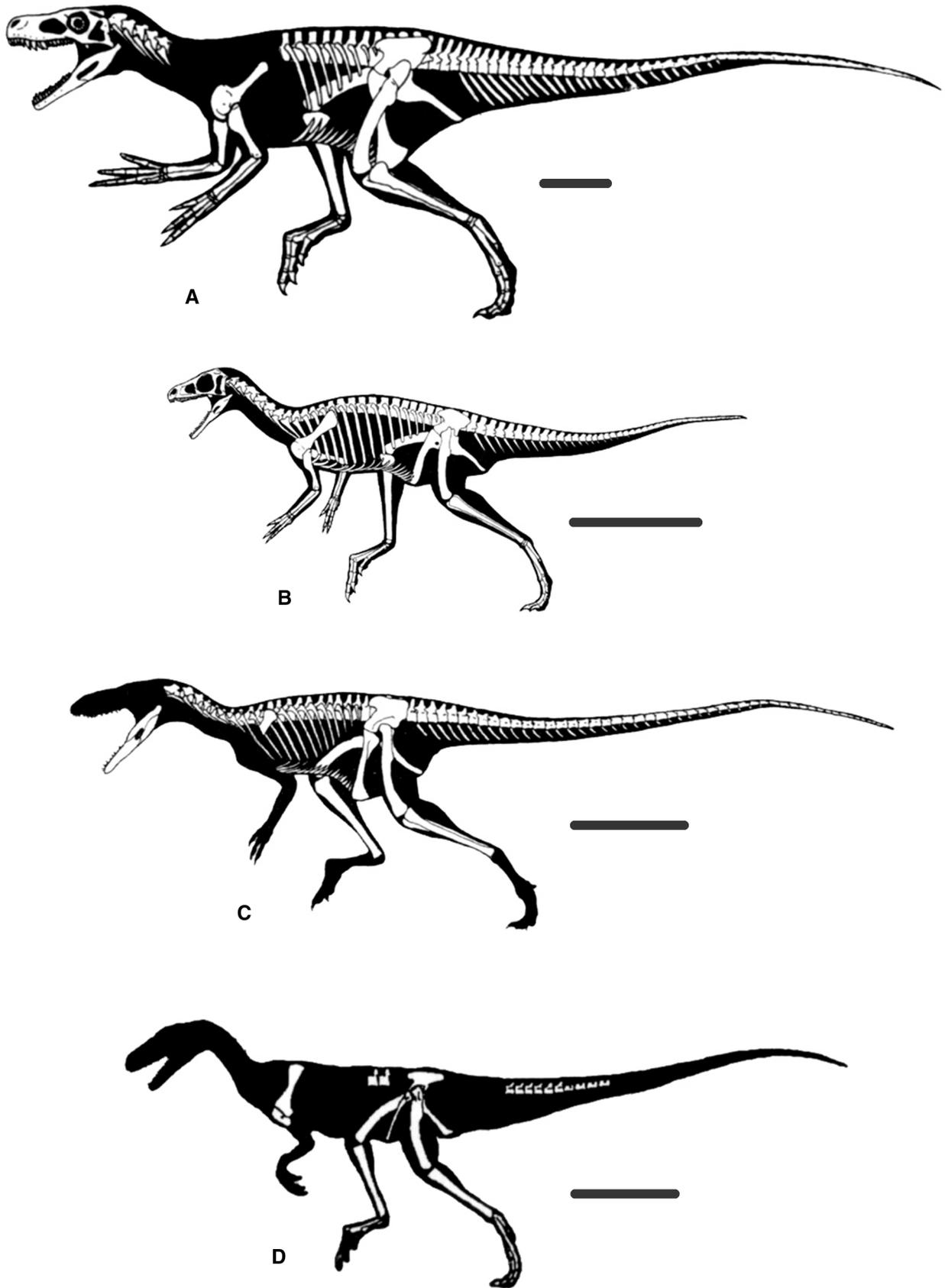


FIGURE 2.1. Body silhouettes of basal saurischians: A, *Herrerasaurus ischigualastensis*; B, *Eoraptor lunensis*; C, *Staurikosaurus pricei*; D, *Guaibasaurus candelariensis*. Scale = 25 cm. (A after Sereno and Novas 1992; B after Sereno et al. 1993; C after Novas 1997a.)

Eoraptor lunensis (fig. 2.1A–B), in which the complete skull and postcranium are known. *Staurikosaurus pricei* and *Guaibasaurus candelariensis* (fig. 2.1C–D) are known from reasonably complete postcranial remains. Where relevant, this section also includes comments on the anatomy of some little-known Late Triassic putative dinosaurs or saurischians, including *Agnosphitys cromhallensis*, *Aliwalia rex*, *Alwalkeria maleriensis*, *Chindesaurus bryan-smalli*, *Saltopus elginensis*, and *Spondylosoma absconditum*.

Skull and Mandible

Among basal saurischians complete skull material is known for *Herrerasaurus* and *Eoraptor*. In addition, fragmentary upper jaws have been assigned to *Aliwalia*, *Alwalkeria*, and *Agnosphitys*, and complete mandibles or portions of the lower jaw are known for *Herrerasaurus*, *Eoraptor*, *Staurikosaurus*, and *Alwalkeria*. In *Herrerasaurus*, *Eoraptor*, and *Staurikosaurus* the head is about the same length as the femur, a size relation apparently also found in *Alwalkeria* (Chatterjee 1987).

The skull of *Herrerasaurus* (fig. 2.2A–B) is slender, with a particularly narrow snout that is almost as deep as the back of the skull. In *Eoraptor* (fig. 2.2H) the skull is shorter, and its caudal portion is much deeper than the rostrum. The premaxilla of *Herrerasaurus* is deep, with a broad laterocaudal process that extends between the maxilla and the nasal, excluding the former from the margins of the external naris. The external naris is not particularly large but bears a well-developed narial fossa. In *Eoraptor*, on the other hand, the external naris occupies a much larger portion of the premaxilla, and the laterocaudal process of that bone is thinner. Both *Eoraptor* and *Herrerasaurus* possess a subnarial foramen, but that of *Herrerasaurus* is much smaller (Fraser et al. 2002) and does not open at the ventral surface of the narial fossa as in most saurischians (Galton 1984b; Madsen 1976a). Instead, it is placed on the lateral surface of the skull, at the lower end of the premaxilla-maxilla contact, almost forming a row with the nutrient foramina of these bones. In addition, above its subnarial foramen *Herrerasaurus* bears a premaxilla-maxilla fenestra (Serenó and Novas 1993) piercing the skull to the premaxillary palate, a feature suggested to represent an autapomorphy of the taxon (Serenó and Novas 1993). No other basal dinosaur is known to possess such a structure, but similar apertures are seen in crurotarsan archosaurs (Gower 2000). In *Eoraptor* the toothless and concave ventral margin of the premaxilla-maxilla contact forms a subnarial gap below the subnarial foramen (fig. 2.2I). A similar condition is seen in coelophysoid theropods (Rowe 1989) and has also been described for *Alwalkeria*. The robust maxilla of *Herrerasaurus* possesses a convex cranial margin and a tapering caudal ramus, whereas that of *Eoraptor* is thinner and has a clear rostroventral projection. Its lateral surface bears a well-developed ridge between the antorbital fenestra and the row of nutrient foramina that is not evident in *Herrerasaurus* and *Alwalkeria*. For its robustness and general morphology (tapering caudal ramus) the large isolated maxilla attributed to *Aliwalia* resembles that of *Herrerasaurus* more than it does that of other basal saurischians. It lacks any clear dinosaur synapomorphies, however, and cannot be safely assigned to the group. The maxillary antorbital fossa of *Eoraptor*, as well as, apparently, that of *Alwalkeria*, is much larger than that of *Herrerasaurus*.

The nasals of basal saurischians are elongate, accounting for about half the length of the skull. Each of those of *Eoraptor* contributes to the dorsal margin of the antorbital fenestra and

possesses a caudolateral process that envelops part of the rostral ramus of the lacrimal. In contrast, the lateral margin of each nasal of *Herrerasaurus* is straight and completely separated from the antorbital fenestra by projections of maxilla and lacrimal. The lateral margin of the lacrimal of both *Eoraptor* and *Herrerasaurus* folds over the caudodorsal portion of the antorbital fenestra. The lacrimal of *Eoraptor* is L-shaped, with a long, vertical ventral ramus, whereas that of *Herrerasaurus* is short and inclined. The supratemporal fenestra of *Herrerasaurus* forms a deep fossa excavating frontal, postorbital, and parietal. The parietal wings are directed caudolaterally and slightly ventrally and articulate to the dorsal borders of supraoccipital and paroccipital processes. Sclerotic plates have been reported for *Herrerasaurus* (Serenó and Novas 1993) but not for *Eoraptor*, which bears large orbits. In fact, if the latter does not represent a juvenile trait, as suggested by Bonaparte (1996b), it might be the single autapomorphic trait of *Eoraptor* recognized so far, the original diagnosis of which (Serenó et al. 1993) includes only features of broad distribution among basal saurischians. The caudal ramus of the jugal is forked in both *Eoraptor* and *Herrerasaurus*. That of *Eoraptor* has, however, a more concave ventral margin, which projects the craniomandibular joint well below the maxillary tooth line. The jugal of *Herrerasaurus* has a marked lateral ridge, and its expanding cranial ramus forms the caudoventral corner of the antorbital fenestra, preventing a lacrimal-maxilla contact. In *Eoraptor*, on the other hand, the lacrimal contacts the maxilla at the caudoventral corner of the antorbital fenestra. In *Herrerasaurus* the squamosal possesses a short subquadratic ventral process that expands cranially into the infratemporal fenestra but does not contact the quadratojugal. Such a subquadratic process is not seen in the squamosal of *Eoraptor*, which might contact the quadratojugal. The quadratojugal of *Herrerasaurus* bears a medially deflected ventral portion that covers the quadrate caudally but does not contribute to the jaw joint. A quadrate foramen laterally bound by the quadratojugal is seen in both *Eoraptor* and *Herrerasaurus*. In *Herrerasaurus* the quadrate forms a smooth articulation for the paroccipital process and a transversally broad ventral articulation for the lower jaw.

In the palate of *Herrerasaurus* the vomers form a vertical median plate on the rostral part of the skull. The pterygoids are laterally constricted in their rostral part, where they form a vertically expanded symphysis, contacting the vomers rostrally and the palatines laterally. Caudally, each pterygoid slopes laterally, forming a broad palate that receives the ectopterygoid and forms the medial border of the postpalatine fenestra. Caudal to this, the quadrate ramus projects caudolaterally to meet the epipterygoid, quadrate, and basisphenoid. The palatine possesses a depressed dorsal surface and forms the palate between the choanae and the postpalatine fenestra. The ectopterygoid is a simple structure bridging the gap between the jugal and pterygoid. Its medial margin is slightly expanded and overlaps the pterygoid. As described by Serenó and Novas (1993), the ventral surface of the ectopterygoid of *Herrerasaurus* is not exposed, and the presence of a ventral recess cannot be confirmed. Such a structure is, however, apparently found in *Eoraptor* (Serenó et al. 1993).

The laterosphenoid of *Herrerasaurus* is set ventral to the parietal and rostral to the prootic, and its smooth rostral tip articulates to the frontal and postorbital. The long and narrow parasphenoid process extends rostrally between the pterygoid palates. It joins the body of the basisphenoid between the basiptyergoid processes, which project rostroventrally and slightly laterally from a central depression in the ventral surface of the bone. The basisphenoid-basioccipital contact forms

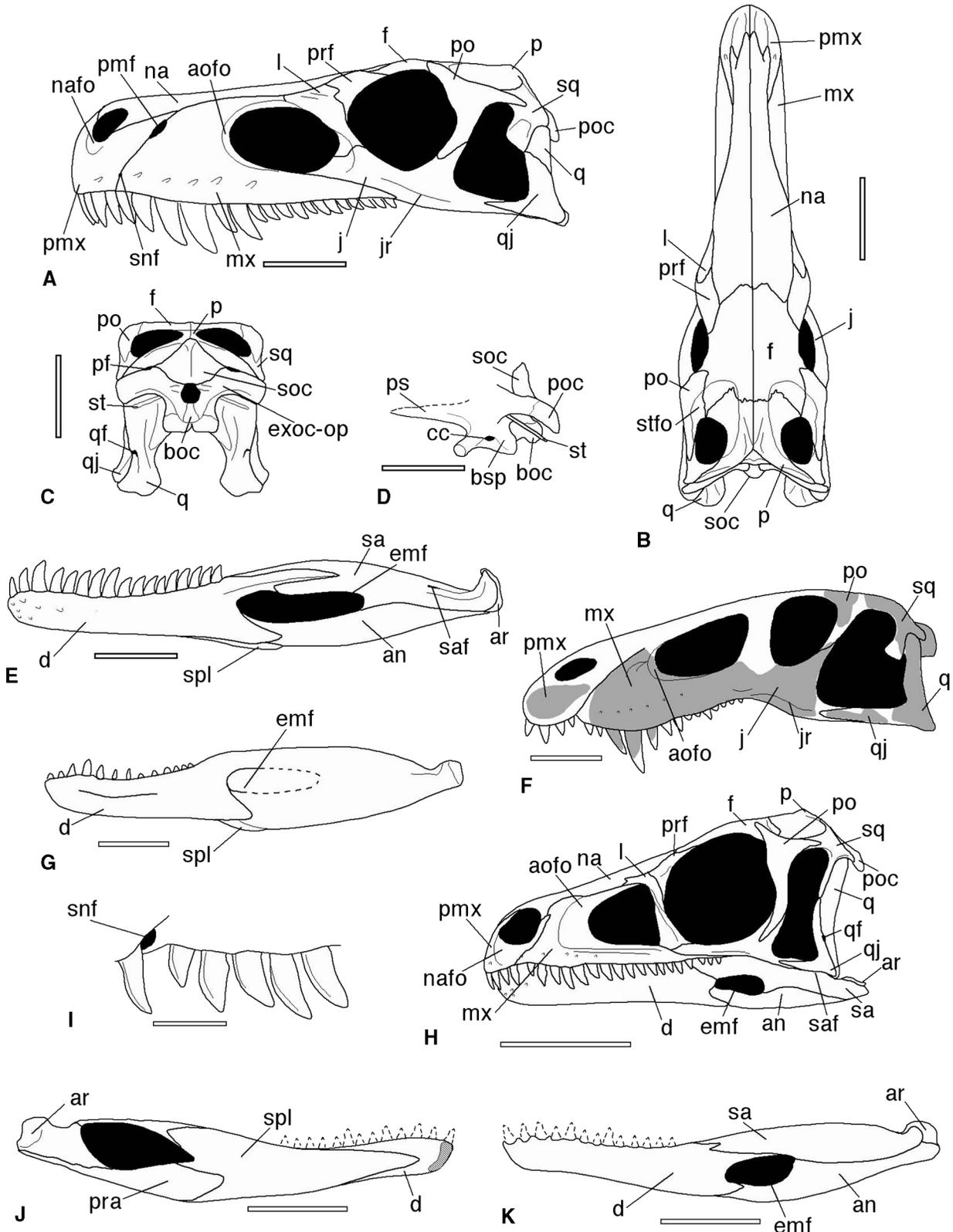


FIGURE 2.2. Skull and mandible. A–E, *Herrerasaurus ischigualastensis*: A–C, skull in A, lateral, B, dorsal, and C, caudal aspects; D, lateral aspect of braincase; E, left mandible in lateral aspect. F–G, *Herrerasaurus ischigualastensis* (= *Frenguellisaurus ischigualastensis*): F, skull (preserved parts in gray); G, mandible. H, I, *Eoraptor lunensis*: H, skull in right lateral aspect; I, right distal premaxillary and mesial maxillary teeth in lateral aspect (reversed). J, K, *Staurikosaurus pricei*: left mandibular ramus in J, medial, and K, lateral aspects. Scale = 5 cm (A–E, H, J, K), 10 cm (F, G), 1 cm (I). (A–E after Sereno and Novas 1993; F, G, after Novas 1986; H, I, after Sereno et al. 1993; J, K, after Colbert 1970.)

large basal tubera. The basioccipital forms the occipital condyle together with the exoccipitals, which are co-ossified to the opisthotics and bear articular facets for the proatlas on the border of the foramen magnum. Each opisthotic has two ridges on its lateral surface that separate the carotid canal rostrally, the foramen for the cranial nerve XII caudally, and the otic apertures in the middle. Each paroccipital process is directed caudolaterally and slightly ventrally. Together with each parietal wing and the supraoccipital it forms a fissurelike posttemporal fenestra that possibly serves the exit of the occipital ramus of the ophthalmic artery. The triangular supraoccipital bears a marked median ridge and is lodged between the parietal wings. A slender stapes extends ventrolaterally from the fenestra ovalis.

The dentary of most basal saurischians occupies a little more than half the length of each mandibular ramus (fig. 2.2E, G, H, K). In most basal saurischians, including *Herrerasaurus* and *Staurikosaurus* (fig. 2.2J), the dentary symphysis is restricted to the distal end of the bone. In *Alwalkeria*, however, it is more caudally extended than that of any other known basal dinosaur, even surpassing the characteristic symphyseal elongation of basal ornithischians (Serenó 1991b). In *Herrerasaurus* the dentary is covered medially by the splenial and forks caudally to envelop the external mandibular fenestra, which is longer in that taxon than in *Staurikosaurus* or *Eoraptor*. The caudoventral process of the dentary of *Herrerasaurus* overlaps the angular laterally, while the caudodorsal process, which is T-shaped in cross section, fits into a smooth slot in the surangular to form a movable articulation. As in most archosaurs (Walker 1961, 1964), the rostral ramus of the angular penetrates between dentary and splenial, but in *Herrerasaurus* its lateral and medial surfaces are polished for a sliding articulation with these bones. The three movable articulations mentioned above form the well-developed intra-mandibular joint of *Herrerasaurus*. In *Staurikosaurus*, despite the poor preservation of its lower jaw, it is possible to recognize a similar movable joint system, as indicated by the sliding articulation between the tongue-like rostral process of the angular and a smooth ventral groove on the caudal process of the splenial. *Eoraptor*, on the other hand, lacks any evidence of an intra-mandibular joint. In *Herrerasaurus* the ventral portion of the surangular is overlapped by the angular, and its caudal portion forms the lateral part of the craniomandibular articulation. The prearticular lies on the internal side of the mandible. It forms the ventral margin of the adductor fossa and the caudal margin of the internal mandibular fenestra. The articular forms the medial part of the jaw articulation and bears an expanded medial prong that is also seen in *Staurikosaurus*.

Herrerasaurus has 4 premaxillary, 17–18 maxillary, and about 16 dentary teeth, all of which are serrated, laterally compressed, and caudally curved. The middle portion of the maxillary series bears long caniniform teeth (fig. 2.2F). Similarly large, serrated, and laterally compressed teeth are seen in the maxilla assigned to *Aliwalialia*, whereas the poorly preserved mandibular teeth of *Staurikosaurus* are like those of other carnivorous taxa. The upper jaw of *Eoraptor*, on the other hand, has a heterodont dentition composed of 4 premaxillary and 18 maxillary teeth. Pre-maxillary and rostral maxillary teeth are lanceolate, resembling those of basal sauropodomorphs. Distal maxillary teeth are shorter and caudally curved, as is usual for theropods. A similar arrangement is seen in basal sauropodomorphs (Gauffre 1993a; Langer et al. 1999b), as well as in *Alwalkeria*, in which the tooth crowns from the rostral part of the jaws are slender, while more distal teeth elements are distally curved. Unlike those of all other basal dinosaurs, however, the teeth of *Alwalkeria* lack serration.

Postcranial Skeleton

AXIAL SKELETON

Although no complete vertebral series is known for basal saurischians, their axial anatomy is well known based on some well-preserved specimens. This is the case with *Staurikosaurus* and especially *Eoraptor*, almost the entire vertebral columns of which have been found. For *Herrerasaurus* only partial vertebral series are known, and the vertebral column is the least understood part of its osteology. Its cervical-dorsal transition and the cranial half of the dorsal series in particular are not well known, and it is not possible to determine the number of presacral vertebrae. For both *Eoraptor* and *Staurikosaurus*, on the other hand, a count of 24 presacral elements, 9–10 of them corresponding to cervical vertebrae, has been suggested (Galton 1977a; Sereno et al. 1993; Novas 1997a). This can be assumed for basal saurischians in general, the number of whose sacral elements varies between 2 and 3. *Herrerasaurus* and *Staurikosaurus* have been reconstructed with about 50 caudal vertebrae, but the tail of *Eoraptor* was apparently shorter, with little more than 40 vertebrae (Novas 1997a). In addition, incomplete portions of the vertebral column are known for *Alwalkeria*, *Chindesaurus*, *Guaibasaurus*, *Saltopus*, and *Spondylosoma*.

The proatlas of *Herrerasaurus* (fig. 2.3A) is transversely compressed and bears a thin ventral margin. The subcircular odontoid process (the atlantal centrum) is fused to the axis and fits into a pit in the occipital condyle. The articular facet for the occipital condyle in the atlantal intercentrum is cup-shaped and faces craniodorsally. Caudally the bone has lateral depressions for a pair of single-headed ribs. The atlantal neural arches have long epiphyses projecting caudal to the postzygapophyses. The axial centrum is fused to its intercentrum and neural arches (fig. 2.3A) and bears low parapophyses and diapophyses for the articulation of double-headed ribs. The intercentrum is much broader than the centrum, and its articulation for the atlantal intercentrum is markedly concave. The neural arches form a broad neural canal and have short and broad prezygapophyses, between which the neural spine projects slightly (fig. 2.3B). The caudal portion of the neural spine is divided into two laminae, which are continuous to the epiphyses.

The postaxial cranial cervical vertebrae (3–6) of basal saurischians (figs. 2.3C, J; 2.4D) are elongate, and their centra are usually about 25% longer than those of the axis and/or cranial dorsal vertebrae. In *Staurikosaurus* the putative third cervical vertebra (Galton 1977a) is the longest, while in *Herrerasaurus* the length of the centra increases between cervical 3 and 6 (Serenó and Novas 1993). The parapophyses are always set on the cranioventral corner of the centrum, while the diapophyses change their position along the series. In the third cervical of *Herrerasaurus* these diapophyses form faint ridges on the cranial portion of the vertebra, while in more caudal elements of *Herrerasaurus*, *Eoraptor*, and *Staurikosaurus* they project as ventrolaterally directed flanges overhanging the centrum laterally. Ridge-like epiphyses are present in postaxial cranial cervical vertebrae of *Herrerasaurus*, *Staurikosaurus*, *Eoraptor*, and *Spondylosoma* and are more developed in the most cranial elements. Those of *Herrerasaurus* are, however, much more elongate and project caudal to the postzygapophyses. Epiphyses are also present in the caudal cervical vertebrae (7–9) of *Herrerasaurus* and *Eoraptor*. In most basal saurischians these vertebrae are not significantly longer than the cranial dorsal elements (fig. 2.3K). Their parapophyses and diapophyses are displaced caudally and dorsally in relation to the position in cranial cervical vertebrae.

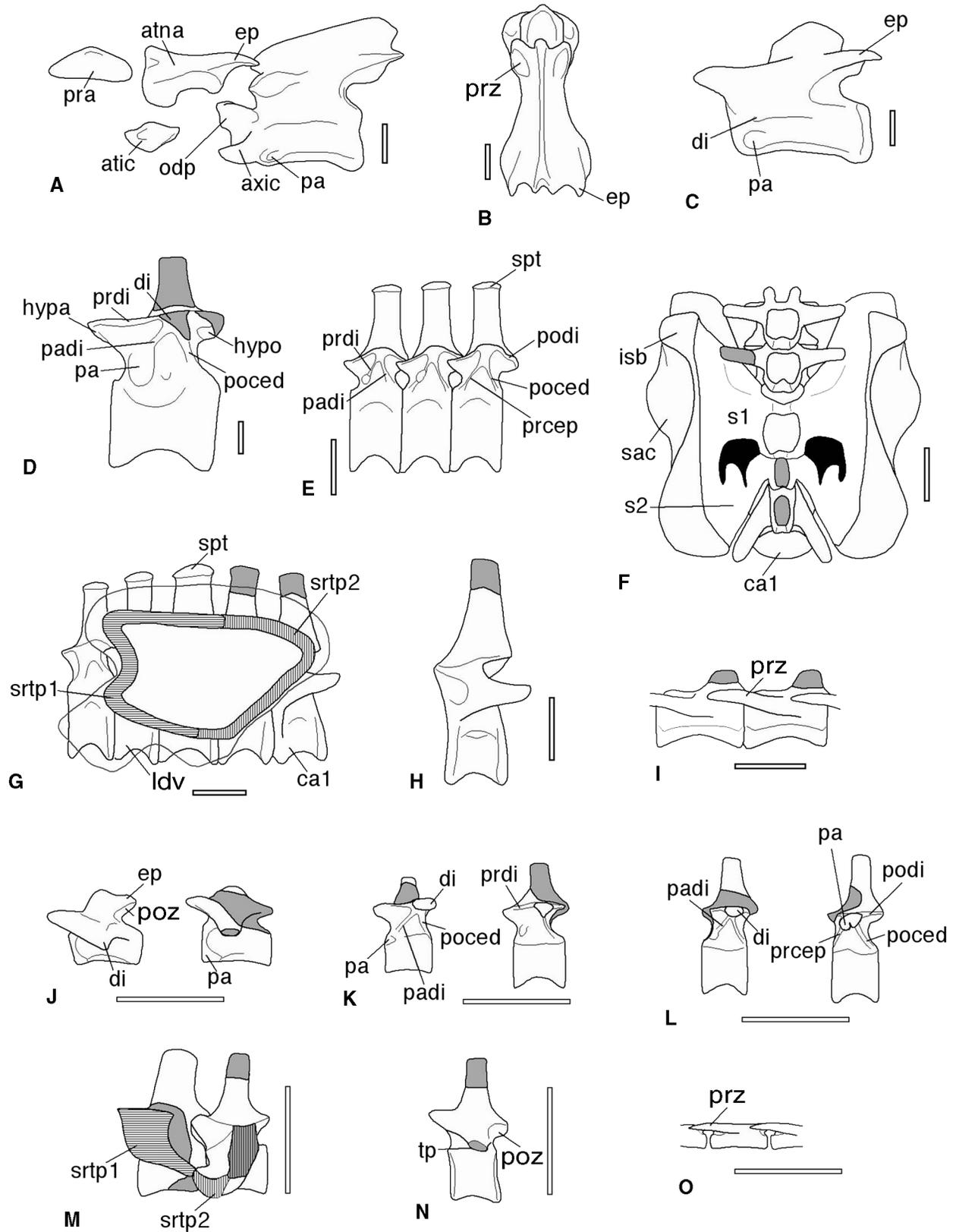


FIGURE 2.3. Vertebral column. A–I, *Herrerasaurus ischigualastensis*: A, atlas and axis in lateral aspect; B, axis in dorsal aspect; C, third cervical vertebra in lateral aspect; D, mid-dorsal vertebra in lateral aspect; E, caudal dorsal series in lateral aspect; F, G, sacrum in F, dorsal, and G, lateral (with an outline of the ilium) aspects; H, proximal caudal vertebra in lateral aspect; I, most distal tail vertebrae in lateral aspect. J–O, *Staurikosaurus pricei*: lateral aspect of J, cranial cervical vertebrae; K, caudal cervical and cranial dorsal vertebrae; L, caudal dorsal vertebrae; M, sacral vertebrae 1 and 2; N, proximal caudal vertebrae; and O, most distal caudal vertebrae. Scale = 1 cm (A–D), 5 cm (E–O). Nonpreserved portions in gray. (A–C after Sereno and Novas 1993; D–I after Novas 1994; J–O after Galton 1977a.)

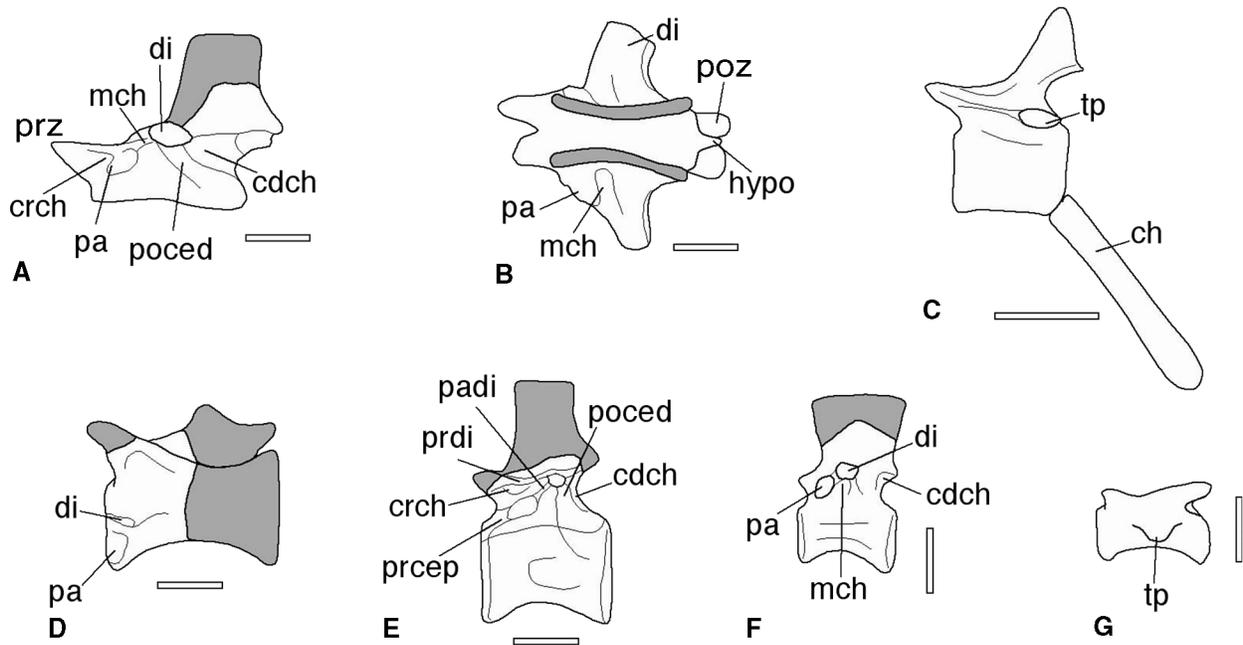


FIGURE 2.4. Vertebral column. A–C, *Guaibasaurus candeliariensis*: A, B, mid-dorsal neural arch in A, lateral, and B, ventral aspects; C, proximal caudal vertebra and chevron in lateral aspect. D–G, *Alwalkeria maleriensis*: lateral aspect of D, cervical, E, F, dorsal, and G, caudal vertebrae. Scale = 2 cm (A–C), 1 cm (D–G). Nonpreserved portions in gray. (A–C after Bonaparte et al. 1999; D–G after Chatterjee 1987.)

The parapophyses are usually set on the cranial end of the neurocentral joint, whereas the diapophyses project laterally, and robust laminae radiate from them. An exception is *Eoraptor*, none of whose 24 presacral vertebrae show marked lamination.

Dorsal vertebrae of all basal saurischians (figs. 2.3D, E, K, L; 2.4A, B, E, F) bear hyposphene-hypantrum auxiliary articulations. The parapophyses are placed on the cranial part of the neurocentral junction in more cranial elements. However, in more caudal vertebrae each of them is displaced caudodorsally along the lamina that links the cranioventral corner of the neural arch to the diapophysis until it merges to the diapophysis in the most caudal elements. The diapophyses are dorsally placed and project laterally. They are linked by robust laminae to the pre- and postzygapophyses and to the cranio- and caudoventral corners of the neural arches. These laminae define deep cranial, medial, and caudal chonoe (Welles 1984), which are characteristic of most basal saurischians. Exceptions are *Eoraptor* and *Guaibasaurus*, whose dorsal vertebrae lack precentroparapophyseal laminae. Most dorsal vertebrae of *Herrerasaurus* possess a certain degree of axial compression. This compression is such that the last dorsal vertebra is placed between the iliac preacetabular processes and its transverse processes articulate to the dorsal surface of the first sacral transverse processes. A less extreme version of this compression is seen in *Staurikosaurus* but not in other basal saurischians such as *Eoraptor*, *Guaibasaurus*, and *Alwalkeria*. In *Eoraptor* the neural spines of the caudal dorsal vertebrae are often axially expanded (Novas 1997), and those at the dorsal-sacrum transition bear well-developed spine tables. Spine tables are also present in the dorsal-sacrum transition of *Herrerasaurus* but not in *Staurikosaurus*. Double-headed ribs are present in the dorsal series of *Herrerasaurus*, and remains of a gastralia have also been reported for that taxon (Novas 1993).

Basal saurischians represent a transitional group in terms of sacral anatomy (fig. 2.3F, G, M). Some taxa retain the two-vertebrae sacrum of more basal archosaurs, whereas other forms have dorsal and/or caudal vertebrae incorporated into the sacral

series, approaching the condition of theropods and sauropodomorphs. However, in no basal saurischian are the sacral vertebrae fused together. *Herrerasaurus* has only two sacral elements, the first of which is axially compressed as the last dorsal vertebrae, while the second element is longer. In other basal saurischians, including *Staurikosaurus*, *Spondylosoma*, and *Chindesaurus*, none of the sacral vertebrae are axially shortened. In these forms the ribs of the two main sacral elements are L-shaped and deep, together forming a U-shaped structure that strongly articulates to the ilium. In *Herrerasaurus* the transverse processes are fused to the ribs in both sacral vertebrae, forming a complex structure fused to the ilium. In lateral aspect this structure is C-shaped in the first sacral vertebra, while that of the second element is almost its mirror image. Together they enclose the space between the ilium and the articulation of the two sacral centra, whose only external communication is through dorsal and ventral fenestrae. In dorsal aspect the transverse processes of *Herrerasaurus* are fan-shaped, expanding over the whole dorsomedial surface of the ilium. The two-vertebrae sacrum of *Saltopus* has similar fan-shaped transverse processes, but its ribs are not as deep as those of most basal saurischians. Among the basal saurischians with three sacral vertebrae *Eoraptor* possesses a dorsosacral element (Serenio et al. 1993), while a caudal vertebra has been added to the sacrum of *Staurikosaurus*, *Guaibasaurus*, and *Spondylosoma*. However, only in *Staurikosaurus* can this condition be clearly determined. *Contra* Galton (1977a), the vertebra caudal to the two main sacral elements has a robust transverse process that attached to the ilium, as indicated by a medial scar on the caudal rim of the postacetabular process of the bone.

Regarding the caudal vertebrae of basal saurischians (figs. 2.3H, I, N, O; 2.4C, G), the most cranial element of *Herrerasaurus* is axially compressed. Like the most caudal dorsal vertebra, it fits between the ilia, but its transverse processes are laterodistally directed and do not touch either the postacetabular process of those bones or the transverse processes or ribs of the second sacral. The neural spines of the most cranial tail vertebrae of

Staurikosaurus and *Herrerasaurus* are nearly vertical, while those of *Guaibasaurus* and *Eoraptor* are more distally oriented. More distal tail vertebrae are usually longer, but the extreme elongation seen in the midcaudal elements of *Saltopus* is not seen in any basal saurischian. In *Herrerasaurus* and *Staurikosaurus* the vertebrae of the rear of the tail have long prezygapophyses that overlap more than a quarter of the preceding centrum. Slightly elongate prezygapophyses are apparently also seen in *Eoraptor* (Sereno, pers. comm.) but not in *Alwalkeria* and *Chindesaurus*. The chevrons are proximally forked in *Herrerasaurus* but bear fused condyles in *Guaibasaurus*.

APPENDICULAR SKELETON

Among basal saurischians *Eoraptor* and *Herrerasaurus* have well-known appendicular skeletons. In addition, fragmentary portions of the pectoral girdle and/or forelimb of *Guaibasaurus*, *Staurikosaurus*, *Saltopus*, *Agnosphitys*, and *Spondylosoma* have also been excavated. The pelvic girdle and hindlimb of *Guaibasaurus* and *Staurikosaurus* are reasonably well known, and less complete remains of these elements are known for most other taxa discussed here.

The pectoral girdle of basal saurischians (fig. 2.5A, B) is formed of a co-ossified scapulocoracoid; no dermal elements have yet been recovered. The scapular blade of *Herrerasaurus* is strap-shaped, and only a subtle dorsal expansion is seen. The scapular blade forms an angle of about 90° with the dorsal margin of the acromion, a feature that is unique to this taxon. The scapular blade of *Guaibasaurus* is also long and slender, while that of *Eoraptor* is short and broad. Although not strong, their dorsal expansion is more substantial than that of the scapular blade of *Herrerasaurus*. The identification of the pectoral girdle and forelimb bones in *Staurikosaurus* and *Spondylosoma* is controversial (Galton 2000a), but their scapular blades are at least as dorsally expanded as that of *Guaibasaurus*. In *Herrerasaurus* and *Guaibasaurus* the ventral margin of the coracoid bears a caudal process that is separated from the glenoid by a notch.

In both *Herrerasaurus* (fig. 2.5C–G) and *Eoraptor* the length of the forelimb is slightly less than half the length of the hindlimb. In *Herrerasaurus* the proximal portion of the humerus is concave craniomedially and has an unusual, possibly autapomorphic (Sereno 1994) prominent medial tuberosity separated from the head by a cleft. The deltopectoral crest is continuous to the head and extends for 40% of the humeral length (measured at the point of major distal inflection), as seen in *Herrerasaurus*. That of *Eoraptor* is slightly shorter, extending for about 35% of the total length of the bone. The deltopectoral crests of *Saltopus* and *Spondylosoma* are, however, shorter than those of all well-known basal dinosaurs. According to Sereno (1994), the distal humerus of *Herrerasaurus* is highly autapomorphic. The lateral epicondyle has a circular pit on its lateral surface, whereas the medial epicondyle bears prominent cranial and caudal depressions and is separated from the saddle-shaped lateral condyle by a shallow groove. The ulna of *Herrerasaurus* has a prominent olecranon process, as well as a concave facet for the radius proximally on the lateral surface. Its convex distal surface shows a sliding articular facet for the smaller, concave proximal surface of the ulnare. The radial shaft is sigmoid in cranial aspect and bears a medial crest (= biceps tuberosity). The carpus of *Herrerasaurus* is composed of two proximal (radiale and ulnare) and five distal elements. The latter are the centrale, placed distally to the radiale-ulnare articulation, and distal carpals 1–4 (distal carpal 5 is apparently lost). Distal carpals 1–3 are small, and their distal articulations are no larger than the proximal surface of a medial

metacarpal. Distal carpal 4 is larger and articulates to the ulnare, distal carpals 2 and 3, and metatarsals IV and V.

The five-digit manus of *Eoraptor* and *Herrerasaurus* is more than half as long as the humerus plus the radius. Metacarpal III is the longest (as is digit III), and those medial to it are successively shorter. Extensor depressions are present in metacarpals I–III. Metacarpal I is slightly broader than the others, and that of *Eoraptor* is stouter than that of *Herrerasaurus*. Its lateral distal condyle, and to a lesser degree that of metacarpal II, expands farther distally than the medial condyle. Metacarpals IV and V are strongly reduced in both *Eoraptor* and *Herrerasaurus*. Those of *Herrerasaurus* are set on the palmar surface of metatarsals III and IV, respectively, while in *Eoraptor* they are mainly lateral to metatarsals III and IV. The nonungual phalanges of the functional digits (I–III) of both *Herrerasaurus* and *Eoraptor* distally bear ginglymoid condyles, collateral ligament pits, and dorsal extensor depressions. For *Herrerasaurus* the phalangeal formula of those digits is 2-3-4, and their penultimate phalanges are elongate, exceeding the length of the preceding metacarpal or phalanx. In *Eoraptor* this condition is not so clear, as indicated by the longer phalanx 1 of digit II. The unguis of *Herrerasaurus* are large, strongly curved, and transversely compressed, a condition not approached by those of *Eoraptor*. The single phalanx of digit IV of *Eoraptor* and *Herrerasaurus* is merely a spur of bone, while digit V lacks phalanges altogether.

The pelvis of basal saurischians (fig. 2.6) usually has a deep and robust ilium bearing a short preacetabular process. The process does not exceed the cranial projection of the pubic peduncle, which, *contra* Huene (1910a), is also the case in *Saltopus*. In addition, in forms such as *Herrerasaurus*, *Staurikosaurus*, and *Chindesaurus* the preacetabular process has a truncated and rugose cranial border that probably allocated the origin of *M. iliobtibialis cranialis* (= avian *M. sartorius*, Vanden Berge and Zweers 1993). From that attachment area a robust lateral ridge extends caudoventrally, bordering the caudal margin of the preacetabular embayment, to reach the craniodorsal border of the acetabulum. The length of the postacetabular process, on the other hand, varies among basal saurischians. In *Eoraptor* and *Staurikosaurus* it is remarkably short, whereas in *Guaibasaurus* and *Chindesaurus* it is rather long, and in *Herrerasaurus* it is intermediate between those two. In *Herrerasaurus* and *Staurikosaurus* *M. caudofemoralis brevis* originates from a mainly vertical area on the ventrolateral surface of the postacetabular process, bounded dorsally by the faint *brevis* shelf and ventromedially by the ventral margin of the bone. In other basal saurischians, including *Eoraptor*, *Guaibasaurus*, and *Chindesaurus*, *M. caudofemoralis brevis* originates from a more lateromedially expanded concave area (the *brevis* fossa). This fossa is bounded medially by the ventral margin of the postacetabular process (equivalent to the medial blade *sensu* Currie and Zhao 1993a) and laterally and dorsally by a marked lateral ridge (the spine *sensu* Welles 1984) that is homologous to the *brevis* shelf of *Staurikosaurus* and *Herrerasaurus*. In addition, the ridge on the medial surface of the ilium of *Chindesaurus* does not mark the medial margin of the *brevis* fossa. Instead, it dorsally bounds the articulation area of the caudal sacral vertebrae, as in *Herrerasaurus* and basal sauropodomorphs (Young 1942a; Galton 2000a; Benton et al. 2000b). A well-developed supracetabular crest is seen in most basal saurischians, and that of *Eoraptor* extends farther through the postacetabular process, to connect to the dorsolateral margin of the *brevis* fossa. In most basal saurischians the acetabulum is semiperforated, but that of *Guaibasaurus* is almost fully closed. The pubic peduncle of basal saurischians is usually long, and there is a marked ventral

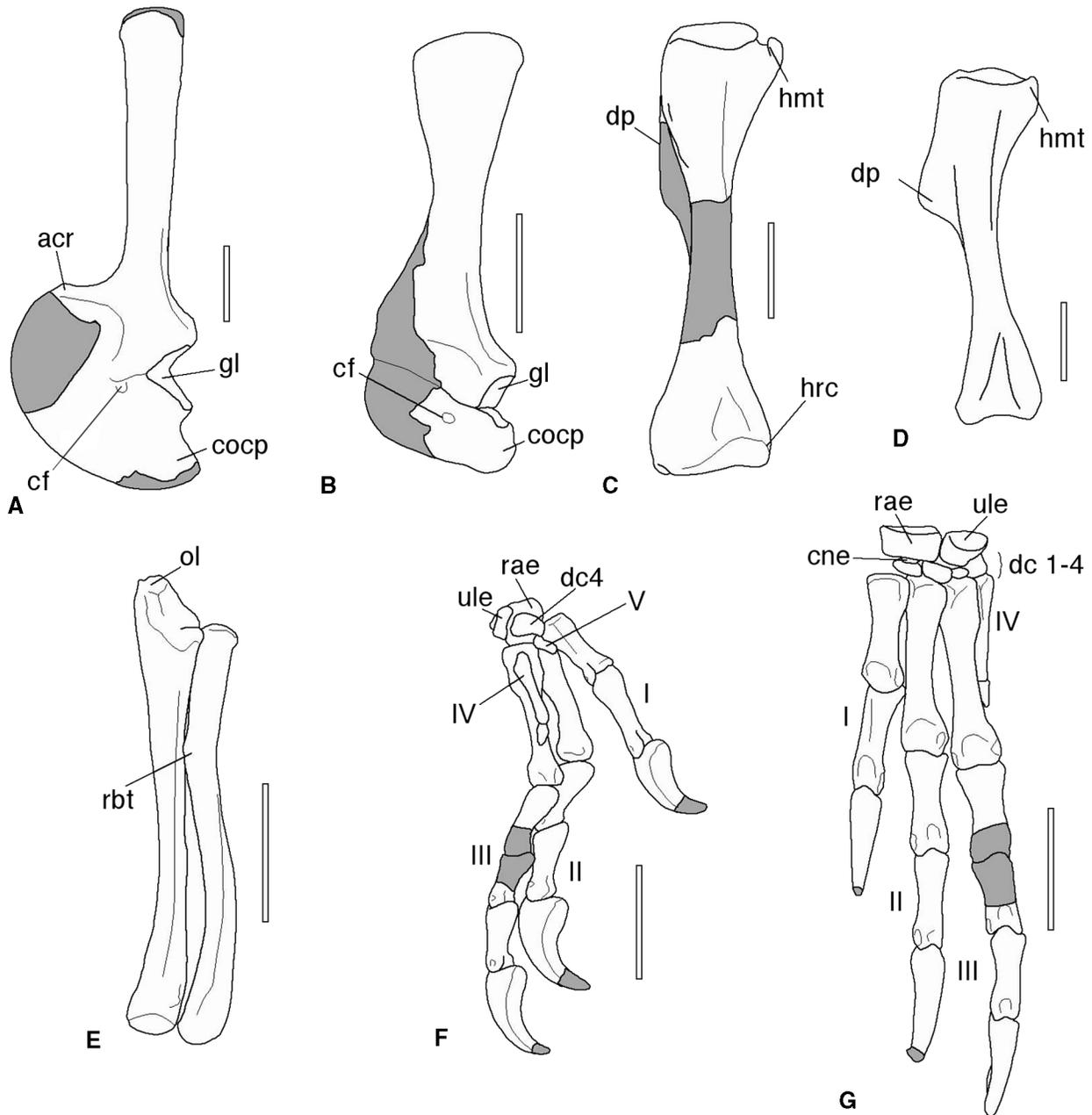


FIGURE 2.5. Pectoral girdle and forelimb. A, *Herrerasaurus ischigualastensis*, left scapulocoracoid in lateral aspect. B, *Guaibasaurus candeleriensis*, partial left scapulocoracoid in lateral aspect. C–G, *Herrerasaurus ischigualastensis*: C, left humerus in caudal aspect; D, left humerus of *Herrerasaurus ischigualastensis* (formerly *Ischisaurus cattoi*) in caudal aspect; E, left radius and ulna in cranial aspect; F, G, left carpus and manus in F, lateral, and G, cranial aspects. Scale = 5 cm (A, E–G), 4 cm (B, C), 3 cm (D). Nonpreserved portions as in fig. 2.3. (A after Sereno 1994 and Brinkman and Sues 1987; B after Bonaparte et al. 1999; C, E–G, after Sereno 1994; D after Reig 1963.)

expansion in *Staurikosaurus* and *Chindesaurus*. The ischial peduncle is shorter and vertically oriented, except in *Eoraptor*, in which it is well expanded caudally.

In most basal saurischians the pubis possesses a knoblike ambiens process on the proximolateral surface of the bone. The obturator process is short and composed of a thin medial lamina that forms the proximal part of the pubic symphysis. The pubic shaft of these dinosaurs, on the other hand, is rather distinct from one another, and that of *Herrerasaurus* is unique. The robust lateral margin of its retroverted pubis is caudally folded, and the cross section of the joint shafts is U-shaped. The folding is more extreme at the distal end of the bone, forming a bootlike

expansion that is markedly compressed in cranial aspect. This condition is approached by the pubis of *Staurikosaurus*, the distal part of whose lateral margin is also caudally folded, but not to the extreme seen in *Herrerasaurus*. In addition, the pubis of *Staurikosaurus* is distinctive among basal dinosaurs because of a marked bevel on its mediolateral corner (Novas 1993). In *Eoraptor* and *Chindesaurus* the pubis is less modified, with no sign of the caudal folding of the lateral margin. In most basal saurischians the acetabular margin of the ischium bears a well-defined antitrochanter that continues dorsally onto the ilium (Novas 1996a; Fraser et al. 2002). Ventrally the obturator process is composed of a medioventral lamina that extends along the proximal

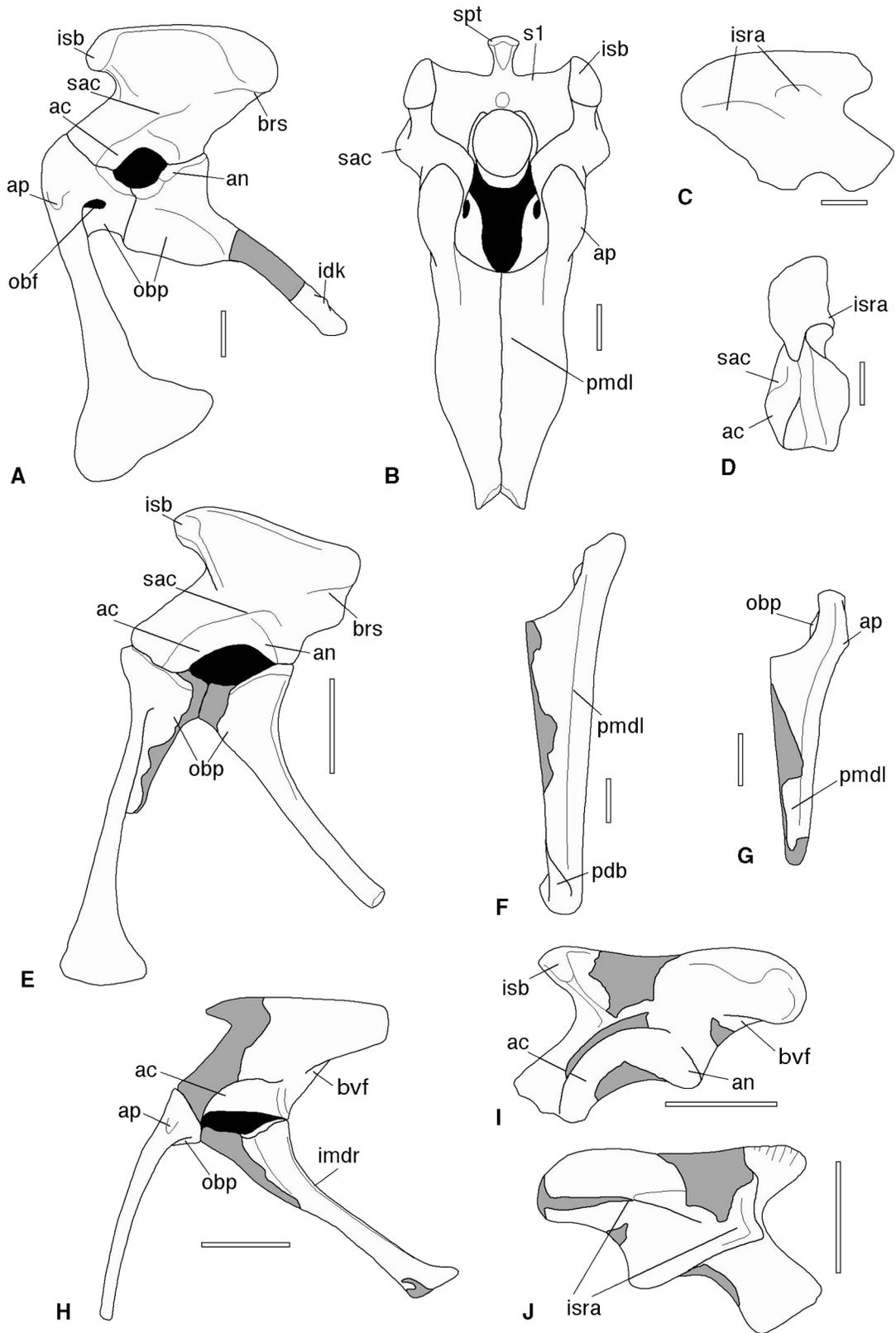


FIGURE 2.6. Pelvis. A–D, *Herrerasaurus ischigualastensis*: A–B, pelvis in A, left lateral, and C, cranial aspects; C, D, right ilium (reversed) in H, medial, and I, caudal aspects. E–F, *Staurikosaurus pricei*: E, pelvis in left lateral aspect; F, right pubis (reversed) in cranial aspect. G–H, *Guaibasaurus candelariensis*: G, partial right pubis (reversed) in cranial aspect; H, partial right (reversed) pelvis in lateral aspect. I, J, *Chindesaurus bryansmalli*: right ilium (reversed) in I, lateral, and J, medial aspects. Scale = 5 cm (A–C, E, I, J), 2 cm (D, F), 4 cm (G, H). Nonpreserved portions in gray. (A–C, F, after Novas 1993; D after Novas 1992a; E after Colbert 1970; G, H, after Bonaparte et al. 1999; I, J, after Long and Murry 1995.)

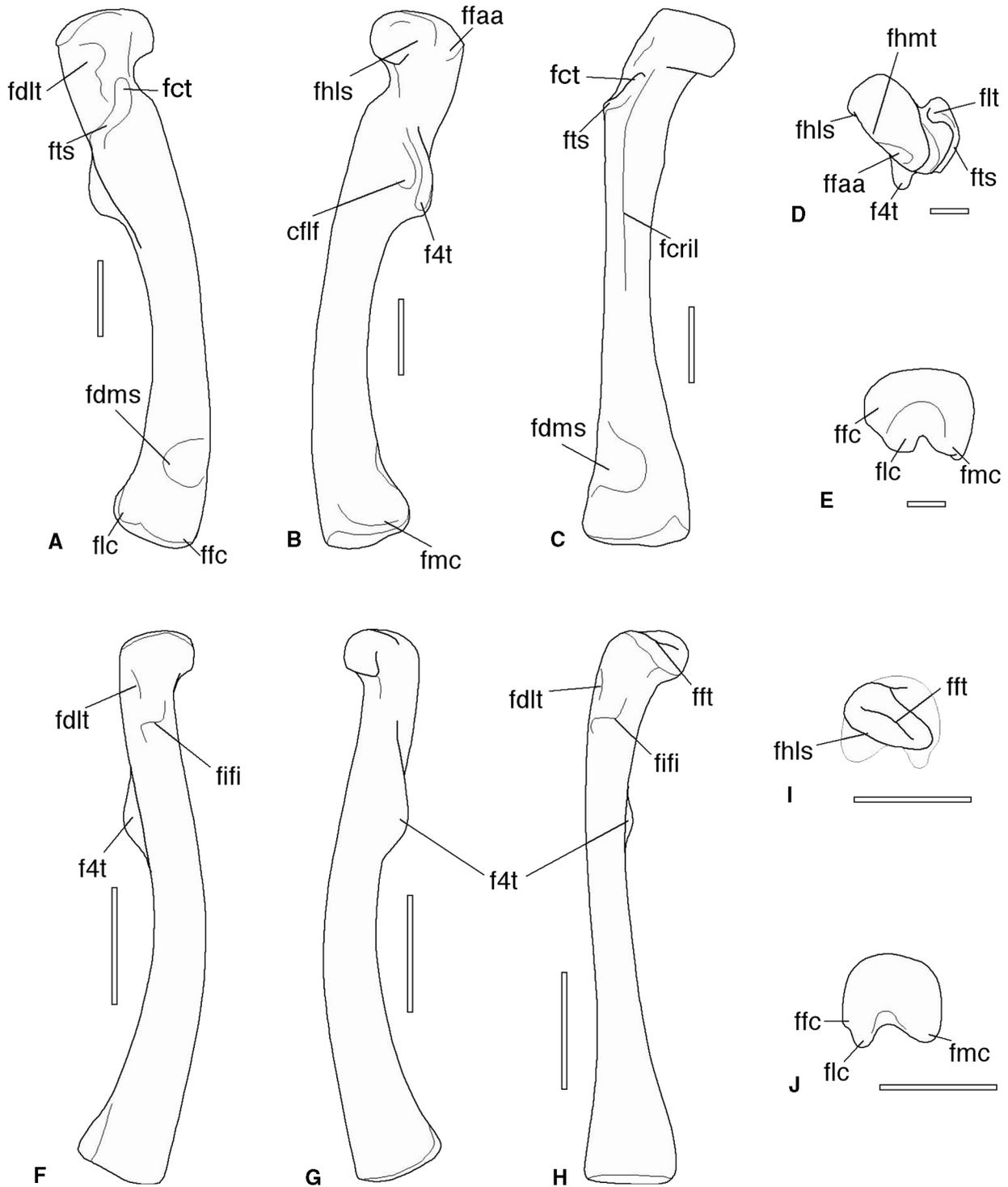


FIGURE 2.7. Femur. A–E, *Herrerasaurus ischigualastensis*: right femur in A, lateral, B, medial, C, cranial, D, proximal, and E, distal aspects. F–J, *Staurikosaurus pricei*: left femur (reversed) in F, lateral, G, medial, H, cranial, I, proximal (with an outline of the distal end), and J, distal aspects. Scale = 5 cm (A–C, F–J), 2.5 cm (D, E). (A–E after Novas 1993; F–J after Galton 1977a.)

third of the bone to form the proximal part of the symphysis. The rodlike ischial shaft forms the rest of the symphysis and bears no sign of medioventral lamination. Its cross section is subtriangular in *Herrerasaurus* and *Guaibasaurus* but more rounded in *Staurikosaurus* and *Eoraptor*. The actual length of the ischium is not known for *Herrerasaurus* (drawings in Reig 1963 and Novas 1993 are reconstructions), but its distal end bears a marked

lateral knob, possibly for the insertion of the caudal branch of *M. flexor tibialis internus*. The distal end of the ischium is not expanded in *Herrerasaurus*, *Staurikosaurus*, or *Eoraptor*, but a clear expansion is present in *Guaibasaurus*.

The femur of basal saurischians (figs. 2.7, 2.8) does not have a completely inturned head, its long axis at an angle of about 45° to the transverse axis of the distal end of the bone. A

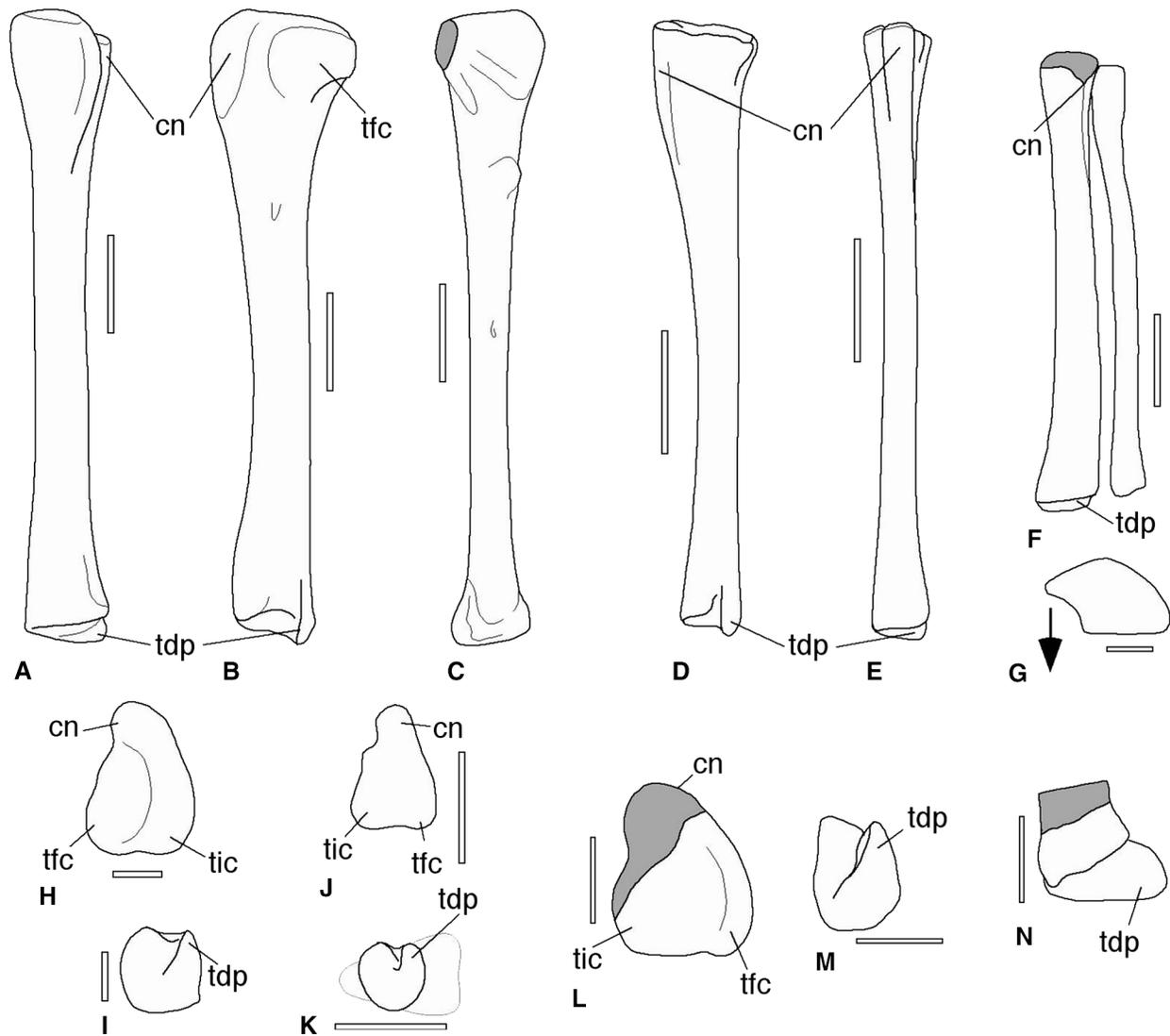


FIGURE 2.9. Crus. A–C, *Herrerasaurus ischigualastensis*: A, B, left tibia in A, lateral, and B, cranial, and C, lateral aspects; C, left fibula in medial aspect. D, E, *Staurikosaurus pricei*: left tibia in D, lateral, and E, cranial aspects. F, G, *Guaibasaurus candelariensis*: F, right tibia and fibula (reversed) in cranial aspect; G, cross section on the distalmost portion of a right (reversed) tibia (arrow points cranially). H, I, *Herrerasaurus ischigualastensis*: left tibia in H, proximal, and I, distal aspects. J, K, *Staurikosaurus pricei*: left tibia in J, proximal, and K, distal (with an outline of the proximal end) aspects. L–N, *Chindesaurus bryansmalli*: L, M, right tibia (reversed) in L, proximal, and M, distal aspects; N, distal end of right tibia (reversed) in cranial aspect. Scale = 5 cm (A–E, J, K), 2.5 cm (H, I), 4 cm (F), = 1 cm (G). Nonpreserved portions in gray. (A–C, H, I, after Novas 1993; D, E, J, K, after Galton 1977a; F, G, after Bonaparte et al. 1999; L–N after Long and Murry 1995.)

branch of *M. iliotochanterici* (Rowe 1986). This muscle scar is also present in *Herrerasaurus* and is homologous to the ridge identified by Galton (1977a) as the cranial trochanter of *Staurikosaurus*. In both *Herrerasaurus* and *Guaibasaurus* a cranial intermuscular line extends distally from the cranial trochanter and probably separated two branches of *M. femorotibialis*. Accordingly, *contra* Novas (1993), the presence of this feature is not considered autapomorphic for *Herrerasaurus*. The fourth trochanter of most basal saurischians is semipendent, with the distal border forming a step angle to the shaft. This condition is seen in *Herrerasaurus*, *Eoraptor*, *Aliwalia*, and *Alwalkeria*, whereas in *Guaibasaurus*, *Staurikosaurus*, and *Chindesaurus* the distal margin of the fourth trochanter slopes gently onto the femoral shaft. In *Herrerasaurus* a subcircular muscle scar is seen on the cranial corner of the distal femur. A similar muscle scar is seen in *Saturnalia*, as well as in some crurotarsans (Sill 1974),

and it might correspond to the insertion of an ansa of *M. iliiofibularis* (see Vanden Berge 1975). In all basal saurischians except *Aliwalia* the intercondylar sulcus does not extend onto the craniodistal surface of the femur.

The crus of basal saurischians (fig. 2.9) is approximately the same length as the femur. Exceptions are *Herrerasaurus*, in which the crus is significantly shorter, and *Saltopus*, in which the contrary is the case. The tibia of most basal saurischians bears a robust but not proximally expanded cnemial crest. The proximal condyles are placed at the caudal margin of the bone, separated by a faint concavity. In *Herrerasaurus* the distal articular facet of the tibia is subquadratic, whereas that of *Staurikosaurus* is subcircular, a feature that is autapomorphic for the taxon. In *Eoraptor* and *Guaibasaurus* the distal tibia is significantly broader than long. In addition, the distal tibia of *Guaibasaurus* possesses other features that are peculiar among basal saurischians, such

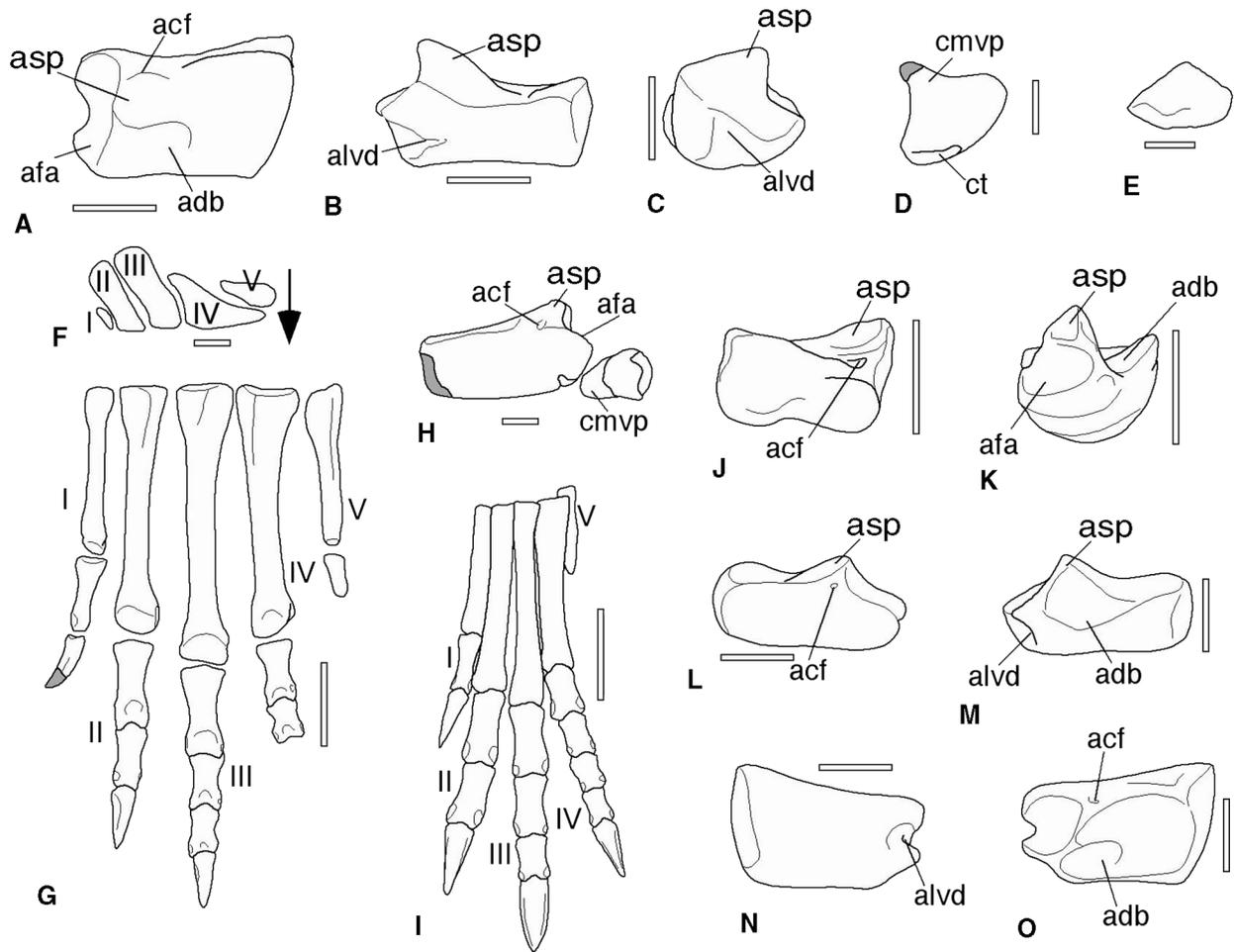


FIGURE 2.10. Tarsus and pes. A–G, *Herrerasaurus ischigualastensis*: A–C, left astragalus in A, proximal, B, caudal, and C, lateral aspects; D, right (reversed) calcaneum in distal aspect of *Herrerasaurus ischigualastensis* (formerly *Ischisaurus cattoi*); E, right (reversed) lateral distal tarsal in distal aspect; F, proximal outline of right (reversed) metatarsals (arrow points cranially); G, right (reversed) pes in flexor aspect. H, I, *Guaibasaurus candeleriensis*: H, left astragalus and calcaneum in cranial aspect; I, left foot in flexor aspect. J, K, *Chindesaurus bryansmalli*: right (reversed) astragalus in J, cranial, and K, lateral aspects. L–O, *Alwalkeria maliensis*: left astragalus in L, cranial, M, caudal, N, distal, and O, proximal aspects. Scale = cm (A–D), 2.5 cm (E–F), 5 cm (G), 1 cm (H, L–O), 4 cm (I), 2 cm (J, K). Nonpreserved portions in gray. (A–D after Novas 1989; G after Novas 1993; H, I, after Bonaparte et al. 1999; J, K, after Long and Murry 1995; L–O after Chatterjee 1987.)

as a craniomedial corner that forms an acute angle and a medial border that is broader than the lateral. In all basal saurischians the tibia possesses a well-defined descending process that fits caudal to the ascending astragalular process. Those of *Herrerasaurus* and *Staurikosaurus* are short and broad and do not extend laterally. In *Eoraptor*, *Chindesaurus*, and *Guaibasaurus* the descending process forms a small postfibular wing. The fibula of basal saurischians is slender and transversely compressed. In *Herrerasaurus* the medial surface of its proximal portion bears ridges for articulation with the tibia, while in *Guaibasaurus* the insertion of *M. iliofibularis* inflects its shaft laterally.

The tarsus of basal saurischians (fig. 2.10A–E, H, J–O) comprises two proximal (astragalus and calcaneum) and two distal elements. The astragalus is a broad, subrectangular bone. It bears a flat medial articular surface for the tibia that continues to the broad, also proximally flat craniolateral ascending process. In various members of the group a marked furrow is present on the cranial surface of the ascending process. Caudal to this process in forms such as *Herrerasaurus*, *Agnosphytys*, and *Alwalkeria* the descending tibial process articulates into a deep elliptical basin. In *Guaibasaurus*, on the other hand, this part of the bone is

rather flat and continuous to the medial tibial articulation. In most basal saurischians the fibular articulation in the astragalus is small and divided by a notch for the calcaneal articulation. An exception is the astragalus of *Alwalkeria*, whose fibular articulation is larger than that of all other basal dinosaurs. The calcaneum of *Herrerasaurus* is a proximodistally flattened triradiate bone. It bears a marked caudal tuber, as well as a medial projection that articulates ventrally to the astragalus. A slightly different condition is seen in *Guaibasaurus*, whose calcaneum retains a defined tuber and medial process but is also significantly compressed lateromedially. The medial distal tarsal of basal saurischians is flat and articulates to metatarsal III. The lateral element is deeper and subtriangular and articulates to metatarsal IV. The pes of basal saurischians (fig. 2.10G, I) has three weight-bearing digits (II–IV), of which metatarsal III is the longest. Metatarsals II and IV are approximately the same length, whereas digits I and V are reduced. An exception is *Saltopus*, in which metatarsal IV is almost as long as metatarsal III. Metatarsal I articulates proximally to the tarsus in all basal saurischians, and its medial distal condyle projects farther distally than the medial. In *Herrerasaurus* it lies partially on the

flexor surface of metatarsal II, in an overlapping pattern that extends along the whole metatarsal series. Metatarsal IV has an L-shaped proximal outline, and metatarsal V articulates to its extensor surface. Extensor pits are seen in metatarsals II–IV, and only metatarsal V lacks distal ginglymoid condyles. The pedal phalangeal formula of *Herrerasaurus* is 2-3-4-5-1 (Novas 1993), whereas digit V of *Guaibasaurus* apparently lacks phalanges altogether. All nonterminal phalanges possess symmetrical ginglymoid condyles, and most of them also bear deep collateral ligament pits and extensor ligament depressions.

Systematics and Evolution

A new phylogenetic study of early dinosaur evolution is presented in this section. The monophyly of Dinosauria as defined by previous cladistic works (Gauthier 1986; Benton and Clark 1988; Sereno et al. 1993; Novas 1996a) is an a priori assumption of the numerical analysis performed here, and basal dinosauromorphs such as *Lagerpeton*, *Marasuchus*, and *Pseudolagosuchus* (Arcucci 1997) compose the hypothetical outgroup.

Two nonsaurischian taxa are included in the analysis as part of the ingroup, namely, *Pisanosaurus mertii* (the oldest well-known ornithischian) and remaining ornithischians. The monophyly of this last group is supported by Sereno (1986, 1999a). Other individual taxa of the ingroup include *Eoraptor lunensis*, *Guaibasaurus candelariensis*, *Herrerasaurus ischigualastensis*, and *Staurikosaurus pricei*. Still other taxa treated in the anatomical section of this chapter are too little known to be confidently included in the analysis. Accordingly, their phylogenetic affinities are discussed afterward.

Other taxa of the ingroup include Neotheropoda (*sensu* Sereno et al. 1994), whose monophyly is supported by most recent cladistic studies (Sereno 1999a, 1999b; Holtz 1998a; Rauhut 2000a), and Sauropodomorpha. This last taxon comprises basal dinosaurs usually regarded as prosauropods, as well as basal sauropods, to the exclusion of *Saturnalia*, the only well-known Ischigualastian sauropodomorph-related dinosaur (Langer et al. 1999a, 1999b), which is treated separately. The monophyly of the clade including prosauropods and sauropods is supported by a series of previous phylogenetic studies (Gauthier 1986; Sereno 1999a, 1999b; Benton et al. 2000b).

The cladistic analysis presented here is based on 107 anatomical characters, most of which were gathered from previous cladistic studies of Dinosauria, mainly Gauthier 1986; Sereno 1986, 1999a; Sereno et al. 1993; Benton and Clark 1988; Benton 1999; Novas 1989, 1992b, 1993, 1996a; Benton et al. 2000b; Holtz 1998a; Rauhut 2000a; and Yates 2003. Some characters are, however, newly proposed here. The data matrix was analyzed using PAUP*4.0b4a (Swofford 2000). The branch-and-bound search option was employed, and all characters were weighted equally. Multistate characters were treated as “uncertainty,” and those in which one derived state (1) is transitional between the primitive (0) and a second derived state (2) were ordered (except in the case of character 76). A single most parsimonious tree was found (fig. 2.11). The robustness of each of its clades was assessed by bootstrapping (Felsenstein 1985) and using decay indexes (Bremer 1994). In addition, a double decay analysis (Wilkinson et al. 2000) was performed using PAUP and RadCon version 1.1.2 (Thorley and Page 2000, 2001), and leaf stability values were defined for each taxon, together with the average value for the entire tree. These values, together with the tree statistics, are given in figure 2.11A.

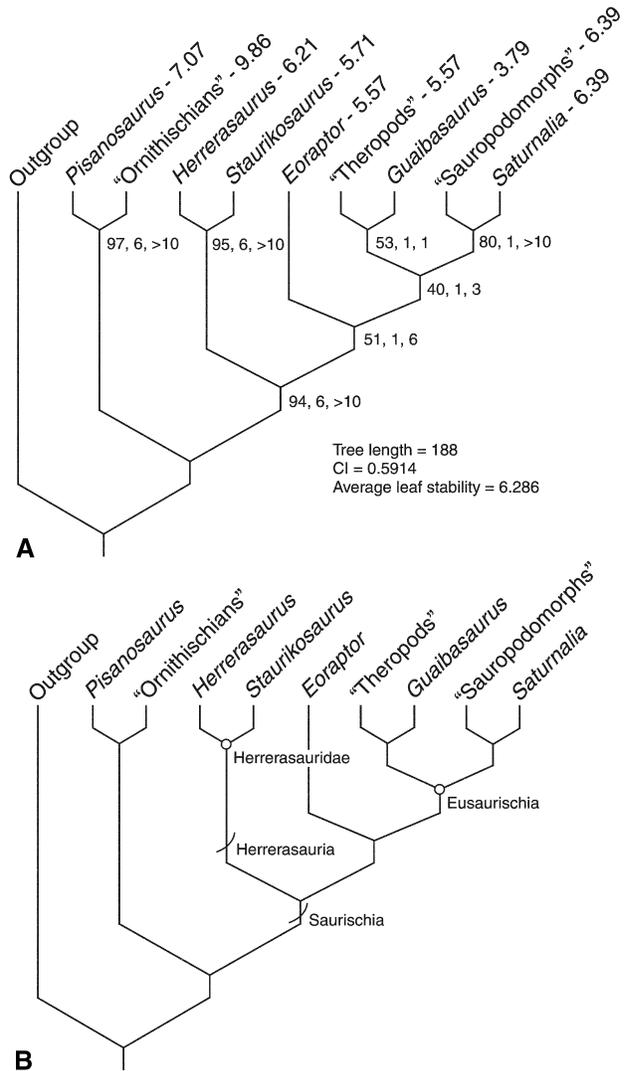


FIGURE 2.11. Early dinosaur evolution as depicted by the single most parsimonious tree found based on the analysis of 107 anatomical characters: A, values of bootstrap (10,000 replicates searched by branch-and-bound method in PAUP*4.0b4a) and Bremer support, based on strict and 50% majority rule consensus, indicated for each clade, and leaf stability indicated for each terminal taxon; B, nomenclature of the basal dinosaur groups discussed in the text based on the phylogenetic arrangement here proposed, with node-based taxa indicated by a white circle and stem-based taxa indicated by a curved line.

Two main alternative hypotheses regarding the phylogenetic position of the dinosaurs considered in this chapter have been proposed under the cladistic paradigm. Early studies (Gauthier 1986; Brinkman and Sues 1987; Benton 1990a; Novas 1992a; see also Fraser et al. 2002) suggested *Herrerasaurus* and/or *Staurikosaurus* to be sister taxa of a monophyletic Dinosauria (= Saurischia + Ornithischia). Since the discoveries of *Eoraptor* (Sereno et al. 1993) and the complete skeleton of *Herrerasaurus* (Sereno and Novas 1992) a new hypothesis in which both *Eoraptor* and herrerasaurids are considered the basalmost theropods has been widely advocated (Sereno et al. 1993; Sereno 1999a, 1999b; Novas 1993, 1996a, 1997a).

More recently, this hypothesis has been questioned by various authors (Padian and May 1993; Holtz 1995a; Bonaparte and Pumares 1995; Langer et al. 1999b), who, although not supported by explicit phylogenetic analyses, suggested that theropods

might share a more recent common ancestor with sauropodomorphs than with herrerasaurids and/or *Eoraptor*. According to some of these studies, these last forms belong to Dinosauria but not to Theropoda and should be assigned instead to the base of Saurischia as the sister taxa of Sauropodomorpha + Theropoda. This hypothesis is supported in the present study.

A monophyletic Saurischia including herrerasaurids, *Eoraptor*, sauropodomorphs, and theropods is strongly supported in the present analysis by high bootstrap and Bremer support values (fig. 2.11A). Accordingly, if the data matrix is analyzed using constraints to the alternative view of herrerasaurids as non-dinosaurs (Brinkman and Sues 1987; Novas 1992a) five most parsimonious trees are found. These trees contain 14 more steps than the most parsimonious tree found by the unconstrained analysis and have much lower bootstrap values (fig. 2.12A). In addition, a comparison of these five topologies with the overall most parsimonious tree using the Templeton test (Templeton 1983) yields *P* values that range from 0.0082 to 0.0164. This suggests that the monophyly of sauropodomorphs + theropods + herrerasaurids, to the exclusion of ornithischians, is significantly better supported by the data presented here than the monophyly of sauropodomorphs + theropods + ornithischians, to the exclusion of herrerasaurids.

Phylogenetic studies favoring a monophyletic Dinosauria, to the exclusion of herrerasaurids, are found in Brinkman and Sues (1987), Novas (1992a), and Benton (1990a). However, most plesiomorphic features of herrerasaurids discussed by those authors are also present in basal members of the major dinosaur groups. These include the well-developed medial wall of the acetabulum (Brinkman and Sues 1987), which is present in basal sauropodomorphs (Galton 1973b; Benton et al. 2000b) and ornithischians (Santa Luca 1984; Sereno 1991b); the unexpanded cranial trochanter (Novas 1992a), present in basal sauropodomorphs (Galton and Upchurch, this vol.) and some theropods (Padian 1986; Rowe 1989); the well-developed trochanteric shelf (Novas 1992a), present in *Saturnalia* (Langer et al. 1999b) and some theropods (Raath 1990; Madsen and Welles 2000); and the unexpanded distal end of the tibia (Benton 1990a), present in some theropods (Padian 1986; Carpenter 1997a) and some sauropodomorphs (Benton et al. 2000b). In particular, the two-vertebrae sacrum of *Herrerasaurus* has been suggested to indicate its primitiveness (Novas 1992a; Fraser et al. 2002). However, this feature can also be interpreted as homoplastic in the early evolution of dinosaurs, as indicated by its presence in at least one sauropodomorph (*Saturnalia*; contra Langer et al. 1999b) and its absence in *Staurikosaurus*, the sister taxon of *Herrerasaurus*. Accordingly, the absence of a well-developed concave area for the insertion of the caudofemoral musculature (brevis fossa) in the ventral surface of the postacetabular iliac process of herrerasaurids (*Staurikosaurus* + *Herrerasaurus*) is the sole trait suggesting that they belong outside Dinosauria.

Although there is strong support for a monophyletic Saurischia, several putative apomorphies of the group present some problems and deserve further discussion. Sereno and Novas (1992; but see Fraser et al. 2002) proposed that a jugal that overlaps the ventral margin of the lacrimal and possesses a forked caudal ramus is unique to saurischians. However, the jugal of the basal ornithischian *Lesothosaurus* clearly overlaps the lacrimal at their articulation, a trait also present in *Scelidosaurus*. Likewise, the caudal ramus of the jugal in both *Scelidosaurus* and *Emausaurus* (Haubold 1991) is forked. The presence of epipophyses on the axis has also been considered apomorphic for Saurischia (Novas 1993). Axial epipophyses are, however, clearly present in basal ornithischians such as *Lesothosaurus* and

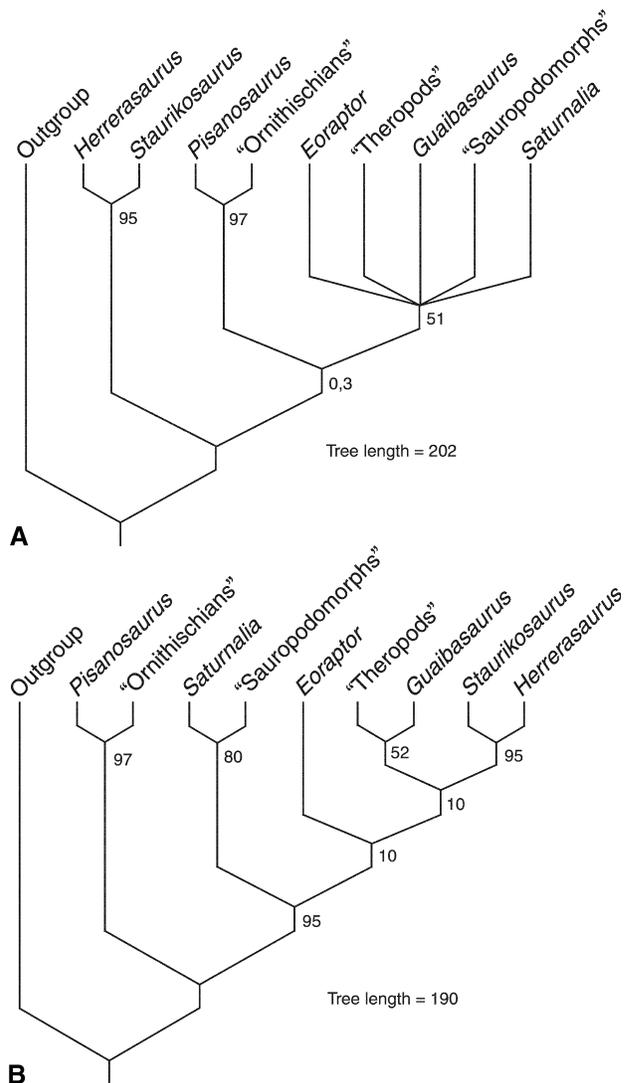


FIGURE 2.12. Early dinosaur evolution as depicted by the analysis of 107 morphological characters with constraints to A, the monophyly of Saurischia + Ornithischia, to the exclusion of Herrerasauridae (strict consensus of five most parsimonious trees), and B, the monophyly of Herrerasauridae + Theropoda, to the exclusion of *Eoraptor*, plus the monophyly of these three to the exclusion of Sauropodomorpha (single most parsimonious tree). Tree length and bootstrap values (10,000 replicates) are indicated.

Scelidosaurus, but they are obscured by marked laminae extending into the caudal part of the neural spines. In addition, Sereno et al. (1993) suggested that metatarsals II–IV with overlapping proximal portions are apomorphic for Saurischia. This feature is, however, plesiomorphic for Dinosauria since it is also present in basal dinosauromorphs (Bonaparte 1975b).

Saurischia is defined as a stem-based taxon: all Dinosauria closer to *Allosaurus* than to *Stegosaurus* (see also Gauthier 1986; Padian and May 1993; and Sereno 1998). Its diagnosis is provided earlier in this chapter. The saurischian clade is divided into two main groups: Herrerasauridae, including *Herrerasaurus* and *Staurikosaurus*, and an unnamed clade comprising *Eoraptor*, *Guaibasaurus*, *Saturnalia*, Theropoda, and Sauropodomorpha. The monophyly of Herrerasauridae was contested by early phylogenetic studies of basal dinosaurs (Brinkman and Sues 1987; Benton 1990a) but has since been firmly established by

thorough cladistic studies (Novas 1992a; Sereno 1999a, 1999b; Rauhut 2000a) and is strongly supported in the present analysis by high bootstrap and Bremer support values (fig. 2.11A). Indeed, if the present data matrix is analyzed with constraints to a paraphyletic Herrerasauridae, four most parsimonious trees are found that are six steps longer than the overall most parsimonious tree.

Some putative apomorphic features of Herrerasauridae present problems, however, including the scapular characters used by Novas (1992a). The 90° angle between the acromion and the scapular blade cannot be adequately measured in the scapular fragments of *Staurikosaurus*. Moreover, as discussed by Galton (2000a), the scapular blade of *Staurikosaurus* expands dorsally as in most saurischians and is not strap-shaped like that of *Herrerasaurus*. Likewise, Sereno (1999a) listed the presence of a crested cranial margin of the proximal femoral shaft as apomorphic for Herrerasauridae, probably based on the femoral keel described for *Herrerasaurus* (Novas 1993). However, as pointed out by Novas (1993), this feature is not clearly seen in *Staurikosaurus*. Moreover, as previously discussed, a similar keel is also present in the femur of *Guaibasaurus*.

Herrerasauridae was erected by Benedetto (1973) to include *Herrerasaurus* + *Staurikosaurus*, and Novas (1992a; see also Novas 1997a) defined a node-based Herrerasauridae as comprising *Herrerasaurus*, *Staurikosaurus*, and all descendants of their most recent common ancestor. However, with Herrerasauridae defined as a node-based taxon, there is no name for the stem leading to its two internal specifiers. This stem may include taxa such as *Aliwalia*, *Chindesaurus*, and new finds. Herrerasauria Galton, 1985 comprises all dinosaurs that share a more recent common ancestor with *Herrerasaurus* than with *Liliensternus* and *Plateosaurus*. These two external specifiers were chosen because they represent well-known Triassic members of the two major saurischian groups (Theropoda and Sauropodomorpha, respectively) and were mentioned by Galton (1985a) in his taxonomic discussions.

If the monophyly of Saurischia, as well as that of Herrerasauridae within it, is strongly supported in the present analysis, this is not the case for some other clades of the most parsimonious hypothesis presented here. In fact, bootstrap and Bremer support values are low for the internal clades of Saurischia, which include *Eoraptor*, Theropoda, and Sauropodomorpha exclusive of Herrerasauridae, as well as Theropoda and Sauropodomorpha exclusive of *Eoraptor* (fig. 2.11A). These are the instances in which the hypothesis presented here differs from that advocated by some other authors (Sereno and Novas 1992; Sereno et al. 1993; Novas 1993, 1996a, 1997a; Sereno 1999a). Indeed, if the present data matrix is analyzed with constraints to this alternative view, the most parsimonious tree is only two steps longer than that found by the unconstrained analysis, although its bootstrap values are lower (fig. 2.12B). In addition, the comparison of the two topologies using the Templeton test (Templeton 1983) yields a nonsignificant *P* value of 0.701. This implies that the favored phylogenetic arrangement is not significantly better supported by the present data than the arrangement advocated by the aforementioned authors.

The lack of statistical support for that part of the chosen phylogenetic hypothesis is not unexpected. In fact, Sereno and Novas (1992, 1993) defined various primary homologies that *Eoraptor* and/or herrerasaurids share with theropods that are unknown among other basal dinosaurs. Most of these have been incorporated into the present analysis, with the coding slightly altered in a few cases to accommodate new data (Langer et al. 1999b; Galton 1999b, 2000a; Benton et al. 2000b). However,

some evidence put forward by those authors in support of their phylogenetic hypothesis presents problems and deserves further attention.

Novas (1993) suggested that the lacrimal of theropods (including herrerasaurids) is more derived than that of other dinosaurs because it is exposed in the skull roof. In fact, the lacrimal of *Herrerasaurus* is not more exposed in the skull roof than that of well-known prosauropods (Huene 1926a; Bonaparte and Pumares 1995) and most basal archosaurs (Ewer 1965; Bonaparte 1972). All of these forms are plesiomorphic in relation to various theropods (Britt 1991; Madsen and Welles 2000), in which the dorsal part of the lacrimal is much more lateromedially expanded and occupies a larger part of the skull roof. In addition, Sereno and Novas (1993) suggested that the dorsally constricted infratemporal fenestra of *Herrerasaurus* indicated its theropod affinity. Similar arrangements are also seen, however, in basal sauropodomorphs (Young 1941a, 1942a; Bonaparte and Vince 1979; Gow et al. 1990; Bonaparte and Pumares 1995). Moreover, Sereno (1999a) claims that an ectopterygoid ventral recess characterizes theropods, including herrerasaurids and *Eoraptor*. However, an ectopterygoid recess is also seen in *Thecodontosaurus* (Yates 2003), while its presence in *Herrerasaurus* cannot be confirmed.

Sereno et al. (1993) proposed the presence of prong-shaped epiphyses in the cervical vertebrae as an apomorphy of Theropoda, including herrerasaurids and *Eoraptor*. This character is, however, present in some prosauropods (*Thecodontosaurus*, *Plateosaurus*, *Sellosaurus*), while it is not present in some basal theropods (*Liliensternus*, *Elaphrosaurus*). In addition, Sereno et al. (1993; see also Novas 1993 and Sereno 1999a) diagnosed the elongate prezygapophyses of the distal caudal vertebrae of herrerasaurids as a theropod trait, but this character is not present in various basal theropods (Welles 1984; Madsen and Welles 2000). In addition, Sereno et al. (1993; see also Sereno 1999a) suggested a strap-shaped scapular blade to be apomorphic for Theropoda, including Herrerasauridae. However, *Staurikosaurus* most probably possesses a dorsally expanded scapular blade, as is the case with various basal theropods (Raath 1969; Welles 1984; Carpenter 1997a). Furthermore, Sereno (1999a) claimed that intermetacarpal articular facets in metacarpals I–III are also apomorphic for theropods, including herrerasaurids and *Eoraptor*. Structures similar to those described for *Herrerasaurus* (Sereno 1993, figs. 11, 14) are, however, clearly seen in other basal dinosaurs (Huene 1932, pl. 11; Santa Luca 1980).

Sereno et al. (1993) suggested the presence of a bootlike expansion of the distal pubis as a theropod feature of herrerasaurids. The primitive condition of theropods is, however, a distal pubis that is not significantly more expanded than that of basal sauropodomorphs (Galton and Upchurch, this vol.), as seen in most basal members of the group (Padian 1986; Carpenter 1997a). In addition, the pubic expansion of herrerasaurids is not homologous (*sensu de Pinna* 1991) to that of more derived theropods (Madsen 1976a; Currie and Zhao 1993a). The herrerasaurid pubic expansion is, in fact, the result of the caudal folding of the lateral margin of the distal end of the bone, as also seen in *Marasuchus*, and not an actual increase of its cranio-caudal width. In addition, this caudal folding also accounts for the reduced transverse width of the distal end of the pubis of herrerasaurids. Accordingly, *contra* Sereno (1999a), the reduction in width of the distal part of the pubic shaft of some basal theropods (Raath 1969; Carpenter 1997a) is not considered homologous to that of herrerasaurids.

Sereno (1999a) indicated that an obturator process in the ischium, an arched brevis fossa, and a distal femoral depression

were theropod apomorphic features in *Eoraptor* and/or Herrerasauridae. However, an ischial obturator process is found in basal sauropodomorphs (Huene 1926a; Cooper 1981b), as well as in basal ornithischians—*Lesothosaurus*, *Scelidosaurus*—although it is not as ventrally expanded in these forms as in most saurischians. Moreover, as already discussed, herrerasaurids possess an area for the insertion of *M. caudofemoralis brevis* that is similar to that of *Marasuchus* and much less lateromedially and dorsoventrally expanded than that of both ornithischians and most saurischians. In addition, the depression on the distal femur mentioned by Sereno (1999a) is interpreted here as the cranioproximal extension of the sulcus intercondylaris. This depression is present in most derived dinosaurs (Galton 1976b; Forster 1990a; Currie and Zhao 1993a) but is absent from the cranial surface of the distal femur of *Herrerasaurus*, *Staurikosaurus*, and several other basal dinosaurs, such as *Saturnalia*, *Liliensternus*, and *Lesothosaurus*.

Finally, Novas (1993) suggested the presence of a trochanteric shelf on the proximal femur as apomorphic for theropods, including *Eoraptor* and Herrerasauridae. Although a sigmoid insertion for *M. iliofemoralis* is seen in all these forms, only in *Herrerasaurus* and some coelophysids—e.g., *Coelophysis* (Padian 1986) and robust *Syntarsus* (Raath 1990)—as well as in the sauropodomorph *Saturnalia* (Langer et al. 1999b), is it raised to form a horizontal shelf. The proximal femur of *Eoraptor* and *Staurikosaurus*, on the other hand, lacks a horizontal platform on its lateral surface, a condition shared by most basal dinosaurs, such as *Liliensternus*, *Thecodontosaurus*, and *Lesothosaurus*.

As concerns *Eoraptor*, previous assessments (Sereno et al. 1993; Novas 1993, 1996a, 1997a; Sereno 1999a; Rauhut 2000a) have defined the taxon as the most basal theropod. However, the present study indicates that regardless of their relation to other members of the group, herrerasaurids are more basal in the dinosaur tree than *Eoraptor*. In fact, herrerasaurids represent the most basal branch in the shortest tree in which *Eoraptor* and herrerasaurids are basal theropods. Especially in the skull, *Eoraptor* shares with some basal sauropodomorphs and/or theropods various apomorphic characters that are absent in *Herrerasaurus*, namely, a thin dorsocaudal premaxillary process, which allows the maxilla to approach the external naris; a subnarial gap similar to that of coelophysid theropods; a maxilla with a concave rostral margin and a horizontal ridge on the lateral surface; a nasal that forms the dorsal border of the antorbital fenestra and bears a caudolateral process enveloping part of the rostral ramus of the lacrimal; a long, subvertical ventral ramus of the lacrimal; and a rostral ramus of the jugal that does not reach the internal antorbital fenestra. In addition, *Eoraptor* shares with theropods and sauropodomorphs a stouter metacarpal I and with theropods a supracetabular ridge continuous with the lateral border of the *brevis fossa* and a caudally expanded ischial peduncle.

In fact, the only characters that support a close relationship between *Herrerasaurus* and more derived saurischians, to the exclusion of *Eoraptor*, are predatory features that *Herrerasaurus* shares with some unambiguous theropod taxa. These include the intramandibular joint, the long penultimate manual phalanges, and the trenchant unguals of the manus. However, these characters were outweighed by those indicating a closer relationship between *Eoraptor* and more derived saurischians and are interpreted as convergences. Indeed, they could well have arisen independently in these forms as adaptations to their more carnivorous diet. Indeed, it is in fact not clear that the intramandibular joints of herrerasaurids and more derived theropods represent homologous structures (Holtz 1998a; Fraser et al. 2002).

As discussed above, the present study defined a close relationship between theropods and sauropodomorphs. Indeed, the monophyly of the clade uniting those two major dinosaur groups, exclusive of *Eoraptor* and herrerasaurids, is supported by several apomorphic characters. This least inclusive group of Saurischia, comprising *Cetiosaurus* and Neornithes, was called Eusaurischia by Padian et al. (1999).

Within Eusaurischia, *Saturnalia* and *Guaibasaurus* were found to represent sister taxa of Sauropodomorpha and Theropoda, respectively (fig. 2.11). The monophyly of Sauropodomorpha + *Saturnalia* is strongly supported by high values of bootstrap and Bremer support (fig. 2.10A). Basal sauropodomorph phylogeny is fully discussed by Galton and Upchurch (this vol.).

The phylogenetic position of *Guaibasaurus* is more controversial. Bonaparte et al. (1999) included the taxon within Saurischia, suggesting its closer relation to sauropodomorphs and theropods than to herrerasaurids. This hypothesis is supported by the present analysis, but Bonaparte et al. (1999) also listed several characters linking *Guaibasaurus* to sauropodomorphs. Among these, a well-developed ambiens process and an unreduced metatarsal I are plesiomorphic for Dinosauria. Likewise, most basal members of the group possess a straight femur (in cranial aspect), a moderately developed cranial trochanter, an elongate fourth trochanter with a medial depression (i.e., insertion of *M. caudofemoralis longus*), and a reduced metatarsal V. As indicated by Bonaparte et al. (1999), however, the distal tibia of *Guaibasaurus* has a craniocaudally compressed lateral margin, and the projections of its calcaneum are reduced. These are, indeed, apomorphic features within Dinosauria, found as they are in both ornithischians and theropods. In addition, a distally expanded massive ischium with a long symphysis is a eusaurischian apomorphy.

In conclusion, there is no strong evidence to support the sauropodomorph affinity of *Guaibasaurus*. Instead, the present analysis found it to represent the most basal theropod. The support for this hypothesis, however, is weak (fig. 2.11A), with few apomorphic features supporting the arrangement. The precise phylogenetic position of *Guaibasaurus* is therefore still ambiguous, although it is clearly more closely related to eusaurischians than to herrerasaurids. Moreover, if considered a theropod, *Guaibasaurus* is also the most basal member of the group since it lacks most synapomorphies of more derived Theropoda.

Among the little-known basal dinosaurs not included in the present phylogenetic analysis, *Alwalkeria maliensis* and *Chindesaurus bryansmalli* possess morphological features indicating a saurischian affinity. However, a substantial problem with these two taxa, as well as with *Spondylosoma absconditum*, is the uncertainty about the association of the various remains attributed to the taxa, which may not belong to a unique specimen or taxon. An even more problematic case is that of *Agnosphytes cromhallensis*, which admittedly is based on dissociated remains (Fraser et al. 2002). Saurischian characters of *Alwalkeria* include an elongate cranial cervical vertebra and dorsal vertebrae with well-developed chonoe. Moreover, features like the subnarial gap, the heterodont dentition, the noncompressed dorsal vertebrae, and the craniocaudally compressed lateral portion of the astragalus suggest that *Alwalkeria* is more related to eusaurischians than to herrerasaurids. Besides, *Alwalkeria* has some plesiomorphic features that are unknown in basal theropods, such as a semipendent fourth trochanter and an astragalus with a well-developed elliptical cavity for the tibial descending process. In conclusion, *Alwalkeria* represents a dinosaur phylogenetically close to *Eoraptor* and to the base of Eusaurischia.

The saurischian affinity of *Chindesaurus* is suggested by features such as the chonoe on the dorsal vertebrae and the expanded transverse processes of the second sacral vertebra, which roofs the space cranial to the caudal margin of its rib. In addition, short dorsal vertebrae and deep sacral ribs of *Chindesaurus* might indicate some affinities with herrerasaurids. However, the shortening of the dorsal vertebrae is not as extreme as that of *Staurikosaurus* or *Herrerasaurus*. Other derived features of herrerasaurids not found in *Chindesaurus* include the folded laterodistal portion of the pubic shaft and the elongate prezygapophyses on the distal caudal vertebrae. Indeed, as proposed by Hunt (1996), *Chindesaurus* might well represent a nonherrerasaurid herrerasaurian. Accordingly, it lacks elongate caudal neck vertebrae, a derived feature of Eusaurischia. However, the fourth trochanter of *Chindesaurus* is placed down the shaft, as in sauropodomorphs, and its distal tibia is narrower laterally than medially, with the descending process partially overlapping the fibula, a condition seen in some basal saurischians but not in herrerasaurids. Thus, *Chindesaurus* is presently best referred to as a Saurischia *incertae sedis*, although its high nesting within any of the major saurischian groups (Herrerasauridae, Theropoda, and Sauropodomorpha) can be dismissed.

Aliwalia rex cannot be safely assigned to Saurischia. It is most probably a dinosaur, as indicated by several features of its femur, such as the ridgelike semipendent fourth trochanter and the head, which is subrectangular, forms an angle of more than 45° to the sagittal line, is well set off from the shaft, and has an angulated proximolateral corner and a reduced medial tuberosity. Within dinosaurs its semipendent fourth trochanter is similar to that of *Herrerasaurus* and prosauropods and distinct from that of basal theropods. Besides, the ridgelike cranial trochanter is similar to that of sauropodomorphs and distinct from that of any other basal saurischian. In contrast, the fourth trochanter of all sauropodomorphs is placed lower on the femoral shaft, while that of *Aliwalia* partially overlaps the cranial trochanter. The distal femoral fragment of *Aliwalia* is also distinct from that of most basal saurischians. Its sulcus intercondylaris extends onto the cranial surface of the bone, a feature more commonly seen in more derived members of the group. In conclusion, the two femoral fragments assigned to *Aliwalia* might well belong together. The taxon likely represents a saurischian but is better referred to as a Dinosauria *incertae sedis*.

As mentioned above, the affinities of *Agnosphitys cromhallensis* cannot be well determined because of the uncertainty about the association of its attributed specimens. The well-developed brevis fossa of the ilium strongly indicates a dinosaur affinity. In addition, the extreme elongation of its postacetabular process is characteristic of eusaurischians, while some of its plesiomorphic features, such as a partially closed acetabulum and a short preacetabular process, are not seen in most theropods. According to Fraser et al. (2002), the maxilla attributed to *Agnosphitys* has no clear dinosaurian features, but its attributed humeri could well be dinosaurian, as suggested by the deltopectoral crest morphology. This is also the case with its attributed astragali, which are clearly dinosaurian, as indicated by the straight caudal margin, the small articular facet for fibula, and the ascending process bounded caudally by an articular facet for the tibial descending process. In fact, this articular facet forms a deep elliptical slot, as seen in *Herrerasaurus*, *Saturnalia*, and prosauropods. Accordingly, even though it is undiagnosable due to its disassociated nature, *Agnosphitys* probably has dinosaur affinities.

The two other little-known taxa dealt with here, *Saltopus elginensis* and *Spondylosoma absconditum*, cannot be safely referred to Dinosauria. *Saltopus* is most probably related to Dinosauri-

formes, as indicated by the well-developed trochanteric shelf on its femur, the elongate crus and metatarsus, and the pes with three weight-bearing digits and a shorter element medial to these (Rauhut and Hungerbühler 2000). In addition, its saurischian affinity is suggested by the anatomy of the ischium, which bears a long symphyseal area composed of a short obturator process and has a rodlike shaft with reduced medioventral lamination. However, *Saltopus* lacks several dinosaur apomorphies, such as a long deltopectoral crest, a fibula significantly thinner than the tibia, and a metatarsal IV shorter than metatarsal III. In addition, the vertebrae of the middle of the tail are elongate, as seen in basal nondinosaur dinosauromorphs (Seren and Arcucci 1994), as well as in *Scleromochlus* (Benton 1999). The assignment of *Saltopus* to Dinosauria is therefore problematic, and it is here considered a Dinosauriformes *incertae sedis*.

Spondylosoma absconditum was first described as a saurischian dinosaur (Huene 1942), and since then its possible dinosaur affinity has often been contemplated (Romer 1966; Charig 1976b; Colbert 1970; Bonaparte 1971b; Galton 1977a; Sues 1990; Novas 1997a). More recently, its affinity to rousuchian archosaurs has been proposed (Galton 2000a). In fact, various features of *Spondylosoma* are found in both saurischian dinosaurs and some crurotarsan archosaurs (Walker 1961; Long and Murry 1995; Alcober and Parrish 1997), including elongate cervical vertebrae with ridgelike epiphyses, dorsal vertebrae with hyposphene-hypantrum auxiliary articulations, well-developed cranial, medial, and caudal chonoe, and ribs of the two main sacral vertebrae forming a U-shaped articulation to the ilium. Galton (2000a) suggested a rousuchian affinity of *Spondylosoma* based on the morphology of the ventral margin of its sacral ribs, which are ventrally bent, so that the pelvic articulation faces in the same direction, as seen in *Stagonosuchus* and *Saurosuchus* (Bonaparte 1981, 1984; see also Parrish 1986). However, the articular areas of the sacral ribs of these forms face mainly ventrolaterally, while those of *Spondylosoma* face mainly laterally. Indeed, this arrangement resembles that of the sacral ribs of *Herrerasaurus* (fig. 2.6B) and to some extent of *Staurikosaurus*, in which the ventral margin is also ventrally bent to articulate to the iliac peduncular area. Accordingly, the dorsal margin of the sacral ribs of *Spondylosoma* is mainly horizontal, as in most archosaurs, and not dorsolaterally inclined, as in the aforementioned rousuchians. On the other hand, the humerus of *Spondylosoma* has a deltopectoral crest that is shorter than that of well-known basal dinosaurs and resembles more that of other archosaurs (Ewer 1965; Bonaparte 1975b; Benton 1999). In conclusion, the taxonomic assignment of *Spondylosoma* is ambiguous, and both rousuchian and dinosaur affinities are possible. Nevertheless, if the latter alternative is confirmed, *Spondylosoma* would be the only Ladinian dinosaur known and the earliest member of the group.

Function and Behavior

Probably the most remarkable functional adaptation of basal saurischians is the sliding intramandibular joint of herrerasaurids. Sereno and Novas (1993) fully discussed this structure in *Herrerasaurus*, suggesting a rotation of about 15° along the plane of the mandibular rami. Comparisons with modern lepidosaurs suggest that such an apparatus allowed the toothed cranial segment of the mandible to flex around the struggling prey, preventing its escape. Apparently, the lateral flexion of the joint was restricted and did not serve to increase the mandibular gape.

As also seen in lizards with an intramandibular joint, the mandibular tooth row of *Herrerasaurus* is much shorter than that of the upper jaw. In addition, larger caniniform teeth are seen in the middle of its tooth rows. The combined presence of particularly short dentary and large maxillary caniniform teeth in *Herrerasaurus* (fig. 2.2F, G) suggests possible functional interdependence between these structures. The larger size of that skull also indicates that such traits could be enhanced in older individuals.

The tooth morphology of basal saurischians is rather variable, and so is their inferred function. The serrated, laterally compressed, and caudally curved teeth of *Herrerasaurus* were surely efficient for sizing prey and slicing animal material. Accordingly, a fully carnivorous habit can be inferred for this taxon, as well as for *Staurikosaurus* and *Aliwalia*, which possesses a similar dentition. The heterodont dentition of *Eoraptor* and *Alwalkeria*, on the other hand, lacks clear herbivorous or carnivorous adaptations, showing some resemblance to that of basal sauropodomorphs (see Barrett 2000a). This condition, together with the body size of these taxa, suggests that they were adapted for a mixed diet including invertebrates and small vertebrates as well as soft plant material.

The rear of the tail of *Herrerasaurus* and *Staurikosaurus* was stiffened by the elongate prezygapophyses of its vertebrae. This device probably acted as a dynamic stabilizer during running and leaping (Ostrom 1969a). The forelimb of *Herrerasaurus* and *Eoraptor* is about half as long as the hindlimb, suggesting a function related to prey capture and manipulation rather than to locomotor support (Sereno 1994). In particular, the long manus with large trenchant unguals of *Herrerasaurus* was surely specialized for powerful grasping and raking.

The femoral head of most basal dinosaurs is craniomedially directed, and its shift to a fully medial orientation occurred independently in ornithischians, theropods, and sauropodomorphs (Carrano 2000). The femoral head combines with a semiperforated acetabulum, which is also seen in various basal members of the group. Despite these primitive features, a fully erect gait with a parasagittal hindlimb motion is usually inferred for basal dinosaurs (Novas 1996a; Carrano 2000). However, during locomotion the movement of the limb on the hip was by no means a simple fore-and-aft, stiff rotation around the acetabulum; there was also strong axial rotation of the femur. During maximum protraction the femoral head sat conformably on the hip, forming an angle of about 45° to the sagittal plane. During retraction, however, the contraction of *M. caudofemoralis longus*, assisted by *M. ilirotrochantericus*, caused medial rotation of the femur, so that its head was transversely oriented by the end of the movement. This arrangement generated important medial movement of the knee and ankle during fast locomotion.

Sereno and Novas (1993) reported the presence of puncture wounds in the skull of *Herrerasaurus*. These were suggested to represent injuries derived from either intraspecific aggression or interaction with other large-sized predators, such as *Saurosuchus*. Evidence of behavioral patterns such as gregariousness, nesting, parental care, or visual display have not been confirmed for the taxa discussed in this chapter.

Paleoecology and Biogeography

The dinosaur taxa discussed in this chapter include forms from the Carnian beds of various parts of the world, which contain the earliest known dinosaur-bearing faunas. Dinosaurs are, how-

ever, not dominant components of those paleocommunities, usually representing fewer than 10% of the known specimens (Bonaparte 1982b; Benton 1983a; Azevedo et al. 1990; Rogers et al. 1993). However, basal dinosaurs are much more abundant and diverse in the South American Ischigualastian beds than in any correlated strata of other parts of the world. Accordingly, the Ischigualasto and Santa Maria Formations yielded several skeletons of well-known taxa (Colbert 1970; Sereno and Novas 1992; Sereno et al. 1993; Langer et al. 1999b), whereas only fragmentary remains, most of unclear affinities, were recovered from other Carnian stratigraphic units (Benton and Walker 1985; Kutty and Sengupta 1989; Gauffre 1993a; Long and Murry 1995; Flynn et al. 1999b). This evidence, together with the occurrence of the sister taxa of Dinosauria—*Lagerpeton*, *Marasuchus*, *Pseudolagosuchus* (Arcucci 1997)—in the Ladinian strata of the Chañares Formation, in Argentina, supports the hypothesis of a South American center of origin for dinosaurs in general and for saurischians in particular.

Early saurischian evolution must have been rapid, since basal representatives of its major groups, with their ecological adaptations, have been found in the strata in which the group as a whole is first recorded. The evidence of a tachytelic early evolution of dinosaurs is consistent with opportunistic scenarios, in which they take advantage of ecological space in the aftermath of an extinction event (Benton 1983a). However, forms such as *Herrerasaurus* shared the landscape in which the Ischigualasto Formation was deposited with similarly sized crurotarsan predators such as *Saurosuchus*, and ecological competition could have partially driven the evolution of both groups. In this sense it is interesting that many of the novel features of the dinosauromorph skeleton are related to the hindlimb anatomy; some of these features clearly involved in enhanced bipedal locomotion. Indeed, competitive and opportunistic scenarios are not mutually exclusive, and the locomotor adaptations of dinosaurs could have provided the members of the group with adequate tools to survive in the changing environment that drove other archosaur forms toward extinction (Bakker 1971b; Charig 1972, 1984).

Regardless of which force drove the origin and early evolution of saurischians, it was not only tachytelic; it also involved rapid geographic dispersion. Indeed, rocks of approximately the same age in various parts of the world “simultaneously” register the first appearance of the group. As mentioned, Carnian saurischians are particularly abundant in South America, but they are also known from North America, northern and southern Africa, and India. Accordingly, from the time of their first record saurischians were distributed through almost the entire western Pangaea.

The South American Ischigualastian terrestrial paleocommunities include medium- to large-sized herbivores such as hyperodapedontid rhynchosaurs and kannemeyeriid dicynodonts, as well as medium-sized, possibly omnivorous forms such as aetosaurs and traversodontid cynodonts. Predators were small- to medium-sized cynodonts, particularly chiniquodontids, and medium- to large-sized archosaurs such as proterochampsids and raiusuchians. Herrerasaurids were the most common dinosaurs of those communities, which were characterized by medium to large size and active bipedal predation (Colbert 1970; Sereno and Novas 1992). *Staurikosaurus* was 2 m long and probably preyed on small- to medium-sized vertebrates such as rhynchosaurs and cynodonts. *Herrerasaurus*, on the other hand, 3–5 m in length, was one of the top predators of its time, surpassed in size only by large raiusuchians such as *Saurosuchus* and *Prestosuchus*. An adult *Herrerasaurus* probably preyed on virtually

any vertebrate in its communities apart from other adult top predators. Novas (1997a) mentioned the discovery of a juvenile *Hyperodapedon* (rhynchosaur) within the rib cage of a specimen of *Herrerasaurus*. Herrerasaurids represent the first important saurischian radiation, and their evolutionary history was mainly restricted to the Carnian of South America.

Much more successful than the herrerasaurids was their sister group, which includes the ancestors of theropods and sauropodomorphs. The early evolution of these dinosaurs was not marked by the increase in size and predation capabilities seen in herrerasaurids. Instead, their basal members were small- to medium-sized omnivores that in various ecological aspects resemble basal dinosauiromorphs and early ornithischians. Ischigualastian basal members of the group include the 1.5 m long facultative biped *Saturnalia* and the slightly smaller biped *Eoraptor*.

From that basal stock the two main, fundamentally distinct groups of saurischian dinosaurs evolved. Theropods were rare during Carnian times, and only dubious and fragmentary remains have been referred to the group (Hunt et al. 1998). By contrast, sauropodomorphs were the most abundant of the major dinosaur groups in the Carnian, having been recorded in strata of that age in northern and southern Africa, as well as in North America. These include records in Madagascar and Zimbabwe (Raath 1996; Flynn et al. 1999b), whose faunas are depauperate versions of the South American Ischigualastian paleocommunities. Langer et al. (1999a, 1999b) tentatively assigned the Zimbabwean sauropodomorph to *Saturnalia*, while Flynn et al. (1999b) described the Malagasy prosauropods as typical members of the group. Both forms were probably subordinate omnivores of their faunas, as was *Azendohsaurus* from the Argana Formation of Morocco (Gauffre 1993a). In fact, *Azendohsaurus* and the Malagasy forms represent the oldest known prosauropods, which are contemporaneous with more primitive taxa such as *Saturnalia*.

Regarding the lesser-known Carnian forms treated in this chapter, the small and lightly built *Marasuchus*-like body of *Saltopus* suggests habits of an agile, probably insectivorous

predator. Based on its size and dentition, *Alwalkeria* might have been a small omnivore like *Eoraptor* and *Saturnalia*.

The trend toward high diversity and abundance of basal sauropodomorphs continued during the latest Triassic, when this group was the protagonist of the first important pulse of dinosaur ascendance. They were apparently the first members of the group to disperse toward the eastern Pangaea (Buffetaut et al. 2000b), and they were a dominant faunal component of most Norian strata in Europe (Hungerbühler 1998b), South America (Bonaparte 1972; Bonaparte and Vince 1979), and southern Africa (Kitching and Raath 1984; Gauffre 1993a). Prosauropods are, however, rarer in other Norian paleocommunities, such as those of the western United States, whose main faunal components are crurotarsan archosaurs such as aetosaurs, phytosaurs, and rauisuchians (Long and Murry 1995). *Chindesaurus*, a putative carnivore about 3 m long, is the only well-known basal saurischian of these faunas and probably preyed on small- to medium-sized individuals of the aforementioned archosaurs. *Chindesaurus* might represent a later wanderer of the herrerasaur lineage, indicating a greater chronological and geographic distribution for the group. Other Norian dinosaurs of uncertain affinity include the enormous *Aliwalia*, which might have been a top predator of the Lower Elliot fauna in southern Africa, which also included prosauropods, rauisuchians, and traversodontid cynodonts (J. M. Anderson et al. 1998).

Guaibasaurus, perhaps the most basal theropod, comes from the Caturrita Formation, in southern Brazil, whose fauna also included prosauropods and kannemeyeriid dicynodonts. It was a medium-sized putative carnivore that probably preyed on small- to medium-sized vertebrates, occupying a similar niche to that of *Staurikosaurus* and coelophysids. Theropods in general are significantly more abundant in the Norian. There are records of the group in various parts of the world (Arcucci and Coria 1997; J. M. Anderson et al. 1998; Rauhut and Hungerbühler 2000), and there is evidence that they were already an important faunal component at the time (Colbert 1989; Schwartz and Gillette 1994).