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Reviewed work(s):
Source: *Journal of Vertebrate Paleontology*, Vol. 13, No. 4 (Jan. 14, 1994), pp. 451-476
Published by: Taylor & Francis, Ltd. on behalf of The Society of Vertebrate Paleontology
Stable URL: http://www.jstor.org/stable/4523532
Accessed: 27/04/2012 22:07

Journal of Vertebrate Paleontology 13(4):451–476, December 1993

THE SKULL AND NECK OF THE BASAL THEROPOD *HERRERASAURUS ISCHIGUALASTENSIS*

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ABSTRACT—We describe the skull and neck of *Herrerasaurus ischigualastensis* from specimens discovered recently in the Upper Triassic Ischigualasto Formation of northwestern Argentina. The skull has a rectangular profile and a transversely narrow snout. Marked supratemporal depressions for jaw adductor musculature on the skull roof and a well-developed, sliding intra-mandibular joint suggest that *Herrerasaurus ischigualastensis* was an active predator. The neck is relatively slender with prominent epipophyses on all of the cervical vertebrae. Diagnostic features of the species include the semicircular shape of the antorbital fossa and the long, slender posterodorsal process of the dentary.

Other features of the skull, such as the loss of the postfrontal and small post-temporal opening, constitute dinosaurian synapomorphies. These synapomorphies, however, remain equivocal at the level of Dinosauria because they cannot be evaluated in immediate dinosaurian outgroups for which cranial information is lacking. Comparisons of the skull and neck of *Herrerasaurus ischigualastensis* to other basal dinosaurs reveals several derived similarities with saurischians and, in particular, theropods. These synapomorphies include a subnarial foramen (between premaxilla and maxilla) shared with saurischians and an intra-mandibular joint shared with theropods. The cervical and cranial anatomy of *Herrerasaurus ischigualastensis,* however, is remarkably primitive compared to that in other basal dinosaurs.

INTRODUCTION

During the early evolution of dinosaurs, the structure of the skull underwent significant modifications. Many dental and osteological specializations are already in place in basal members of the three major dinosaurian clades, Ornithischia, Sauropodomorpha, and Theropoda. To discern the unique features shared by these dinosaurian cranial patterns is a challenging comparative exercise. Few dinosaurian cranial synapomorphies have ever been proposed. The recent discovery of well-preserved cranial material of the early dinosaur *Herrerasaurus ischigualastensis* provides an opportunity to explore these comparisons and to shed more light on the phylogenetic affinity of herrerasaurids.

We describe below the skull and neck of *Herrerasaurus ischigualastensis,* based primarily on materials discovered recently in the Ischigualasto Formation of northwestern Argentina (Novas, 1986; Sereno et al., 1988a).

Institutional abbreviations—**CM**, Carnegie Museum of Natural History, Pittsburgh; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge; **PVL**, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart; **USNM**, National Museum of Natural History, Washington, D.C.

MATERIAL

The skull and neck were poorly represented in the initial reports on the herrerasaurids *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei* (Reig, 1963; Colbert, 1970). The only cranial bone of *H. ischigualastensis* figured by Reig (1963:fig. 1) appears to have been incorrectly referred to this species (Novas, 1993).

Although not recognized until recently, cranial and cervical material of *H. ischigualastensis* had been collected many years ago. The first skull and partial skeleton was collected by A. S. Romer in 1958 in the lower levels of the Ischigualasto Formation (logged as an "indeterminate skeleton" in his field notes of 1958). The skull, which is complete but poorly preserved (MCZ 7063), is associated with an axis and partial postcranial skeleton (MCZ 7064) that was recently described as cf. *Staurikosaurus* sp. (Brinkman and Sues, 1987). In addition, Reig (1963:10) indicated that the holotype of *Ischisaurus cattoi* (MACN 18.060) included some cranial fragments, and these are also now referred to *H. ischigualastensis* (Novas, 1993). More recently, an additional partial skull and fragmentary postcranial skeleton was collected and described as *Frenguellisaurus ischigualastensis* (Novas, 1986; PVSJ 53). This material also belongs to *H. ischigualastensis* (Novas, 1993).

The following description of *H. ischigualastensis* is

TABLE 1. Measurements (mm) of the skull of *Herrerasaurus ischigualastensis* (PVSJ 407). Measurements of paired structures are from the left side. ( ) = estimated.

Abbreviation:	
Maximum skull length	300
Preorbital length	171
Maximum height of posterior skull	(95)
Maximum transverse width of occiput	75
Vertical diameter of orbit	60
Maximum length of antorbital fenestra	70
Length of upper tooth row	180
Length of lower tooth row	(122)
Depression of jaw articulation from maxillary alveolar margin	(21)

based principally on one skeleton (PVSJ 407; see also Sereno, 1993) that includes a well-preserved skull and neck. The skeleton was collected in 1988 during an expedition to the Ischigualasto Formation in northwest Argentina (Ischigualasto-Villa Unión Basin; Stipanicic, 1983). The skull is preserved with articulated lower jaws, a partial sclerotic ring in the right orbit, and the left stapes with the footplate lodged in the fenestra ovalis. Postmortem distortion of the skull is limited to some transverse compression of the snout and mandibular rami and some elevation of the right side of the skull. Checkered bone surfaces suggest that the skull may have been exposed subaerially before final burial. PVSJ 407 was buried within a medium-grained sandstone lens, and most of the skull and postcranial skeleton was enveloped in a hematite precipitate.

The cervical column was preserved in articulation with the skull. The anterior cervical vertebrae are better preserved than the posterior cervical vertebrae, and nearly all of the ribs are lacking. Parts of the axis, atlas, and several cervical centra are also preserved in other individuals (MACN 18.060, PVSJ 53, 373; MCZ 7064, Brinkman and Sues, 1987:fig. 1A).

DESCRIPTION

Skull

The skull is nearly four times as long as deep as seen in lateral view, and the snout is particularly narrow (Figs. 1–9). In posterior view, the skull is deeper than it is wide (Figs. 6, 7C, 8C; Table 1).

Dorsal Skull Roof—The *premaxilla* has two principal processes, a broad triangular posterolateral process and a narrow internarial process. The posterolateral process extends between the maxilla and nasal, excluding the former from the external naris by a broad margin as in ornithischians. The slender internarial process inserts between the nasals in the midline, but the distal end of the premaxilla-nasal suture cannot be discerned. Whether the tips of the internarial processes are separated in the midline by the premaxillae, as occurs in most theropods, cannot be determined. Although the ventral aspect of the premaxilla is not exposed, the narrow width of the snout suggests that the premaxillary palate was narrow (Figs. 7D, 8D).

The *maxilla* contacts the premaxilla anteriorly, nasal dorsally, lacrimal and jugal posteriorly, and palatine medially. The maxilla forms the posterior border of an oval fenestra, located posterior to the external naris (Figs. 1A, B, 7A, 8A). This large oval fenestra, a unique feature of the species, is positioned posterior to the external naris and opens internally above the premaxillary palate. As in most saurischians (e.g., *Allosaurus*, Madsen, 1976), a small subnarial foramen is located along the premaxilla-maxilla suture and opens internally at the posterior end of the premaxillary palate (Figs. 1A, B, 7A, 8A). Several larger foramina exit above the tooth row and pass anterioventrally in a shallow grooves.

The antorbital fossa (the depression bordering the antorbital fenestra) is very narrow in *H. ischigualastensis*. The maxillary portion of the fossa forms a narrow band along the anterior and dorsal margins of the antorbital fenestra (Figs. 1A, B, 2, 3, 7A, 8A). The anterior margin of the fossa is invaginated, as occurs in many other dinosaurs (Fig. 10A, B).

The medial aspect of the maxilla is exposed in PVSJ 53 and shows distinct interdental plates. Contact with the palatine along the lateral margin of the palate is visible through the antorbital fenestra in PVSJ 407 (Figs. 1A, 2).

The *nasal* forms the narrow snout roof, spanning approximately two-thirds of the length of the skull. Sutural contacts of the nasal include the premaxilla, maxilla, lacrimal, prefrontal, and frontal. The anterior two-thirds of each nasal is transversely arched, resulting in a shallow median depression. The lateral margin of the nasal approaches the dorsal rim of the antorbital

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FIGURE 1. **A–C**, **F–G**, skull of *Herrerasaurus ischigualastensis* (PVSJ 407) in left lateral (**A**), right lateral (**B**), dorsal (**C**), ventral (**F**), and posterior (**G**) views; **D**, posterodorsal process of the right dentary in cross-section (lateral to the right); **E**, midsection of left mandibular ramus in ventral view. Abbreviations: **a**, angular; **ar**, articular; **bo**, basioccipital; **bs**, basisphenoid; **d**, dentary; **emf**, external mandibular fenestra; **ec**, ectopterygoid; **eo**, exoccipital; **ept**, epipterygoid; **f**, frontal; **imf**, internal mandibular fenestra; **j**, jugal; **l**, lacrimal; **ls**, laterosphenoid; **m**, maxilla; **n**, nasal; **op**, opisthotic; **p**, parietal; **pl**, palatine; **pm**, premaxilla; **po**, postorbital; **pra**, prearticular; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **qf**, quadrate foramen; **qj**, quadratojugal; **sa**, surangular; **saf**, surangular foramen; **scp**, sclerotic plate; **sf**, subnarial foramen; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **st**, stapes; **stf**, supratemporal fossa; **tm**, tooth mark; **v**, vomer. Double–bar pattern indicates matrix. Cross–hatching indicates broken bone surface. Scale bar for **A–C** and **F–G** (below **G**) equals 5 cm; scale bars in **D** and **E** equal 1 cm.

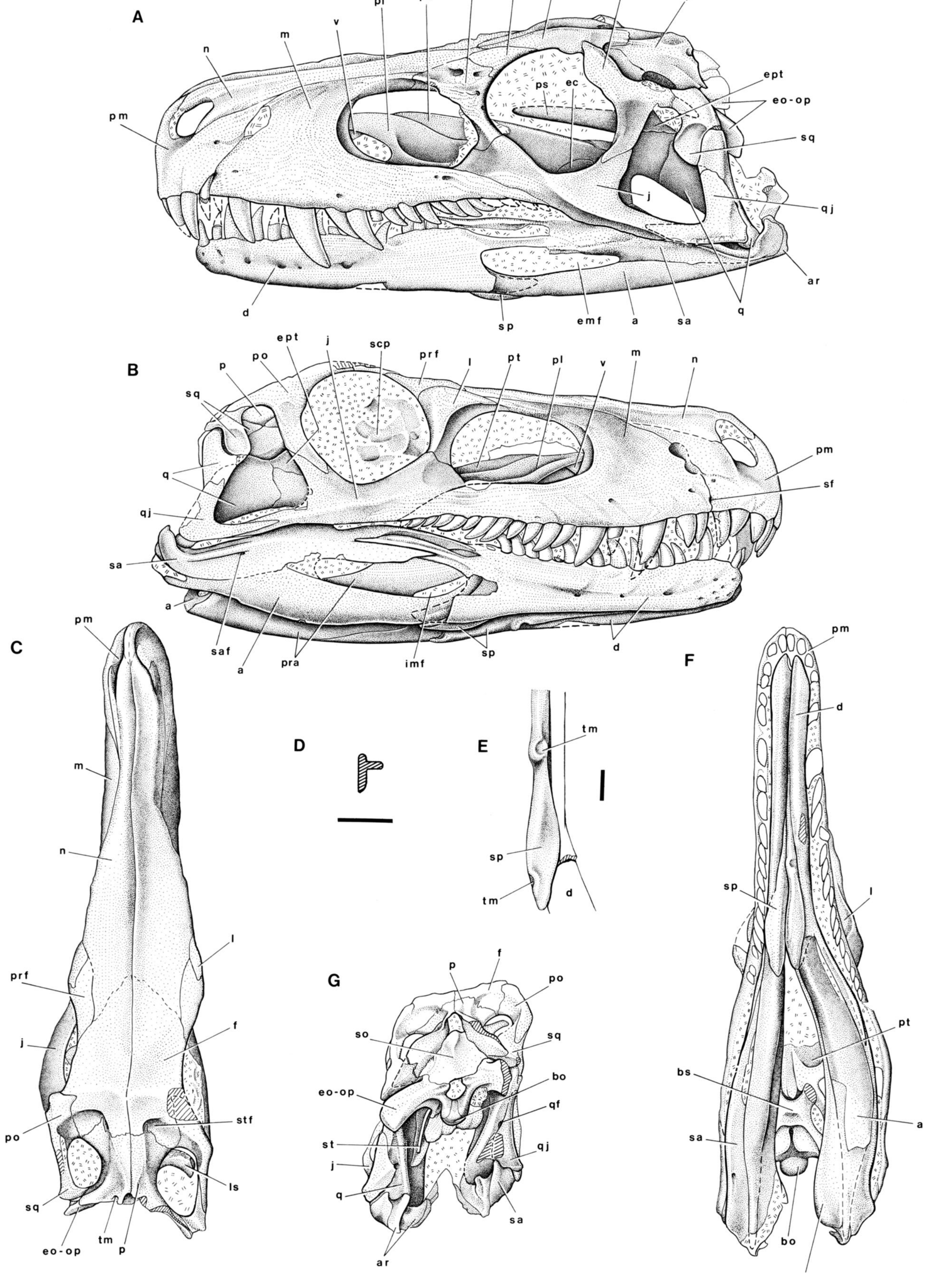
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FIGURE 2. Stereopairs of the skull of *Herrerasaurus ischigualastensis* (PVSJ 407) in left lateral view. Scale bar equals 5 cm.

fossa. Posteriorly, the nasal broadly overlaps the frontal.

The L-shaped *lacrimal* contacts the maxilla anteriorly, the nasal and prefrontal medially, and the jugal ventrally. The external surface of the lacrimal is rugose and pitted, but there is no development of crests or fossae as occur in many theropods. The ventral process of the lacrimal is broadly overlapped by a thin anterior lamina of the jugal, which separates the maxilla and lacrimal in lateral view. A short lateral wall of the lacrimal encloses the posterodorsal corner of the fossa. Ventral to this invagination, the antorbital fossa opens laterally as a shallow depression on the ventral process of the lacrimal and anterior process of the jugal. The lacrimal foramen is not exposed.

The sutural contacts of the *prefrontal* include the nasal, lacrimal, and frontal. Portions of these sutural contacts have been obscured by surface damage. The prefrontal has a lenticular shape in dorsal view, and its external margin forms part of the orbital rim. In lateral view, the prefrontal has a short triangular ventral process that overlaps the lacrimal on the anterior margin of the orbit (Figs. 1A, 7A, 8A).

The *frontal* is approximately twice as long as wide and is overlapped by the nasal, prefrontal, and postorbital, with the latter two bones set in notches on the frontal. The frontal and parietal join along an interdigitating suture. The supratemporal fossa is broad and sharply incised on the frontal. The fossa has an angular, rather than arcuate, anteromedial corner and is sharply incised laterally on the postorbital (Figs. 1C, 7B, 8B). The posterior extremity of the frontal reaches the supratemporal fenestra but does not form a significant part of its anterior wall. Another shallow depression is present on each frontal immediately anterior to the supratemporal fossa.

The paired *parietal* joins the frontal anteriorly, the laterosphenoid ventrally, and the squamosal, supraoccipital, and paroccipital process posteriorly. The contacts with the braincase (supraoccipital, paroccipital process) are partially disarticulated. The medial portion of each parietal is flat, but to each side, the supratemporal fossa is incised. A sharp crest along the medial margin of the supratemporal fossa converges toward the midline at the posterior skull margin (Figs. 1C, 4, 7B, 8B). There is no evidence of a median pineal foramen between the parietals.

The posterolateral wings of the parietal are separated

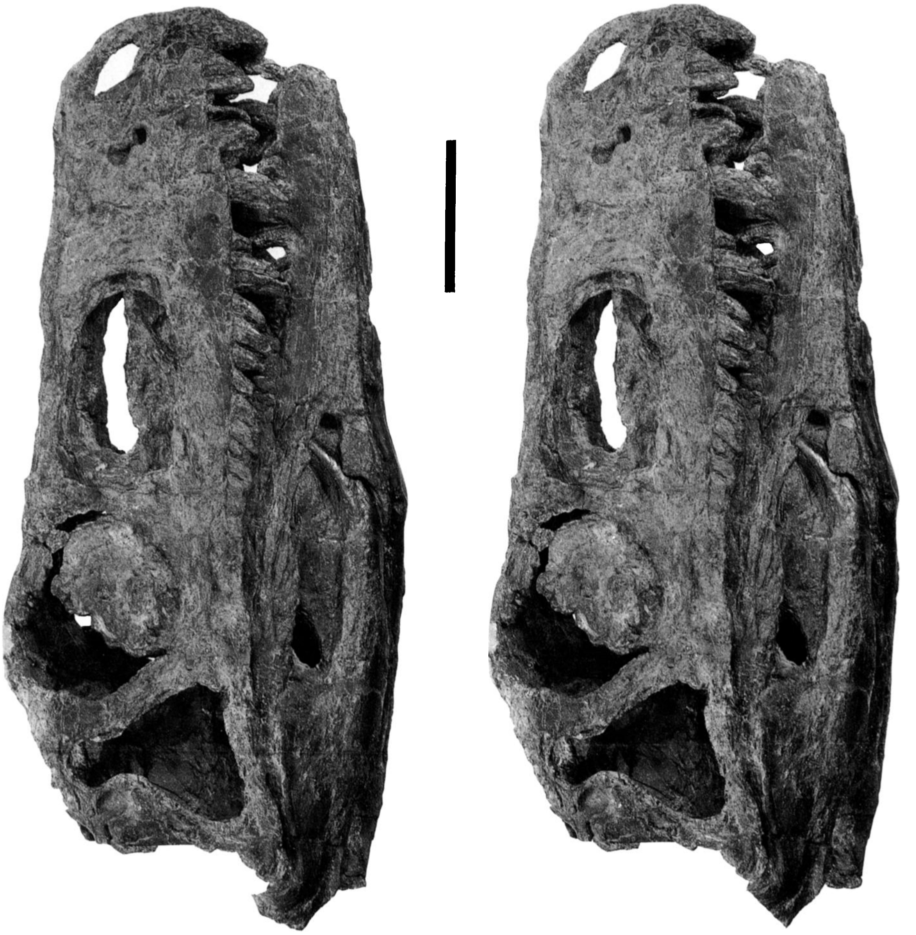

FIGURE 3. Stereopairs of the skull of *Herrerasaurus ischigualastensis* (PVSJ 407) in right lateral view. Scale bar equals 5 cm.

by a shallow median notch. Each wing of the parietal twists into a vertical plane, with its ventral edge resting on the lateral margin of the supraoccipital. Its distal end passes posterior to the squamosal, resting on the dorsal margin of the paroccipital process and forming the dorsal rim of the post-temporal foramen.

The triradiate *postorbital* contacts the frontal medially, the squamosal posteriorly, and the jugal ventrally. On the anterior wall of the supratemporal fossa, the postorbital and parietal share a narrow contact. The postorbital also receives the head of the laterosphenoid, judging from the position of the disarticulated right laterosphenoid (Fig. 1C). The posterior process is the shortest and most slender. It rests in a slot on the anterior process of the squamosal and bridges the narrow dorsal part of the laterotemporal fenestra. The tongue-shaped anteromedial process is slightly longer and, unlike other dinosaurs, is excavated medially by the supratemporal fossa. The ventral process is longest and overlaps the ascending process of the jugal. The distal tip of the ventral process remains superficial and does not insert into a shallow socket, as occurs in some early dinosaurs (e.g., *Lesothosaurus,* Sereno, 1991a).

The *squamosal* has three prominent processes. The short anterior process is the most slender and receives the posterior process of the postorbital in a slot on its lateral surface. Diagnostic features of the squamosal in *H. ischigualastensis* include the subquadrate shape of the ventral process and the subtriangular depression that occupies most of its lateral surface (Fig. 7A). The head of the quadrate articulates against the concave posterior margin of the ventral process, forming a rounded joint that may have allowed minor movement. The ventral process approaches, but does not contact, the dorsal tip of the quadratojugal, as is best preserved on the left side (Figs. 1A, 2). The long, tongue-shaped medial process overlaps the anterior surface of the posterolateral process of the parietal and extends anteriorly along the side wall of the braincase. Its anterior extremity approaches the laterosphenoid (Fig. 1B), as also occurs in early sauropodomorphs (Huene, 1926).

The short, hook-shaped posterior process curves over

FIGURE 4. Stereopairs of the skull of *Herrerasaurus ischigualastensis* (PVSJ 407) in dorsal view. Scale bar equals 5 cm.

the top of the quadrate head (best preserved on the right side), but unlike most dinosaurs, it does not extend ventrally between the quadrate head and paroccipital process. In *H. ischigualastensis,* the paroccipital process articulates directly against the posterior aspect of the quadrate head.

The anterior, dorsal, and posterior processes of the *jugal* contact the maxilla, lacrimal, postorbital, and quadratojugal on the external skull surface and the palatine and ectopterygoid internally. The sheetlike anterior process broadly overlaps the maxilla and lacrimal and increases in depth anteriorly, from mid-orbit toward the antorbital fenestra. A low, rugose ridge passes along the long axis of the jugal. The jugal contributes to the posterior margin of the antorbital fenestra, where it contacts the posterior end of the palatine. The posteroventral corner of the antorbital fossa continues as a shallow depression across the anterior end of the jugal. The jugal-postorbital contact is bevelled, and the postorbital bar is transversely compressed. The ventral margin of the jugal is gently sinuous.

The posterior process is the most slender and is forked to receive the slender anterior process of the quadratojugal, as occurs in saurischians (Fig. 10B, *Plateosaurus*). The dorsal prong of the forked end of the jugal overlaps the quadratojugal. The ventral prong, in contrast, is trough-shaped proximally and planar distally, where it is overlapped laterally by the quadratojugal.

The dorsal process of the L-shaped *quadratojugal*

FIGURE 5. Stereopairs of the skull of *Herrerasaurus ischigualastensis* (PVSJ 407) in ventral view. Scale bar equals 5 cm.

has a maximum width nearly twice that of the anterior process. The dorsal process completely overlaps the ventral one-half of the quadrate shaft. Unlike other dinosaurs, the posterior margin of the bone is deflected medially onto the posterior aspect of the quadrate shaft (Figs. 1A, B, G, 7A, C, 8A, C). The slender anterior process inserts into the forked distal end of the jugal as described above. The posteroventral corner of the quadratojugal approaches, but does not contribute to, the articulation with the lower jaw.

Palate—The *quadrate* is divided into two parts, a vertical shaft and plate-like pterygoid ramus. The shaft ends dorsally in a rounded head, which is exposed in lateral view of the skull (Figs. 1B, 7A, 8A). In proximal view of the disarticulated quadrate, the head is subtriangular with the narrowest apex directed posteriorly. The flattened medial side of the shaft near the head is butted against the paroccipital process. The smooth, planar articular surface between the quadrate head and paroccipital process may indicate that some movement of the quadrate head was possible.

The straight shaft of the quadrate angles slightly anterodorsally in lateral view (Figs. 1A, 2, 7A, 8A). Below the head, the shaft expands anteriorly and the ventral one-half is overlapped by the quadratojugal. In posterior view, the shaft expands toward the distal condyles. The quadrate foramen forms a deep notch in the lateral margin of the shaft and is bordered laterally by

FIGURE 6. Stereopairs of the skull of *Herrerasaurus ischigualastensis* (PVSJ 407) in posterior view.

the quadratojugal (Figs. 1G, 6, 7C, 8C). The distal condyles form two anteromedially angling crests (PVSJ 53, 407), as in other archosaurs.

The quadrate head and condyles extend about 1 cm dorsal and ventral to the pterygoid ramus, respectively. The pterygoid ramus extends from the medial side of the shaft, overlapping the pterygoid and contacting the epipterygoid anterodorsally (Figs. 1B, 7A, 8A). The ventral margin of the pterygoid ramus is deflected medially, forming a shelf that narrows toward the basipterygoid articulation.

The *pterygoid* contacts the vomer anteriorly, the palatine and ectopterygoid laterally, and the epipterygoid, quadrate, and basisphenoid posteriorly. Dorsal to the basipterygoid articulation, the pterygoid is constricted, with quadrate and palatal rami projecting posterolaterally and anteriorly, respectively. The palatal ramus is composed of two perpendicular planar sheets. The first sheet forms the palate proper, a triangular surface broadly exposed in ventral view, angling ventrolaterally away from the midline (Figs. 7D, 8D). The lateral margin is overlapped dorsally by the ectopterygoid and palatine, and contributes to the border of a large postpalatine fenestra. The second sheet is vertically disposed and articulates with its opposite, forming a low, median palatal keel that projects anteriorly between the palatines and vomera. This vertical sheet, present in all archosaurs, is partially exposed through the antorbital fenestra.

The *palatine,* only partially exposed in dorsal view through the antorbital fenestra (Figs. 1A, 7A, 8A), forms a trapezoidal sheet that angles ventrolaterally away from the midline. It contacts the vomer and pterygoid medially and the maxilla and jugal laterally. It may have contacted the lacrimal on the medial side of the jugal, but this latter contact is not exposed. As is common among dinosaurs (e.g., *Lesothosaurus*; Sereno, 1991a), the dorsal surface of the palatine is depressed, with upturned lateral and anterior margins. The palatine must have formed the anterior margin of a postpalatine fenestra, given the preserved margins of the pterygoid and ectopterygoid (Figs. 7D, 8D).

The *ectopterygoid* is fully exposed in dorsal view on the left side. It has a strong, hook-shaped lateral process that abuts against the jugal just below the orbital margin. Medially, the ectopterygoid expands as a thin fan-shaped plate that overlaps the dorsal surface of the pterygoid and extends toward the tip of the mandibular flange. The ventral surface is not exposed.

The posterior end of the right *vomer* is exposed in lateral view through the antorbital fenestra (Fig. 1B). Most of the vomera are hidden from view and so their shape and degree of co-ossification cannot be determined. They form a vertical, median plate that reaches a maximum depth of about 14 mm posteriorly. Assuming that the vomera extended anteriorly to reach the premaxilla, they would span approximately one-third of the length of the palate.

The triangular *epipterygoid* has a thin, fan-shaped base that overlaps the lateral surface of the quadrate ramus of the pterygoid and contacts the corner of the pterygoid ramus of the quadrate (Figs. 1A, B, 7A, 8A). The spine-shaped dorsal projection of the epipterygoid approaches, but does not appear to contact, the lateral process of the laterosphenoid.

Braincase—In PVSJ 407, the braincase has been dislodged 6 to 8 mm from its natural articulation with the dorsal skull roof and palate (Figs. 1G, 6). Most of the cranial foramina are not exposed, due to the narrow space between the pterygoquadrate ramus and the side wall of the braincase.

The triangular *supraoccipital* angles posteroventrally and contacts the parietal and exoccipital-opisthotic. Its ventrolateral apex reaches the small post-temporal foramen (Figs. 7C, 8C). A strong median ridge is present in the dorsal one-half of the supraoccipital for attachment of nuchal ligaments. The wedge is lodged in a posterior notch between the parietals and is visible in dorsal view of the skull (Figs. 7B, 8B).

The exposed contacts of the *basioccipital* include the exoccipital-opisthotic and basisphenoid. The basioccipital forms the ventral two-thirds of the occipital condyle. The basal tubera project ventrally a few mm below the condyle in posterior view (Figs. 7C, E, 8C, E). The tubera, which are separated by a median cleft, are each composed of a medial columnar thickening and a lateral plate-like tab. The lateral margin of the tab continues dorsally as a ridge on the lateral side of the braincase posterior to the fenestra ovalis (Figs. 7E, 8E).

The *basisphenoid* contacts the basioccipital posteriorly and the pterygoids anteriorly at the basipterygoid articulation. In ventral view, a shallow central depression is present in the center of the basisphenoid; the basipterygoid processes and posterolateral buttresses to the basal tubera radiate away from the central depression, forming a symmetrical cross in ventral view (Figs. 7D, 8D). The short basipterygoid processes are slightly flattened dorsoventrally and oval in cross-section. In lateral view, they project anteroventrally at about 45° from the vertical (Figs. 7E, 8E). In ventral view, they project anterolaterally at about 45° from the midline (Figs. 7D, 8D), and, in posterior view, they project at about 45° ventrolaterally from the sagittal plane, extending slightly below the level of the occipital condyle (Figs. 7C, 8C). The transversely compressed *parasphenoid* rostrum projects anteriorly from the body of the basisphenoid toward the converging palatal rami of the pterygoids (Figs. 1A, 2, 7A, 8A).

As in all dinosaurs, the *exoccipital-opisthotic* is completely co-ossified. It contacts the basioccipital ventrally, the quadrate, squamosal, and prootic anteriorly, and the parietal dorsally. It forms the lateral border of the foramen magnum and has an articular facet on each side for the anterior end of the proatlas (Fig. 8C, apro). A notch in the dorsal margin of the paroccipital process forms the ventral border of the post-temporal foramen, which is enclosed dorsally by the parietal. On the side wall of the braincase, two crests, or flanges of bone, are present on the exoccipital-opisthotic (Figs. 7E, 8E). The more posterior crest separates the otic openings from the posterior foramina for N. hypoglossus XII, and the more anterior descends from the paroccipital process anterior to the fenestra ovalis. None of the cranial foramina are exposed, except the foramen for the internal carotid artery.

The *prootic* is partially exposed in the right supratemporal fossa. The right *laterosphenoid* is also exposed anterior to the prootic and ventral to the parietal in the center of the right supratemporal fossa (Fig. 1C). The transversely expanded articular head of the laterosphenoid is smooth and rounded and articulated in a socket on the ventral side of the frontal and postorbital, as in most ornithischians and sauropodomorphs.

Sclerotic Ossicles—Several disarticulated sclerotic plates are preserved in the anteroventral one-half of the right orbit (Fig. 1B). One of the better exposed plates is subrectangular, the long axis of which is approximately 1 cm in length. Little else can be said about the shape of the individual plates or the arrangement of the ring.

Lower Jaw—The lower jaws are preserved in several individuals (PVSJ 53, 407; MACN 18.060). In PVSJ 407, the anterior half of the lower jaws are pressed together, such that only the posterior half of the lower jaw is exposed in medial view (Figs. 1F, 5). As a result, the presence or absence of a coronoid bone cannot be determined. A striking feature of the lower jaw is the well-developed intra-mandibular joint.

The *dentary,* the longest and most robust element of the lower jaw, is slightly upturned anteriorly. Several vascular foramina open along its length, the largest positioned posteriorly and connected to more anterior foramina by a groove. Several smaller foramina open near the symphysis, as in small theropods such as *Deinonychus* or *Velociraptor.* Medially, the dentary is overlapped by the splenial, and the symphysis is restricted to a bevelled surface at the distal end of the dentary (Fig. 1F).

Posteriorly, the dentary is forked. The arched margin between the posterior processes forms the anterior margin of the mandibular fenestra (Figs. 1B, 3, 7A, 8A). An unusually elongate and slender posterodorsal process, which reaches a maximum depth of only 7 mm, inserts into a slot on the surangular. It slides against smooth surfaces on the lateral side of the dorsal prong of the surangular and on the medial side of the ventral prong. The slender dentary process is reinforced by a prominent lateral rib (4 mm in depth), which extends along the length of the dentary process. The posterodorsal process of the dentary thus is T-shaped in cross-section (Fig. 1D), a condition unique

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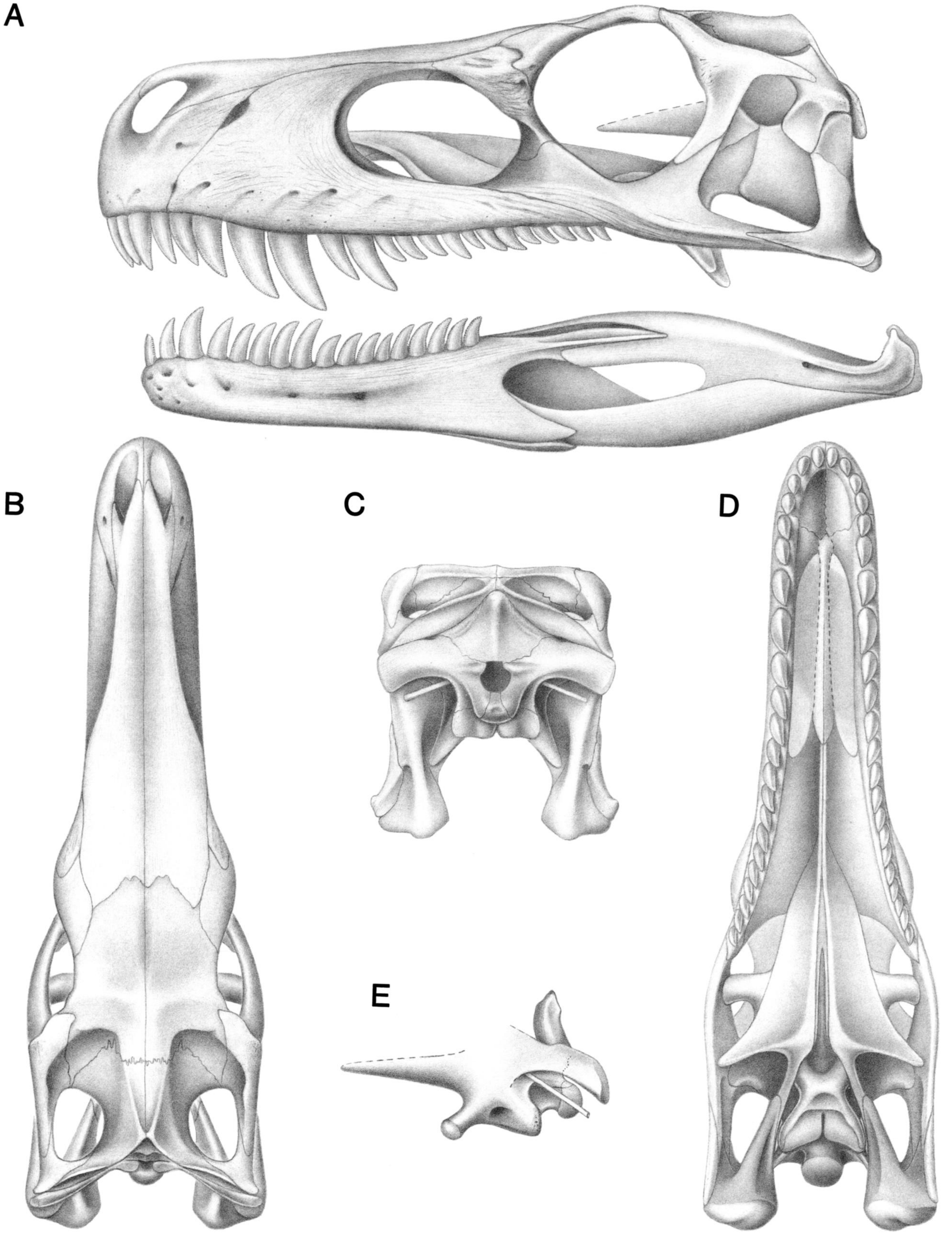
FIGURE 7. **A–D**, Skull reconstruction of *Herrerasaurus ischigualastensis* (based on PVSJ 407) in left lateral (**A**), dorsal (**B**), posterior (**C**), and ventral (**D**) views. **E**, left lateral view of disarticulated braincase. See Figure 8 for bone identifications.

FIGURE 8. **A–D**, Skull reconstruction of *Herrerasaurus ischigualastensis* (based on PVSJ 407) in left lateral (**A**), dorsal (**B**), posterior (**C**), and ventral (**D**) views. **E**, left lateral view of disarticulated braincase. Abbreviations: **antfo**, antorbital fossa; **apro**, articular surface for the proatlas; **fica**, foramen for the internal carotid artery; **ppf**, postpalatine fenestra; **pra**, prearticular; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **ptf**, post-temporal foramen. Other abbreviations as in Figure 1.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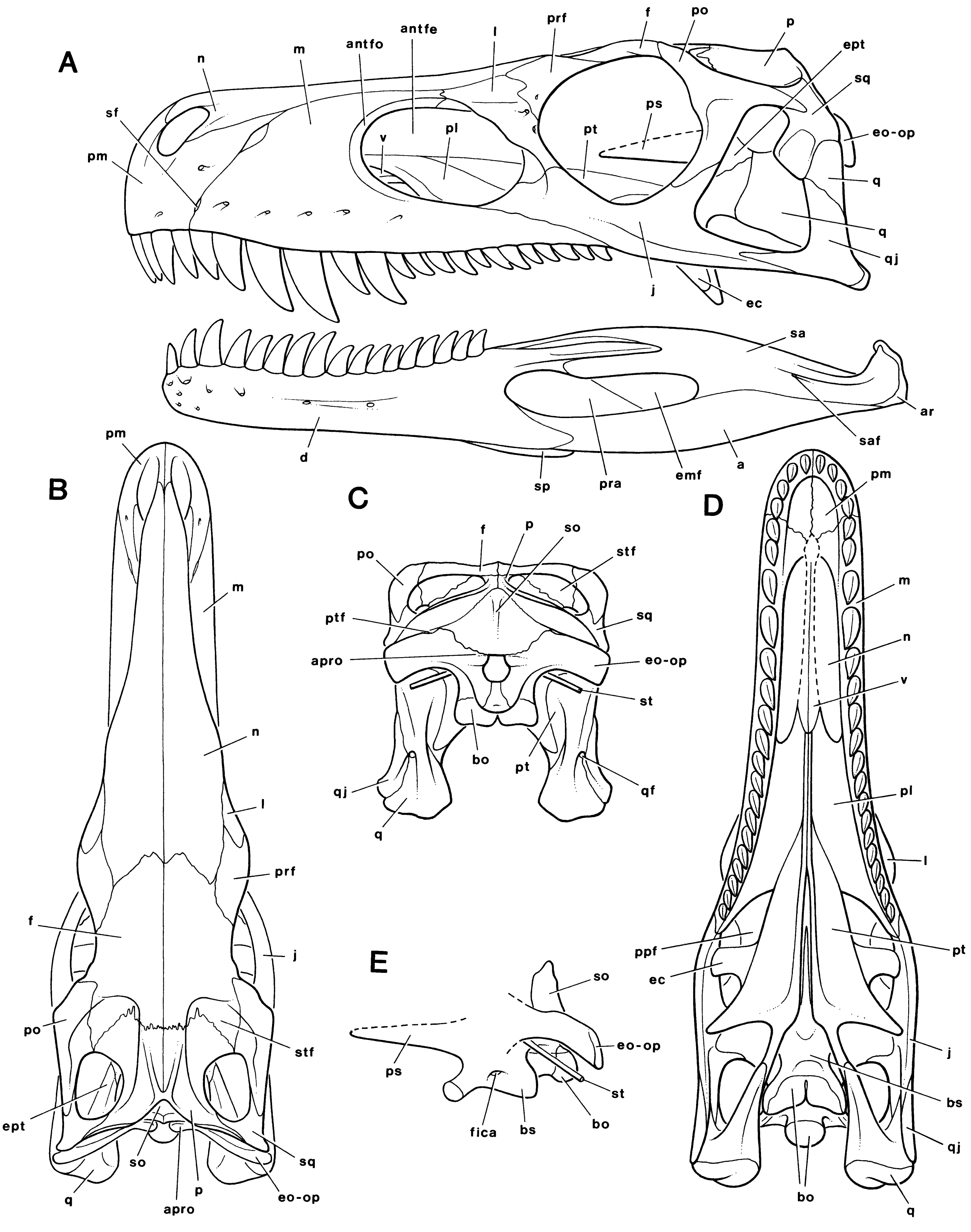
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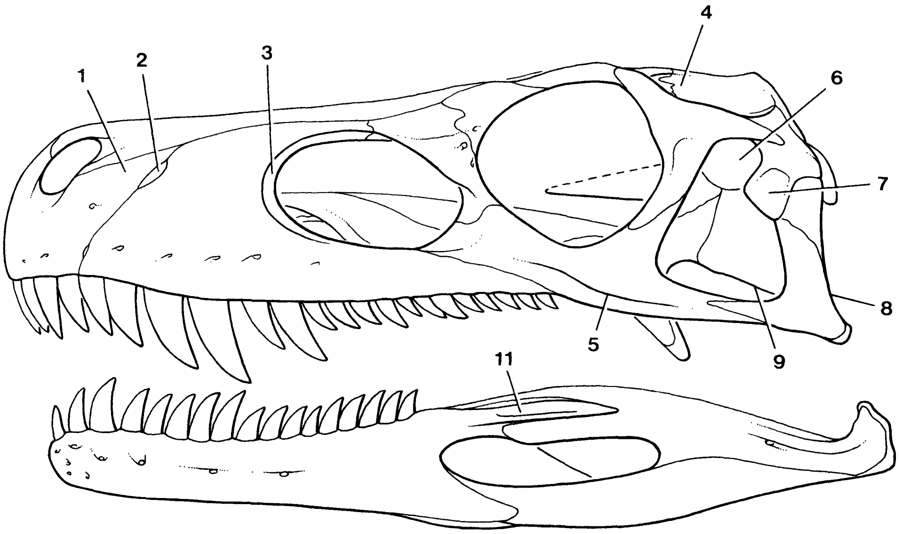

FIGURE 9. Skull reconstruction of *Herrerasaurus ischigualastensis* showing the location of autapomorphies 1–8 and 10.

to *H. ischigualastensis.* During flexion of the intramandibular joint, it abuts against the ventral prong of the surangular, resisting further ventral rotation of the dentary. The thin, subtriangular posteroventral process of the dentary slides against a polished articular surface on the lateral side of the angular.

The *surangular* forms the lateral portion of the jaw articulation where it contacts the lateral condyle of the quadrate (Figs. 1A, B, F, G, 7A, 8A). It curls dorsally behind the jaw articulation, overlapping the lateral aspect of the articular. Just below the jaw articulation, a rounded ridge is developed and disappears anteriorly. A small surangular foramen is present under the ridge. The ventral margin of the surangular is overlapped by the angular posteriorly and forms most of the dorsal margin of the external mandibular fenestra. Anteriorly, the surangular is deeply cleft to receive the posterodorsal process of the dentary. The entire lateral surface of the dorsal prong of the surangular is bevelled for smooth articulation with the posterodorsal process of the dentary.

The *angular* extends from the intra-mandibular joint to the posterior extremity of the retroarticular process. Anteriorly, the angular curves dorsally to form a polished hook-shaped process that articulates laterally with the dentary and ventrally with the splenial (Figs. 1B, 3). Posteriorly, the angular continues as a narrow strip to the distal end of the retroarticular process, where it overlaps the articular, surangular, and prearticular (Fig. 1F).

The *splenial* extends anteriorly at least as far as the seventh dentary tooth, where it tapers in width to a thin plate. Posteriorly, the splenial wraps around the ventral margin of the dentary as a tongue-shaped process (Figs. 1E, 5), with a trough-shaped articular surface for the angular. The tongue-shaped process of the splenial is transversely concave and the angular is transversely convex, which is opposite the condition in other theropods. This tongue-shaped process of the splenial is visible in lateral view ventral to the dentary (Figs. 7A, 8A) and articulates on the ventral aspect of the angular, as in dromaeosaurid theropods (Colbert and Russell, 1969; Ostrom, 1969). The remainder of the posterior end of the splenial is exposed between the posterior processes of the right dentary (Fig. 1B). Judging from this exposure, the splenial appears to have contacted the prearticular on the dorsal margin of the internal mandibular fenestra.

The *prearticular,* a thin plate-like bone on the medial aspect of the lower jaw, extends from the coronoid region anteriorly to the distal end of the retroarticular process posteriorly (Fig. 1B, F). Anteriorly, the prearticular is broad, as seen through the external mandibular fenestra (Figs. 1B, 3). Dorsally, it borders the adductor fossa and, ventrally, it forms the margin of the internal mandibular fenestra. The internal mandibular fenestra appears to be at least 25 mm in anteroposterior length, or more than one-third the length of the external mandibular fenestra. Posteriorly, the prearticular twists onto the ventral side of the retroarticular process. Here it overlaps the articular and, in turn, is overlapped by the angular.

The *articular,* best exposed in posterior view (Fig. 1G), is overlapped by the surangular, angular, and prearticular. The medial surface of the articular is crescentic and extends posterior to the jaw articulation, curving dorsally as a vertical process. A second vertical process, formed by the articular and surangular, is equal in height and positioned laterally (Figs. 1G, 6).

Stapes—The left stapes is preserved with the proximal end in place in the fenestra ovalis and the shaft hanging ventrolaterally alongside the left basal tuber (Figs. 1G, 6). The foot-plate is not exposed. Judging from the position of the proximal shaft, the foot-plate

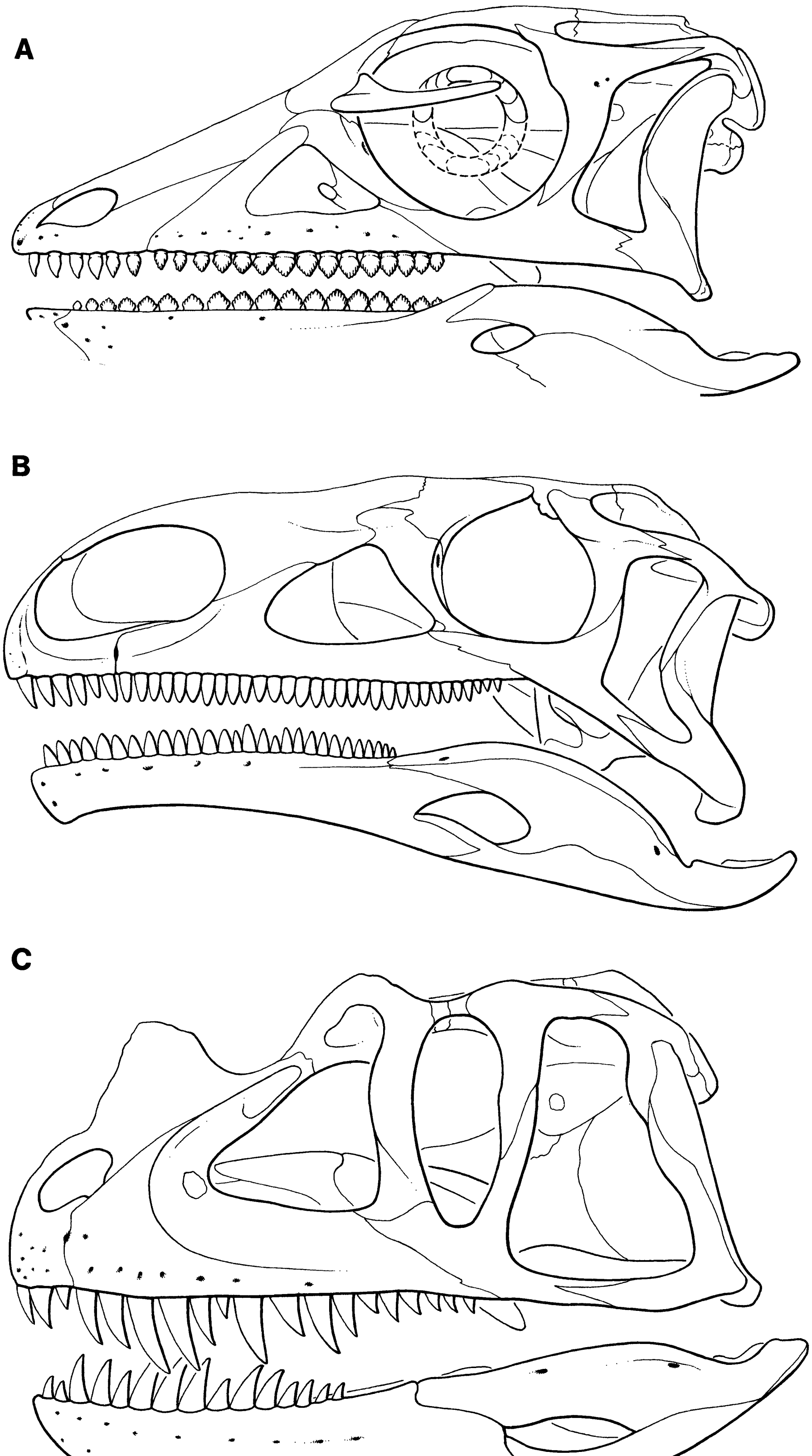

FIGURE 10. Comparative skull reconstructions of the basal dinosaurs (**A**) *Lesothosaurus diagnosticus* (after Sereno, 1991a), (**B**) *Plateosaurus engelhardti* (based on SMNS 13200), and (**C**) *Ceratosaurus nasicornis* (based on USNM 4735).

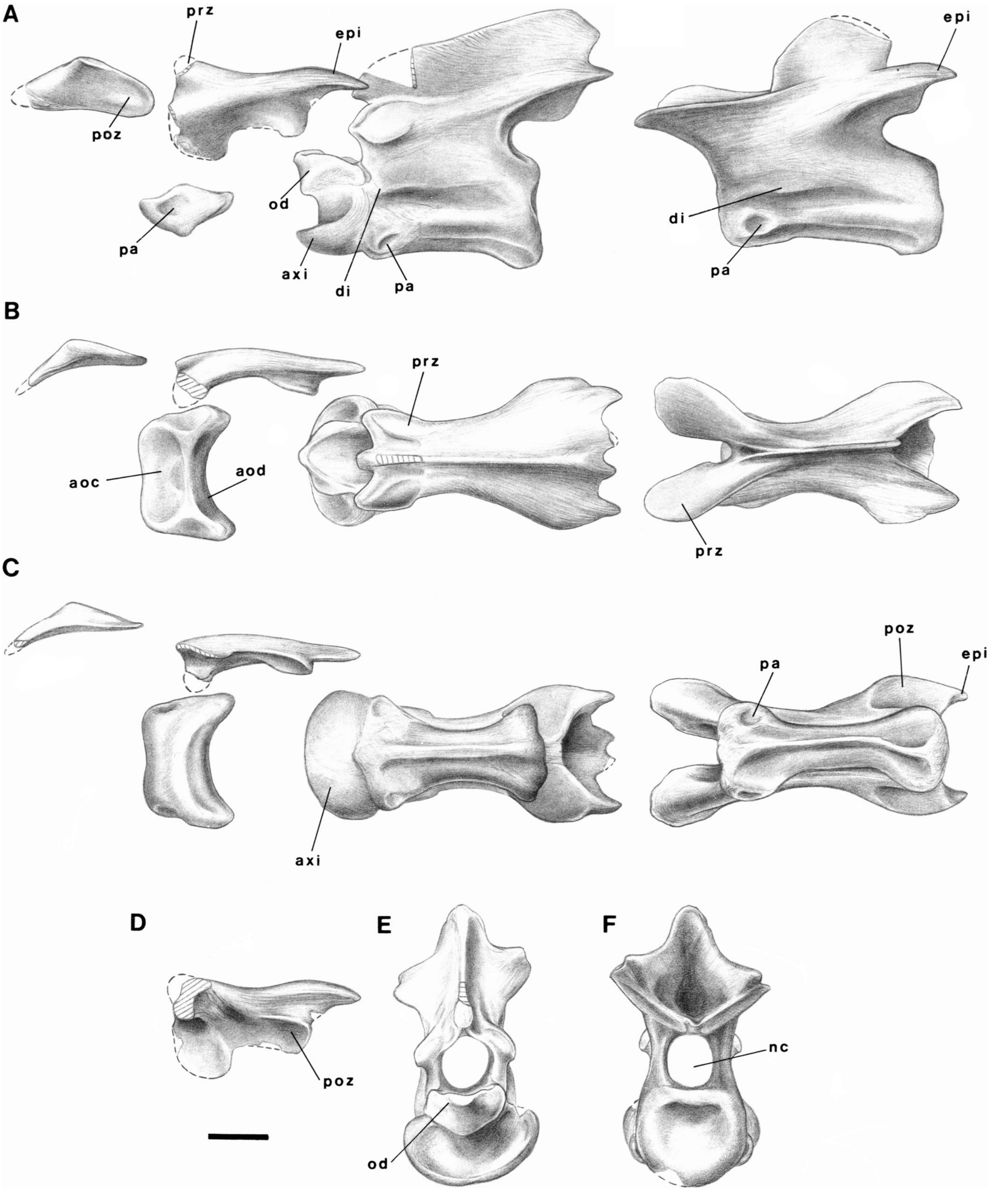

FIGURE 11. Anterior cervical column of *Herrerasaurus ischigualatensis* (PVSJ 407). **A**-**C**, "exploded" views of the proatlas, atlas, axis, and third cervical vertebrae in left lateral (**A**), dorsal (**B**), and ventral (**C**) views; **D**, right atlantal neural arch in medial view; **E**-**F**, axis in anterior (**E**) and posterior (**F**) views. Abbreviations: **aoc**, articular surface for the occipital condyle; **aod**, articular surface for the odontoid; **axi**, axial intercentrum; **di**, diapophysis; **epi**, epipophysis; **nc**, neural canal; **od**, odontoid;

is probably seated in the fenestra ovalis in natural articulation. The slender columelliform shaft has a diameter somewhat less than 2 mm and a preserved length of 28 mm. The stapes with its foot-plate, thus, is approximately 30 to 32 mm long, which nearly spans the distance from the side wall of the braincase to the posterior margin of the quadrate shaft, where the tympanum must have been located. The cartilagenous extrastapes could not have been very long.

Teeth—There are four *premaxillary teeth.* Because of poor preservation, some structural characteristics and virtually all surface details are lacking. The anteriormost tooth is positioned very near the midline and is the least transversely compressed of the premaxillary teeth. In lateral view, the crown is gently recurved with a rounded anterior margin. Because the posterior margin is not exposed, it is impossible to determine whether the crown was elliptical or had a D-shaped cross-section. The second, third, and fourth premaxillary teeth are transversely compressed, with rounded anterior and sharp posterior margins and increase in size from the second to the fourth tooth. The transition between premaxillary and maxillary tooth rows is continuous, without an intervening diastema or noticeable change in crown structure.

There are 17 or 18 *maxillary teeth.* Despite some variation in crown height due to tooth replacement, maximum tooth size (measured from the crown base or alveolus) occurs in the third or fourth maxillary tooth position, posterior to which tooth size gradually decreases. The posterior maxillary teeth under the orbit are relatively short and posteriorly directed. The serrations are not particularly well-preserved. The proximal half of the anterior margin is rounded and appears to lack serrations. The distal halves of anterior and posterior margins have approximately five serrations per mm.

There are approximately 16 *dentary teeth,* which are somewhat shorter than the opposing maxillary teeth. The short first dentary tooth is slightly procumbent and only gently recurved. The anterior margin of this tooth is rounded and lacks serrations. The posterior margin forms a sharp edge a short distance above the base of the crown and has approximately six serrations per mm. Dentary tooth size increases to a maximum in the third and fourth tooth positions, slightly in advance of the largest maxillary tooth. The anterior end of the dentary ramus is slightly swollen to accommodate the roots of these large dentary teeth. Posterior to the fourth tooth, the lateral alveolar margin is gently concave, and tooth size decreases posteriorly. Serrations are exposed on the posterior margins of several dentary crowns and are equal in size and form to those on maxillary crowns.

TABLE 2. Measurements (mm) of cervical vertebrae in *Herrerasaurus ischigualastensis* (PVSJ 407, MACN 18.060). Measurements of paired structures are averages of both sides. Abbreviations: c = calculation based on proportions of third cervical vertebra; r = measurement from right side only.

	PVSJ 407	
Proatlas		
Maximum length		26
Maximum depth		10
Atlas		
Maximum length of neural arch		34r
Maximum length of ventral surface of intercentrum		10
Maximum length of odontoid		10
Maximum width of odontoid		14
Axis		
Maximum length of intercentrum		11
Maximum width of intercentrum		25
Maximum length of centrum		33
Maximum depth of anterior and posterior centrum faces		15
Maximum width across prezygapophyses		13
Maximum width across postzygapophyses		27
Postaxial cervical vertebrae		
	Maximum centrum length	Maximum length between pre- and postzygapophyses (excluding epipophyses)
Cervical 3	40	53
4	43c	56
5	44c	58
6	43c	57
7	—	—
8	31	43
9	—	46
10	—	—
	MACN 18.060	
	Maximum centrum length	Maximum centrum height (posterior face)
Cervical 4?	37	19
5?	35	19

Cervical Column

Proatlas—Both proatlantal elements were preserved near the foramen magnum, but neither was in natural articulation with the skull or atlas (Fig. 11A–C; Table 2). Each element is subtriangular and transversely flattened. The dorsal margin and apex are thickened, in contrast to the thin ventral margin. The anterior end

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←

pa, parapophysis; **poz**, postzygapophysis; **prz**, prezygapophysis. Cross-hatching indicates broken bone surface. Scale bar equals 1 cm.

is narrower than the tablike posterior end and has a ridge on its external surface near the ventral margin (Fig. 11A). The tip of the anterior end articulates against a shallow facet lateral to the foramen magnum (Figs. 1G, 6, 8C, apro). The posterior end is rounded laterally and flat medially (Fig. 11C). The flat medial surface of the posterior end overlaps the prezygapophysis of the atlantal neural arch. In natural articulation, the proatlantal elements would converge slightly toward their cranial articulation (Fig. 11B, C).

Atlas—The atlas is composed of a centrum, intercentrum, and paired neural arches (Fig. 11A–E; Table 2). The centrum, or odontoid, is completely co-ossified with the axis (Fig. 11A, E; Brinkman and Sues, 1987: fig. 1A). The odontoid is subcircular in dorsal view with a distinct anteromedian projection. This rounded projection fits into a pit on the occipital condyle. Ventral to this projection, the anterior surface of the odontoid forms a broad, U-shaped trough, which is concave dorsoventrally and convex transversely (Fig. 11A, E). The occipital condyle articulates posteriorly against this trough-shaped surface during lateral rotation of the skull. Ventral to the trough-shaped surface, the odontoid is slightly concave dorsoventrally and strongly convex transversely and articulates with the rounded posterodorsal rim and posterior surface of the atlantal intercentrum.

The atlantal intercentrum is U-shaped in anterior view (PVSJ 407; MACN 18.060). The articular surface for the occipital condyle is cup-shaped and faces anterodorsally (Fig. 11B). The articular surface for the odontoid faces posterodorsally and has rounded dorsal and ventral margins (Fig. 11B). The broad, U-shaped trough between these margins accommodates the ventral crest on the odontoid. The articular surface for the axial intercentrum is also U-shaped and faces posteroventrally (Fig. 11C). It is dorsoventrally convex, in contrast to the articular surfaces for the occipital condyle and odontoid, and is separated from the nonarticular ventral surface of the intercentrum by a deep groove which receives the anterior rim of the axial intercentrum. The elliptical surface for the pedicels of the neural arches is exposed in dorsal view and angles somewhat ventrolaterally (Fig. 11B). The single-headed atlantal rib articulates against a circular depression on the lateral side of the intercentrum (Fig. 11A).

The atlantal neural arch is approximately twice as long as deep in lateral view (Fig. 11A). The medial surface of the tab-shaped pedicel is dorsoventrally concave and forms the wall of the neural canal. The anteroventral margin of the pedicel is not preserved well enough to determine if the pedicel participated in the articular cup for the occipital condyle. The postzygapophyseal articular surface is elliptical and slightly concave and faces ventromedially (Fig. 11D). A well-developed, arched epipophysis is present and projects posteriorly. The short, tab-shaped prezygapophysis curves dorsomedially. A subtriangular depression on its lateral side marks the articular surface for the proatlas (Fig. 11A).

Axis—The axial centrum is almost twice as long as deep (Fig. 11A–C, E, F; Table 2). A strong ventral keel is present in PVSJ 407 (Fig. 11C), but the keel is less pronounced in other specimens (PVSJ 53, MACN 18.060). The parapophysis is a raised rugosity positioned low on the anterior end of the centrum (Fig. 11A). The weakly developed diapophysis indicates that the axial rib is double-headed. The side of the centrum between the parapophysis and diapophysis is deeply excavated, and the posterior face of the centrum is concave.

The axial intercentrum is fused to the anterior end of the axis. As measured in the midline, it is approximately one-third the length of the axial centrum (Fig. 11C; Table 2). It is very broad, exceeding the width of both the anterior and posterior faces of the axial centrum. Anteriorly, it is deeply cupped to receive the atlantal intercentrum (Fig. 11E). In lateral view, it is subtriangular and projects anteriorly under the atlantal intercentrum (Fig. 11A).

The neural arch is completely co-ossified with the centrum on each side of a spacious neural canal that has a diameter one-half that of the posterior face of the centrum (Fig. 11E–F). Raised, elliptical prezygapophyses face dorsolaterally with the long axis of the facet angling anterolaterally (Fig. 11A). The articular surface is gently convex along its long axis, accommodating the concave atlantal postzygapophyseal facet during rotation of the atlas against the axis. The neural spine projects anteriorly as a short prong between the prezygapophyses and angles posterodorsally at approximately 25°. At its posterodorsal extremity, the neural spine divides into two ventrolaterally inclined laminae. These laminae terminate ventrally as strong epipophyses that project posterior to the postzygapophyses. In posterior view, a deep triangular fossa is located between the apex of the neural spine and the postzygapophyses (Fig. 11F). The subtriangular postzygapophyseal facets are flat and angle ventrolaterally at 20 to 30° from the horizontal (Fig. 11C, F). A thin lamina joins the medial edges of the postzygapophyses and floors the fossa at the base of the neural spine (Fig. 11C).

Postaxial Cervical Vertebrae—The postaxial cervical vertebrae are best preserved in PVSJ 407, although a complete cervical series is not available (Figs. 11A–C, 12; Table 2). Because the cervical-dorsal transition in vertebrae or ribs is not preserved, we regard the first ten presacral vertebrae as cervical vertebrae, based on the condition in other basal dinosaurians. Disarticulated postaxial cervical vertebrae (MACN 18.060, PVSJ 373) have been numbered by comparison to PVSJ 407.

The third cervical vertebra is longer than the axis, and centrum length increases slightly in the fourth to the sixth cervical vertebrae (Figs. 11, 12; Table 2). A portion of the seventh cervical centrum (PVSJ 407) suggests that it was shorter than the sixth centrum, and the eighth centrum is substantially shorter than the mid-cervical vertebrae. The postaxial cervical centra are parallelogram-shaped in lateral view, with eleva-

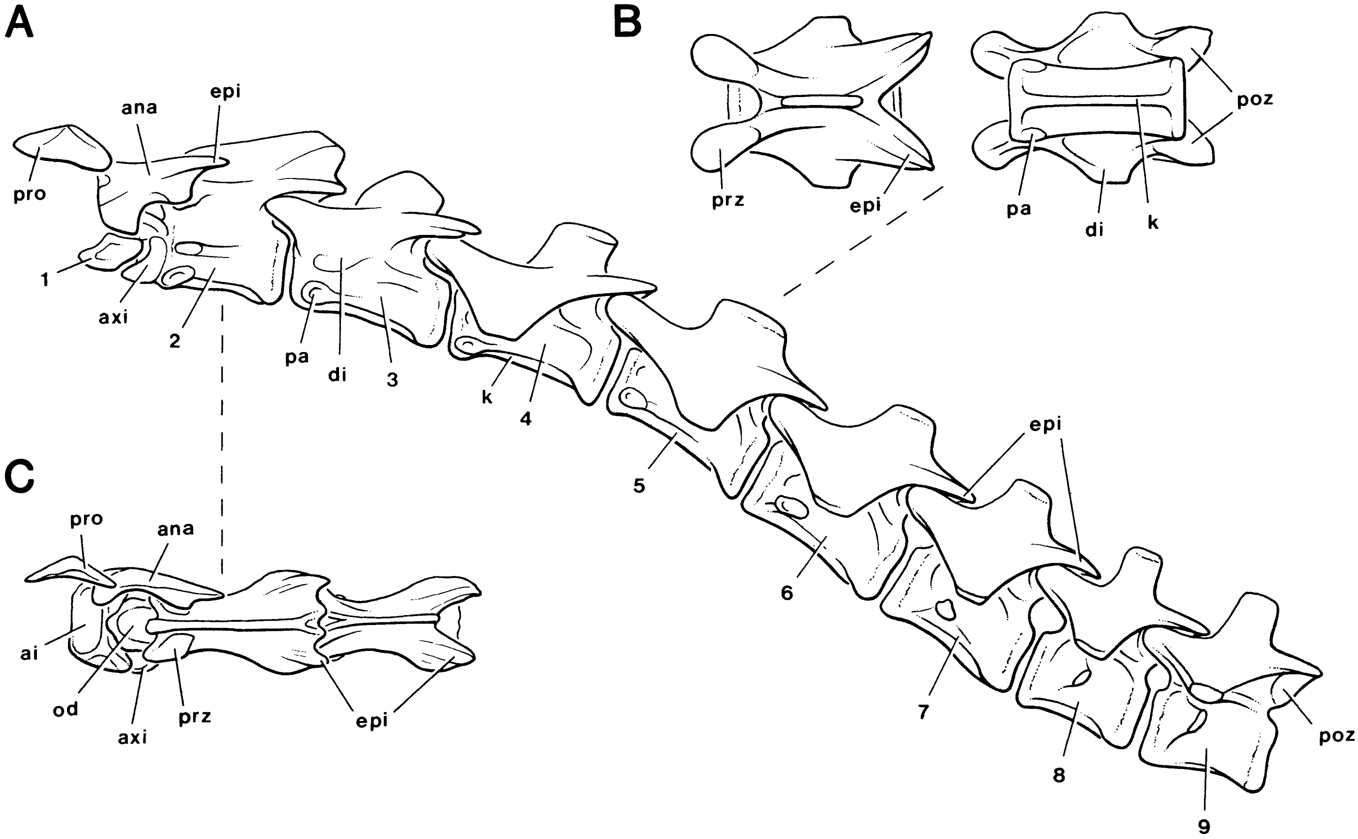

FIGURE 12. Reconstruction of the cervical vertebrae of *Herrerasaurus ischigualastensis* (based on PVSJ 407 and MACN 18.060). **A**, cervical vertebrae in lateral view. **B**, cervical 5 in dorsal and ventral views. **C**, right proatlas and cervicals 1–3 in dorsal view. Abbreviations: **1-9**, cervical vertebrae 1–9; **ai**, atlantal intercentrum; **ana**, atlantal neural arch; **k**, keel; **pro**, proatlas. Other abbreviations as in Figure 11.

tion of the anterior centrum face (Fig. 12A). Excavation of the sides of the centrum is marked in the axis and third cervical but gradually diminishes in posterior cervical vertebrae. Both the anterior and posterior faces of the centrum appear to be weakly concave in all postaxial vertebrae. As on the axis, a strong ventral keel is present on the third cervical centrum but is reduced in depth in more posterior cervical vertebrae.

The parapophyses of the posterior cervical vertebrae are positioned posterior to the centrum rim and are elevated to mid-height on the centrum (Fig. 12A; PVSJ 407, MACN 18.060). The parapophyses are larger in posterior cervical vertebrae but reduced in prominence. The diapophyses, which are developed as crests in the axis and third cervical vertebra, project as ventrolaterally directed flanges in the fourth and fifth cervical vertebrae (PVSJ 407, MACN 18.060). In the seventh and eighth cervical vertebrae, the diapophyses are anteroposteriorly shortened, and in the ninth and tenth cervical vertebrae, they project dorsolaterally. Four laminae extend from the transverse process to pre- and postzygapophyses and to the anteroventral and posteroventral corners of each neural arch. These cross-shaped laminae are rudimentary in the fifth cervical vertebra but are well-developed by the eighth cervical vertebra. The transverse processes appear broadly triangular in dorsal view (Fig. 12B), because the lamina between the prezygapophysis and transverse process is particularly broad.

The prezygapophyses project beyond the anterior face of the centrum in the third cervical vertebra, a condition which is progressively reduced in mid- and posterior cervical vertebrae (Figs. 11, 12). The oval articular surfaces in the third vertebra are flat and face dorsomedially, permitting transverse movement against the postzygapophyses of the axis. A narrow fossa is present at the base of the neural spine between the prezygapophyses. In contrast to the axis, the postzygapophyses of the postaxial cervical vertebrae do not project behind the posterior centrum face. Arched epipophyses are present in the third cervical vertebra and remain prominent as far posteriorly as the eighth cervical vertebra.

The plate-like neural spine of the third cervical vertebra is subquadrate in lateral view and posterodorsally inclined (Fig. 11A). In more posterior vertebrae, the neural spines decrease in length and thicken transversely, particularly in the sixth to the eighth cervical vertebrae. Posterodorsal inclination of the neural spines decreases along the cervical series such that by the fifth cervical vertebra the spine axis is vertical. As in the axis, a deep fossa is present at the base of the neural spine between the postzygapophyses. The fossa is diamond-shaped, rather than triangular, due to the steeper inclination of the laminae between the postzygapophyses.

DISCUSSION

The new skull and neck materials of *H. ischigualastensis* are compared below to other basal dinosaurs and successive dinosaurian outgroups. First, we describe diagnostic characters in the skull and neck of *H. ischigualastensis.* Second, we discuss cranial characters that are unique to dinosaurs and that are relevant to the phylogenetic position of *H. ischigualastensis* within Dinosauria. Finally, we consider the function of the well-developed intra-mandibular joint and the occurrence of tooth injuries on the skull.

Unfortunately, comparative skull materials among immediate outgroups to *H. ischigualastensis* are limited. Only the lower jaws are known in the herrarasaurid *Staurikosaurus pricei* (Colbert, 1970), and only the maxilla and braincase are preserved in the dinosauriform "*Lagosuchus*" *lilloensis* (Bonaparte, 1975; Sereno and Arcucci, 1994). No part of the skull is known in *Lagerpeton chanarensis* (Sereno and Arcucci, 1993). Cranial comparisons to non-dinosaurian archosaurs thus are often limited to pterosaurs and various crurotarsal archosaurs.

Autapomorphies of the Skull and Neck of *Herrerasaurus ischigualastensis*

Several characters of the skull and neck of *H. ischigualastensis* are not present in other basal dinosaurs or immediate dinosaurian outgroups and are regarded here as autapomorphies (see Appendix for character-state distributions). It should be kept in mind, however, that because the cranium is not known in the close relative *Staurikosaurus,* autapomorphies in the cranium (Fig. 8) may eventually characterize Herrerasauridae.

(1) *Broad posterolateral process of premaxilla* (Figs. 7A, 8A, 9). In *H. ischigualastensis,* a broad triangular process of the premaxilla extends between the maxilla and nasal posterior to the external naris, separating the maxilla from the border of the external naris by a significant distance. A similar process is present in ornithischians but generally is narrow or short in saurischians (Fig. 10B, C). Notable exceptions among saurischians include ornithomimids (Barsbold and Osmólska, 1990), oviraptorids (Barsbold et al., 1990), and dromaeosaurids (Ostrom, 1990), although only ornithomimids have a broad, triangular premaxillary process similar to that in *H. ischigualastensis.* The premaxillary process in ceratosaurs and tetanurans, in contrast, is very short and does not extend posterior to the external naris (e.g., *Ceratosaurus,* Fig. 10C; *Allosaurus,* Madsen, 1976). Pterosaurs also lack a broad premaxillary posterolateral process, as do nearly all crurotarsal archosaurs with rare exceptions among suchians (e.g., *Saurosuchus,* Sill, 1974; Crocodylomorpha).

In summary, a broad posterolateral process of the premaxilla is present among dinosaurs in ornithischians and in a few advanced theropod subgroups. This condition does not seem to occur in theropods or saurischians, plesiomorphically. The broad process appears to have arisen independently in *H. ischigualastensis* and Ornithischia.

(2) *Premaxilla-maxilla fenestra* (Figs. 7A, 8A, 9). An oval fenestra is present between the premaxilla and maxilla posterior to the external nares in *H. ischigualastensis.* A similar fenestra has not been reported in other dinosaurs or immediate dinosaurian outgroups. Of course, no data are available for *Staurikosaurus,* "*Lagosuchus,*" and *Lagerpeton.* As mentioned above, this fenestra should not be confused with the saurischian subnarial foramen, which is located ventral (rather than posterior) to the external naris, with an internal opening ventral (rather than dorsal) to the premaxillary palate.

(3) *Narrow, U-shaped anterior antorbital fossa* (Figs. 7A, 8A, 9). The anterior portion of the antorbital fossa in *H. ischigualastensis* is narrow and U-shaped. The external rim of the fossa and margin of the fenestra closely parallel one another. In other dinosaurs, the external margin of the fossa is asymmetrical. In basal ornithischians, for example, the fossa is subtriangular (Fig. 10A). In saurischians, the fossa has a rounded corner anteroventrally and a more open curve dorsally where it approaches the skull roof (e.g., *Syntarsus,* Rowe, 1989; *Allosaurus,* Madsen, 1976). In *Ceratosaurus* (Fig. 10C), the external margin of the fossa is semicircular as in *H. ischigualastensis.* The margin of the fenestra, however, does not closely parallel the external rim of the fossa as in *H. ischigualastensis.* In "*Lagosuchus,*" the antorbital fossa probably had a subtriangular shape, judging from the shape of the maxilla and antorbital fenestra (Bonaparte, 1975:fig. 2). In pterosaurs, the antorbital fossa is reduced or absent anteriorly (Witmer, 1987); the anterior margin of the antorbital fenestra, however, is asymmetrical (Wellnhofer, 1978:figs. 2, 4).

(4) *Broad supratemporal depression* (Figs. 1C, 4, 7B, 8B, 9). In *H. ischigualastensis,* the supratemporal fossa is inset sharply into the skull roof as a broad, flat surface anterior to the supratemporal opening. This depressed surface exceeds the area occupied by the supratemporal opening. No other dinosaur or dinosaurian outgroup exhibits the same proportionately broad depression anterior to the supratemporal opening.

(5) *Jugal ridge* (Figs. 7B, 8B, 9). In *H. ischigualastensis,* a rugose ridge passes across the center of the jugal beneath the orbit. A similar jugal ridge is not known in other basal dinosaurs or in pterosaurs.

(6) *Narrow dorsal portion of laterotemporal fenestra* (Figs. 7A, 8A, 9). In *H. ischigualastensis,* the latero-

temporal fenestra is trapezoidal, with the narrow dorsal portion of the fenestra less than one-half the anteroposterior width of the ventral margin. The proportionately narrow dorsal extent of the fenestra is related to the short postorbital-squamosal bar and the anterodorsal tilt of the quadrate shaft. *Ceratosaurus* (Fig. 10C) and *Abelisaurus* (Bonaparte and Novas, 1985) are the only other dinosaurs with strong constriction of the dorsal portion of the laterotemporal fenestra (Fig. 10C). The condition is not known in *Staurikosaurus, "Lagosuchus,"* or *Lagerpeton.*

(7) *Subquadrate ventral process of squamosal with lateral depression* (Figs. 7A, 8A, 9). In *H. ischigualastensis,* the ventral process of the squamosal has an unusual subquadrate shape with a shallow depression on its lateral surface. The only other dinosaur that approaches this condition is *Dilophosaurus* (Welles, 1984). The squamosal is not preserved in *Staurikosaurus, "Lagosuchus,"* or *Lagerpeton.* It has a slender ventral process in pterosaurs.

(8) *Quadratojugal overlapping posterior side of quadrate shaft* (Figs. 1G, 7C, 8C, 9). The posterior portion of the quadratojugal in *H. ischigualastensis* is deflected medially, overlapping the posterior side of the quadrate shaft. This condition has not been reported elsewhere among dinosaurs or dinosaurian outgroups.

(9) *Basal tuber and occipital condyle subequal in width* (Figs. 6, 7C, 8C, 9). In *H. ischigualastensis,* the basal tubera form a pair of broad plates, with each tuber equal to the occipital condyle in width. In other dinosaurs and in "*Lagosuchus*" (PVL 3870), the width of each tuber is usually considerably less than the width of the occipital condyle (e.g., *Allosaurus*; Madsen, 1976). A few dinosaurs have relatively broad tubera (e.g., *Tyrannosaurus*; Osborn, 1912), but none have achieved the proportions described above in *H. ischigualastensis.*

(10) *Slender, ribbed posterodorsal dentary process and slotted surangular* (Figs. 1D, 7A, 8A, 9). In *H. ischigualastensis,* the posterodorsal process of the dentary is very elongate and slender and has a strong lateral rib along its length. It articulates in a deep slot on the anterior end of the surangular. This configuration of the dentary and surangular is unknown elsewhere among archosaurs. As described below, *Staurikosaurus* has an intra-mandibular sliding joint as in *H. ischigualastensis,* but the posterodorsal process of the dentary is not preserved.

Dinosaurian Synapomorpies

Although the skull is quite distinctive within each of the three major dinosaurian clades (Ornithischia, Sauropodomorpha, and Theropoda), cranial characters that unite all dinosaurs are not obvious. Recent information on the skull in several early dinosaurs allows a more thorough comparison with *H. ischigualastensis* (*Lesothosaurus*; Thulborn, 1970; Sereno, 1991a; *Sellosaurus, Plateosaurus*; Galton, 1973, 1985; Galton and Bakker, 1985; *Coelophysis,* Colbert, 1989; *Allosaurus,* Madsen, 1976). Because the skull is practically unknown in basal dinosauromorphs such as "*Lagosuchus,*" nevertheless, it is effectively impossible to identify unequivocal cranial synapomorphies for Dinosauria.

TABLE 3. Skull and neck characters cited by previous authors as synapomorphies of Dinosauria. Abbreviations: B = Benton, 1984; G = Gauthier, 1986; P1 = Paul, 1984a; P2 = Paul, 1984b.

Skull
1. Anteroventrally expanded antorbital fossa (P1).
2. Tall lacrimal with short anterior prong (P1).
3. Three-pronged jugal (P1).
4. Postfrontal absent (B).
5. Lightly built palate (P1).
6. Vomera elongate (P1, G).
7. Slender pterygoid (P1).
8. Vertical quadrate (P2).
9. Narrow, elongate opisthotic wings (P2).

Neck
10. Curved neck (P1).

Recent cladistic surveys have listed several cranial and cervical synapomorphies for Dinosauria (Table 3, synapomorphies 1–10). Except for the absence of the postfrontal, however, we cannot support these as dinosaurian synapomorphies. Most of the characters are absent in *H. ischigualastensis* and do not describe variation that is distinctive for dinosaurs. In *H. ischigualastensis* and other basal dinosaurs, for example, the antorbital fossa is not expanded anteroventrally (character 1; Figs. 7, 10), as compared to "*Lagosuchus*" (Bonaparte, 1975:fig. 2), pterosaurs (Wellnhofer, 1978), or various crurotarsal archosaurs (e.g., ornithosuchids; Walker, 1964; Bonaparte, 1972; Sereno, 1991b). Compared to other archosaurs, the lacrimal is not especially tall relative to snout height (character 2) in *H. ischigualastensis* or in many other dinosaurs (Figs. 7A, 10A, B). The jugal is not strictly "three-pronged" (character 3) in *H. ischigualastensis.* Rather, the anterior end of the bone has a rudimentary dorsal (fourth) process that overlaps the lacrimal on the orbital margin (Fig. 7A). Although ornithischians and sauropodomorphs lack any development of this jugal process (Fig. 9A, B), several basal theropods show a condition similar to *H. ischigualastensis* (e.g., *Carnotaurus,* Bonaparte et al., 1990; *Dilophosaurus,* Welles, 1984). The supposedly plesiomorphic "four-pronged" condition of the jugal is well-developed in pterosaurs and ornithosuchids (Wellnhofer, 1978; Walker, 1964; Bonaparte, 1972) but is poorly developed or absent in many crurotarsal archosaurs such as phytosaurs (Chatterjee, 1978), *Gracilisuchus* (Romer, 1972), basal suchians (e.g., *Sphenosuchus*; Walker, 1990), proterochampsids (Romer, 1971), and *Euparkeria* (Ewer, 1965). The palate is not especially "lightly-built" (character 5) and the pterygoid is not particularly "slender" (character 7) in *H. ischigualastensis* (Figs. 7D, 8D) or in other basal dinosaurs (e.g., *Lesothosaurus*; Sereno, 1991a:fig. 11D) as compared to basal archosaurs. Although the anterior end of the vomer is not exposed in *H. ischigualastensis,* the length of the vomer (character 6) does not appear to be more than 25 percent of skull length, a proportion that is not unusual among various short-snouted archosaurs. In *H. ischigualastensis,* the shaft of the quadrate slopes anterodorsally, as in several theropods (Fig. 10C), and is not erect (character 8). Finally, the length of the paroccipital processes (character 9) is not relatively greater than in many crurotarsal archosaurs (e.g., *Ornithosuchus, Parasuchus*; Walker, 1964; Chatterjee, 1978; Sereno, 1991b) or proterochampsids (*Chanaresuchus*; Romer, 1971).

We outline below several potential cranial synapomorphies for Dinosauria (see Appendix for character-state distributions).

(11) *Postfrontal absent* (Figs. 7, 8, 10). There is no postfrontal bone on the skull roof between the orbit and supratemporal fossa in *H. ischigualastensis* and other dinosaurs. Most basal archosaurs, in contrast, retain the bone (e.g., parasuchians, ornithosuchids, *Gracilisuchus,* rauisuchians), albeit reduced in some groups (e.g., aetosaurs, Walker, 1961; *Saurosuchus,* PVSJ 32). Reduction or loss of the postfrontal has long been noticed as a general pattern among archosaurian subgroups (Romer, 1956:130). Crocodylomorphs have independently lost the postfrontal (Gauthier, 1986; Sereno, 1991b), and the condition in pterosaurs is not obvious. The posterior orbital margin is not well-preserved in the basal pterosaurs *Eudimorphodon* (Wild, 1978) and *Campylognathoides* (Wellnhofer, 1974), and the presence or absence of this bone cannot be determined. Other pterosaurs show one or two slender ossifications along the dorsal and posterior orbital margin (Wellnhofer, 1978). These bones have been interpreted either as neomorphic ossifications (Gauthier, 1984:175) or (at least one of them) as the postfrontal. In a well-preserved pterodactyloid cranium, a slender, curved element is present along the posterodorsal margin of the orbit, articulating with the frontal and postorbital (Wellnhofer, 1985:figs. 31, 32). These relations are consistent with the position and sutural contacts of the postfrontal in other archosaurs, and we consider this element to represent the postfrontal.

(12) *Ectopterygoid dorsal to transverse flange of pterygoid* (Figs. 7A, D, 8A, D). In *H. ischigualastensis,* the ectopterygoid arches from the infraorbital bar to the dorsal aspect of the pterygoid. It curves posteriorly and extends to the tip of the transverse flange of the pterygoid, maintaining its dorsal position relative to the pterygoid. The same relation between the ectopterygoid and pterygoid occurs in early sauropodomorphs (e.g., *Plateosaurus,* Galton, 1985), theropods (e.g., *Allosaurus,* Gilmore, 1920:24, *contra* Madsen, 1976; *Dromaeosaurus,* Colbert and Russell, 1969:fig. 10B; *Tyrannosaurus,* Osborn, 1912:fig. 6), and ornithischians (e.g., *Lesothosaurus,* Sereno, 1991a; *Hypsilophodon,* Galton, 1974). Sauropods appear to represent the exception among dinosaurs, with the transverse flange of the pterygoid positioned dorsal to the ectopterygoid (e.g., *Camarasaurus,* CM 11338; *Brachiosaurus,* Janensch, 1935–1936:fig. 60). The condition in diplodocids is less certain, with the ectopterygoid apparently positioned on the "anterior border of the transverse process of the pterygoid" (McIntosh and Berman, 1975).

Among dinosaurian outgroups, the relation between the pterygoid and ectopterygoid generally resembles that in sauropods, with the pterygoid overlapping the dorsal side of the ectopterygoid. In pterosaurs, the ectopterygoid appears to be positioned on the ventral aspect of the pterygoid (*Campylognathoides, Scaphognathus, Gnathosaurus, Nyctosaurus*; Wellnhofer, 1978: figs. 3, 6). On the other hand, the the ectopterygoid passes above the pterygoid in at least some pterodactyloids (*Pteranodon,* Eaton, 1910; *Araripesaurus, Santanadactylus,* Wellnhofer, 1985:figs. 3b, 32a). The condition in pterodactyloids, however, is difficult to assess. In other dinosaurian outgroups, the ectopterygoid passes ventral to the transverse flange of the pterygoid, as observed in sphenosuchians (Wu, 1986), ornithosuchids (*Riojasuchus,* PVL 3827; *Ornithosuchus,* Walker, 1964), phytosaurs (*Parasuchus,* Chatterjee, 1978), and proterochampsids (*Chanaresuchus,* PVL 4586). Although the ectopterygoid is shown with a dinosaurian position in *Postosuchus* passing dorsal to the transverse flange of the pterygoid (Chatterjee, 1985:fig. 5b), the identification of the ectopterygoid is questionable (shown as larger than the palatine) and its relation with the pterygoid apparently has been reconstructed from disarticulated materials.

(13) *Quadrate head laterally exposed* (Figs. 7A, 8A, 10). In *H. ischigualastensis* and other dinosaurs, the articular head of the quadrate is exposed in lateral view. The head of the quadrate is smooth, suggesting that a synovial joint existed between the quadrate and squamosal. In pterosaurs and other basal archosaurs, the quadrate head is hidden in lateral view by the squamosal.

(14) *Post–temporal foramen* (Figs. 7C, 8C). In *H. ischigualastensis,* the post-temporal opening is represented by a foramen between the paroccipital process and parietal near the lateral corner of the supraoccipital. The opening in *H. ischigualastensis* and other dinosaurs is much smaller than the foramen magnum. In some thyreophoran ornithischians, the foramen is closed. In dinosaurian outgroups, the post-temporal opening has a maximum diameter more than one-half that of the foramen magnum, as seen in pterosaurs (Wellnhofer, 1978; see also *Araripesaurus,* Wellnhofer, 1985:fig. 34) and crurotarsal archosaurs (*Saurosuchus, Gracilisuchus,* aetosaurs, ornithosuchids, and phytosaurs). Proterochampsids (*Proterochampsa,* Sill, 1967; *Chanaresuchus,* PVL 4575, 4586) and crocodylomorphs (e.g., *Sphenosuchus,* Walker, 1990) have independently reduced the post-temporal opening to a foramen.

Synapomorphies within Dinosauria

Several derived characters are present only in *H. ischigualastensis* and saurischians or saurischian subgroups.

(15) *Subnarial foramen* (Figs. 7A, 8A, 10). A small subnarial foramen is present along the premaxilla-maxilla suture in *H. ischigualastensis.* Nearly all saurischians have a subnarial foramen, which is usually slightly larger than in *H. ischigualastensis* (e.g., *Ceratosaurus,* USNM 4735; *Camarasaurus,* CM 11338). The foramen is absent in some advanced ceratosaurs that have acquired a substantial premaxilla-maxilla diastema (e.g., *Dilophosaurus,* Welles, 1984; *Coelophysis,* Colbert, 1989). A subnarial foramen is absent in ornithischians, pterosaurs, and nearly all crurotarsal archosaurs. Some suchians have evolved a similar foramen (e.g., *Saurosuchus,* Sill, 1974).

(16) *Lateral overlap of lacrimal by jugal* (Figs. 7, 10). In *H. ischigualastensis,* the anterior end of the jugal broadly overlaps the ventral end of the lacrimal at the posteroventral corner of the antorbital fossa. Broad jugal overlap is also present in saurischians (Fig. 10B, C; *Plateosaurus,* Galton, 1985; *Camarasaurus,* Gilmore, 1925; *Carnotaurus,* Bonaparte et al., 1990; *Allosaurus,* Madsen, 1976). The lacrimal-jugal articulation among ornithischians is usually rugose or interdigitating, with minimal overlap. In the basal ornithischian *Lesothosaurus,* the ventral edge of the lacrimal extends somewhat lateral to the jugal (Sereno, 1991a:fig. 2B). Likewise, in the ceratopsian *Psittacosaurus,* the lacrimal appears to extend slightly further on the lateral side, although the articulation is grooved (Sereno, 1987). In other ornithischians, however, the anterior end of the jugal clearly overlaps the lacrimal (e.g., hadrosaurs, Ostrom, 1961) as in *H. ischigualastensis* and other dinosaurs. Many ornithischians do not have a broadly overlapping lacrimal-jugal articulation, and thus this character is too transformed for interpretation of this character.

In pterosaurs and crurotarsal archosaurs, the ventral end of the lacrimal broadly overlaps the jugal in pterosaurs (Wellnhofer, 1985:figs. 31, 32), opposite to the condition in *H. ischigualastensis* and most other dinosaurs. In *Ornithosuchus,* the lacrimal articulates on the posterolateral side of the jugal, such that when the jugal is disarticulated, the articular surface for the lacrimal is only exposed in lateral view (Walker, 1964: fig. 3c, d). In *Saurosuchus* (PVSJ 32), the lacrimal broadly overlaps the jugal. Thus, lateral overlap of the lacrimal by the jugal appears to be the most common condition in crurotarsal archosaurs, with a notable exception among sphenosuchian crocodylomorphs (Wu, 1986; Walker, 1990).

(17) *Posterior process of jugal forked* (Figs. 7, 8, 10). In *H. ischigualastensis,* the posterior process of the jugal is forked for the reception of the anterior process of the quadratojugal. Most saurischians exhibit a similar condition (e.g., *Plateosaurus, Ceratosaurus,* Fig. 10B, C; *Allosaurus,* Madsen, 1976). Sauropods constitute an exception in which the jugal is not forked posteriorly and is broadly overlapped by the quadratojugal (e.g., *Camarasaurus,* Gilmore, 1925). Among ornithischians, the articular relation between the jugal and quadratojugal is the opposite of that in sauropods, with the jugal overlapping the quadratojugal. A forked posterior process occurs in only a few forms (e.g., *Psittacosaurus*; Sereno et al., 1988b), and in these cases the jugal processes are broad, unlike the condition in *H. ischigualastensis* and other saurischians. The broadly overlapping or interdigitating jugal-quadratojugal suture in many ornithischians may be too transformed for comparison, for it does not resemble the outgroup condition described below.

A forked posterior process of the jugal is absent among dinosaurian outgroups. The jugal-quadratojugal articulation is narrow and apparently planar in pterosaurs (Wellnhofer, 1978, 1985). In other basal archosaurs, the jugal overlaps the quadratojugal with an approximately planar articular surface (*Sphenosuchus,* Walker, 1990; *Prestosuchus,* Barbarena, 1978; *Ornithosuchus,* Walker, 1964:fig. 3d; *Riojasuchus,* PVL 3827; *Parasuchus,* Chatterjee, 1978; *Chanaresuchus,* PVL 4586, 4575).

Finally, one cranial and one cervical synapomorphy unite *H. ischigualastensis* and Theropoda.

(18) *Well-developed intra-mandibular joint between the dentary and surangular and between the splenial and angular* (Figs. 7A, 8A). In *H. ischigualastensis,* a well-developed intra-mandibular joint separates the lower jaw into anterior and posterior functional units. Broad sliding articulations are present between the dentary and surangular above the external mandibular fenestra and between the splenial and angular below. The splenial-angular articulation is developed between a tongue-shaped posterior process of the splenial and a hook-shaped anterior process of the angular. The splenial process wraps around the ventral margin of the angular, sliding against its smooth, convex ventral margin. The same articular configuration between the splenial and angular is preserved in the right lower jaw of *Staurikosaurus* (MCZ 1669).

Kinetic dentary-surangular and splenial-angular articulations are also present in theropods (e.g., *Ceratosaurus,* Fig. 10C; *Carnotaurus,* Bonaparte et al., 1990). In theropods, however, the articular surfaces of the splenial-angular sliding joint are the reverse of that in *Herrerasaurus* and *Staurikosaurus*; the tongue-shaped process of the splenial has a convex dorsal articular surface that slides against a concave depression on the angular. The dentary-surangular joint is also present in theropods, but the posterodorsal process of the dentary is not elongated as in *H. ischigualastensis.* The unusual intra-mandibular joint described above is found only in herrerasaurids and theropods among dinosaurs. Dinosaurian outgroups (pterosaurs, crurotarsal archosaurs) also lack an intra-mandibular joint.

(19) *Prominent postaxial cervical epipophyses* (Figs. 11, 12). In *H. ischigualastensis,* prominent, arched epipophyses are present in the cervical series from the

atlas to at least the eighth cervical vertebra. The tips of these epipophyses extend posterior to the articular facet of the postzygapophysis and decrease in strength in the posterior cervical vertebrae. Axial and, especially, atlantal epipophyses are common among dinosaurs. Prominent epipophyses in postaxial cervical vertebrae occur principally among theropods. In *Staurikosaurus* (MCZ 1669), cervical epipophyses have been reported as absent (Sues, 1990). The cervical vertebrae and postzygapophyses, however, are poorly preserved. Among theropods, postatlantal cervical epipophyses are present in ceratosaurs and most tetanurans (*Ceratosaurus,* Gilmore, 1920; *Dilophosaurus,* Welles, 1984; *Procompsognathus,* Sereno and Wild, 1992; *Allosaurus,* Madsen, 1976; *Deinonychus,* Ostrom, 1969).

Although some basal dinosaurs have short epipophyses on the third cervical, they are poorly developed or absent in other cervical vertebrae. In the ornithischians *Lesothosaurus* (Thulborn, 1972:fig. 3A, C; Sereno, 1991a:fig. 8A) and *Heterodontosaurus* (SAM 1332), low epipophyses are present on the third cervical vertebra but are absent in the axis and in mid- and posterior cervical vertebrae. In basal sauropodomorphs, epipophyses are present on the axis but are either absent or very weak in postaxial cervical vertebrae (e.g., *Plateosaurus, Riojasaurus, Camarasaurus*). Gauthier (1986:16) cited the presence of epipophyses on anterior cervical vertebrae as a saurischian synapomorphy, but postaxial epipophyses are usually absent in basal sauropodomorphs. Except for low epipophyses in the third cervical vertebra of some basal ornithischians and sauropodomorphs, prominent postaxial epipophyses occur elsewhere in Dinosauria only among theropods.

Among dinosaurian outgroups, postaxial cervical epipophyses are absent in "*Lagosuchus*" (Bonaparte, 1975; Sereno and Arcucci, 1994) and apparently in most pterosaurs (Wild, 1978; Wellnhofer, 1978). Several advanced short-necked pterodactyloids have well-developed postaxial epipophyses (Howse, 1986), which is regarded here as an independent acquisition.

The Intra-Mandibular Joint

A sliding intra-mandibular joint is well-developed in *H. ischigualastensis* (Figs. 1, 3, 7), which closely resembles that in theropods. Two articulations are developed between anterior and posterior segments of the lower jaw dorsal and ventral to the external mandibular fenestra. In the dorsal articulation, the slender, finger-shaped posterodorsal ramus of the dentary articulates in a deep slot in the surangular. The slender dentary process is strengthened by an elongate, perpendicular strut (Fig. 1D), which appears to limit extension of the joint. In the ventral articulation, a flat subtriangular process of the dentary and a tongue-shaped posterior process of the splenial articulate against the lateral and ventral aspects, respectively, of the polished, hook-shaped anterior end of the angular.

The shape of the articular processes and the orientation of the intra-mandibular articular surfaces suggest that movement between anterior and posterior mandibular segments was primarily in the plane of the mandibular ramus. In the dorsal articulation, the articular surfaces between the dentary and surangular are anteroposteriorly elongate with a near vertical orientation; lateral deviation at this joint does not seem possible. Similarly, the ventral articulation appears to be designed for flexion in the plane of the mandibular ramus; the plate-shaped posteroventral dentary process overlaps the lateral surface of the angular hook. Significant lateral deviation of these joints would result in disarticulation. Thus, the intra-mandibular joint seems to be designed for flexion and extension of the mandibular ramus in a vertical, or near vertical, plane, with approximately 15° of rotation.

In anguimorph lepidosaurs, a hinge-like intra-mandibular joint is present (McDowell and Bogert, 1954: fig. 32). In several regards, it is functionally analogous to the sliding joint in *H. ischigualastensis* and theropods. Except for the enlarged coronoid bone, the joint in anguimorphs is developed between the same elements and divides the lower jaw into the same anterior and posterior segments. Mandibular flexion in lepidosaurs appears to be an adaptation for a grasping, as opposed to a crushing, bite (McDowell and Bogert, 1954:106). The toothed anterior segment of the mandible flexes around struggling prey, preventing escape from the open anterior ends of the jaws. The dentary tooth row is proportionately shorter in anguimorphs with a flexible intra-mandibular hinge, a condition also present in *H. ischigualastensis,* where the dentary tooth row is only two-thirds as long as the opposing maxillary tooth row (Figs. 7A). Thus, a mandibular adaptation for securing live prey in anguimorph lepidosaurs may be the best functional hypothesis for the sliding joint in the lower jaw of *H. ischigualastensis.* An alternative explanation, that the intra-mandibular joint allowed lateral flexion for increasing gape, is not tenable given the vertical articular surfaces between the dentary, angular, and surangular. In *H. ischigualastensis,* as in extant lepidosaurs, flexion of the intra-mandibular joint must have been accomplished largely by elastic ligaments that spanned the joint, because adductor musculature could not have extended far enough anteriorly to insert on any part of the anterior segment of the lower jaw. The elastic connecting ligaments may have also functioned to absorb, or soften, impact during biting.

Tooth Injuries

Three healed puncture wounds are present on the new skull of *H. ischigualastensis* (Figs. 1B, C, E, 5; tm). One is located on the posterior margin of the left parietal, and two occur on the left splenial. These puncture wounds were inflicted independently, as evidenced by their disparate locations and orientations.

The parietal puncture passes through the free posterior margin of the left parietal. Natural lineations in the surface texture of the parietal are deflected around the wound, suggesting that some bone remodeling had occurred after the injury. The splenial wounds are located on the distal one-half of the bone along the ventral margin of the left lower jaw. The anterior wound was sustained from a ventral direction; the posterior wound is located 4 cm away near the distal end of the tongue-shaped process and was sustained from a medial direction, nearly perpendicular to the axis of the first wound (Figs. 1E, 5). The porous swollen rim around each of the wounds suggests that the injury was followed by an initial infection that later healed with some deposition of new bone (Rothschild and Tanke, in press). No additional puncture marks are evident on the dorsal aspect of the snout or elsewhere on the skull.

The large rauisuchian *Saurosuchus* is the only other known contemporary predator in the Ischigualasto Formation with a gape large enough to produce these puncture wounds. However, the moderate size of the puncture wounds, and the fact that the wounds were not responsible for the death of the animal, suggest that they may have been sustained during intraspecific aggression.

CONCLUSIONS

The skull and neck of *Herrerasaurus ischigualastensis* confirm that herrerasaurid dinosaurs were active predators. The skull is long and narrow, with diagnostic features that include the semicircular anterior margin of the antorbital opening, the narrow proportions of the dorsal half of the laterotemporal opening, and the broad depression anterior to the supratemporal opening. The neck is relatively slender with prominent processes (epipophyses) for attachment of cervical musculature.

Dinosaurian synapomorphies in the skull include the absence of the postfrontal, lateral exposure of the articular head of the quadrate, and reduction in the size of the post-temporal opening. The functional significance of these characters remains obscure. All of these potential dinosaurian synapomorphies may eventually be shown to occur in immediate dinosaurian outgroups, such as "*Lagosuchus,*" when more complete material is discovered.

Within dinosaurs, only one apomorphy is shared between *H. ischigualastensis* and ornithischians, the broad, triangular posterolateral process on the premaxilla. This feature appears to have arisen independently in *H. ischigualastensis* and ornithischians, in the light of other character evidence. Three apomorphies are shared with saurischians, the most notable being the presence of a subnarial foramen. Finally, two apomorphies are shared with theropods, an intra-mandibular joint and prominent postaxial epipophyses. The intra-mandibular joint in *H. ischigualastensis* allowed the toothed anterior segment (composed of dentary and splenial) to rotate about 15° and is interpreted here as a mechanism enhancing prey capture, as appears to be the case in some extant anguimorph lizards with analogous intra-mandibular flexibility.

In summary, *H. ischigualastensis* cannot be positioned as the sister group to other dinosaurs on the basis of the skull and neck (Sereno and Novas, 1992). Cranial and cervical evidence suggests, to the contrary, that *H. ischigualastensis* is a basal theropod.

ACKNOWLEDGMENTS

We thank C. Abraczinskas and C. Vanderslice for skilled execution of the finished illustrations. We also thank A. Monetta, J. Powell, and C. Schaff for access to fossils in their care and H.-D. Sues and D. B. Brinkman for access to fossils under their study. For critical review of the manuscript, we are indebted to P. Currie, C. Forster, and H.-D. Sues. This research was supported by National Science Foundation Research Grant BSR-8722586, The David and Lucile Packard Foundation, and the National Geographic Society (to P. S.). Acknowledgment is also made to the Donors of The Petroleum Research Fund, administered by the American Chemical Society (grant ACS-PRF 22637-G8 to P. S.), for partial support of this research.

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Received 28 May 1992; accepted 20 October 1992.

APPENDIX

CHARACTERS AND TAXON–CHARACTER MATRIX

We show below the coding and distribution of 19 binary characters for *Herrerasaurus ischigualastensis, Staurikosaurus pricei,* several basal dinosaurs (*Ceratosaurus nasicornis, Plateosaurus englehardti, Lesothosaurus diagnosticus*), and immediate dinosaurian outgroups ("*Lagosuchus*" *lilloensis,* Pterosauria, Crurotarsi). Characters 1–10 are interpreted as autapomorphies of *Herrerasaurus ischigualastensis.* Characters 11–19 are interpreted as synapomorphies supporting Dinosauria or a dinosaurian subgroup. The equivocal status of a number of the characters due to missing data is underscored and treated in more detail elsewhere.

Herrerasaurus ischigualastensis

1. Posterolateral process of premaxilla: short (0); long and broad (1).
2. Premaxilla-maxilla fenestra: absent (0), present (1).
3. Anterior margin of antorbital fossa: asymmetrical (0); semicircular (1).
4. Supratemporal depression: less than (0), or equal to or greater than (1) the area of supratemporal opening.
5. Jugal ridge: absent (0), present (1).
6. Dorsal portion of laterotemporal fenestra: subequal to (0), or less than one-half of (1) ventral portion.
7. Ventral process of squamosal, shape: tapered (0); subquadrate with lateral depression (1).
8. Posterior portion of quadratojugal, orientation: lateral (0); deflected strongly medially (1).
9. Basal tuber width: less than (0), or equal to (1) width of occipital condyle.
10. Slender, ribbed posterodorsal process of dentary and slotted surangular: absent (0), present (1).

Dinosauria

11. Postfrontal: present (0); absent (1).
12. Pterygoid-ectopterygoid articular relation: ectopterygoid ventral (0); ectopterygoid dorsal (1).
13. Lateral exposure of quadrate head: hidden by squamosal (0); laterally exposed (1).
14. Size of post-temporal opening: fenestra (0); foramen (1).

Saurischia

15. Subnarial foramen: absent (0); present (1).
16. Jugal-lacrimal articular relation: lacrimal overlaps jugal (0); jugal overlaps lacrimal (1).
17. Shape of posterior process of jugal: tapering (0); forked (1).

Theropoda

18. Intra-mandibular joint: absent or poorly developed (0); well-developed (1).
19. Postaxial cervical epipophyses: rudimentary or absent (0), prominent (1).

	5	10	15	
Herrerasaurus ischigualastensis	11111	11111	11111	1111
Staurikosaurus pricei	?????	?????	?????	??1?
Ceratosaurus nasicornis	00000	10000	11111	1111
Plateosaurus engelhardti	00000	00000	11111	1100
Lesothosaurus diagnosticus	10000	00000	11110	XX00
"*Lagosuchus*" *lilloensis*	?0???	?????	?????	???0
PTEROSAURIA	00000	00000	00000	0000
CRUROTARSI	00000	00000	00000	0000

Character-state abbreviations: 0 = plesiomorphic state; $\underline{0}$ = plesiomorphic state for a clade with some ingroup variation; 1 = apomorphic state; ? = not preserved/unknown; X = unknown due to transformation.