

The earliest-known duck-billed dinosaur from deposits of late Early Cretaceous age in northwest China and hadrosaur evolution

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Abstract

A new dinosaur of Early Cretaceous age was recently discovered in the Gobi Desert of northwest China. It is more closely related to Late Cretaceous hadrosaurids than to Early Cretaceous iguanodontids. It occupies the most basal position in the phylogeny of all duck-billed dinosaurs, or the Hadrosauroida. This early hadrosauroid sheds new light on the origin of the herbivorous feeding specializations of the Late Cretaceous duck-billed dinosaurs, and corroborates the view that the Iguanodontidae and the Hadrosauroida are monophyletic clades, with the former characterized by an enlarged maxilla as the main mechanism for mastication, and the latter diagnosed by a smaller yet more mobile maxilla with an elaborate dental battery, separated by a diastema from the enlarged premaxilla. Our study also suggests that the Hadrosauroida had most likely originated in Asia in the Early Cretaceous before this clade diversified and spread to other Laurasian continents during the Late Cretaceous.

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1. Introduction

Duck-billed dinosaurs (Hadrosauroida) were the most abundant and diverse group of herbivorous dinosaurs on Laurasian continents during the Late Cretaceous (Sereno, 1999; Weishampel & Jianu, 2000; Barrett & Willis, 2001). Hadrosauroids consist of those dinosaurs that are more closely related to Hadrosauridae than to *Iguanodon*. They are a sub-group of iguanodontians, which are, in turn, nested within the ornithomimid ('bird-foot') dinosaurs (Norman & Weishampel, 1990; Weishampel & Horner, 1990;

Weishampel et al., 1993; Godefroit et al., 1998; Head, 1998; Norman, 1998). Members of the hadrosauroid clade are characterized by an improved mobility of upper jaw (pleurokinetic mechanism) with an elaborated dental battery specialized for herbivorous feeding (Norman, 1984; Weishampel, 1984). Despite their importance for Cretaceous dinosaur evolution, the earliest history of the duck-billed dinosaurs was not fully understood because of their poor records in the Lower Cretaceous.

Here we describe *Equijubus normani* gen. et sp. nov., which is represented by a complete skull and partial postcranium. It was discovered in the Lower Cretaceous of northwest China (Dong, 1997; Tang et al., 2001). Our study shows that *Equijubus* is more closely related to Hadrosauridae than to *Iguanodon*. As such it is the earliest-known and most primitive of all hadrosauroid dinosaurs.

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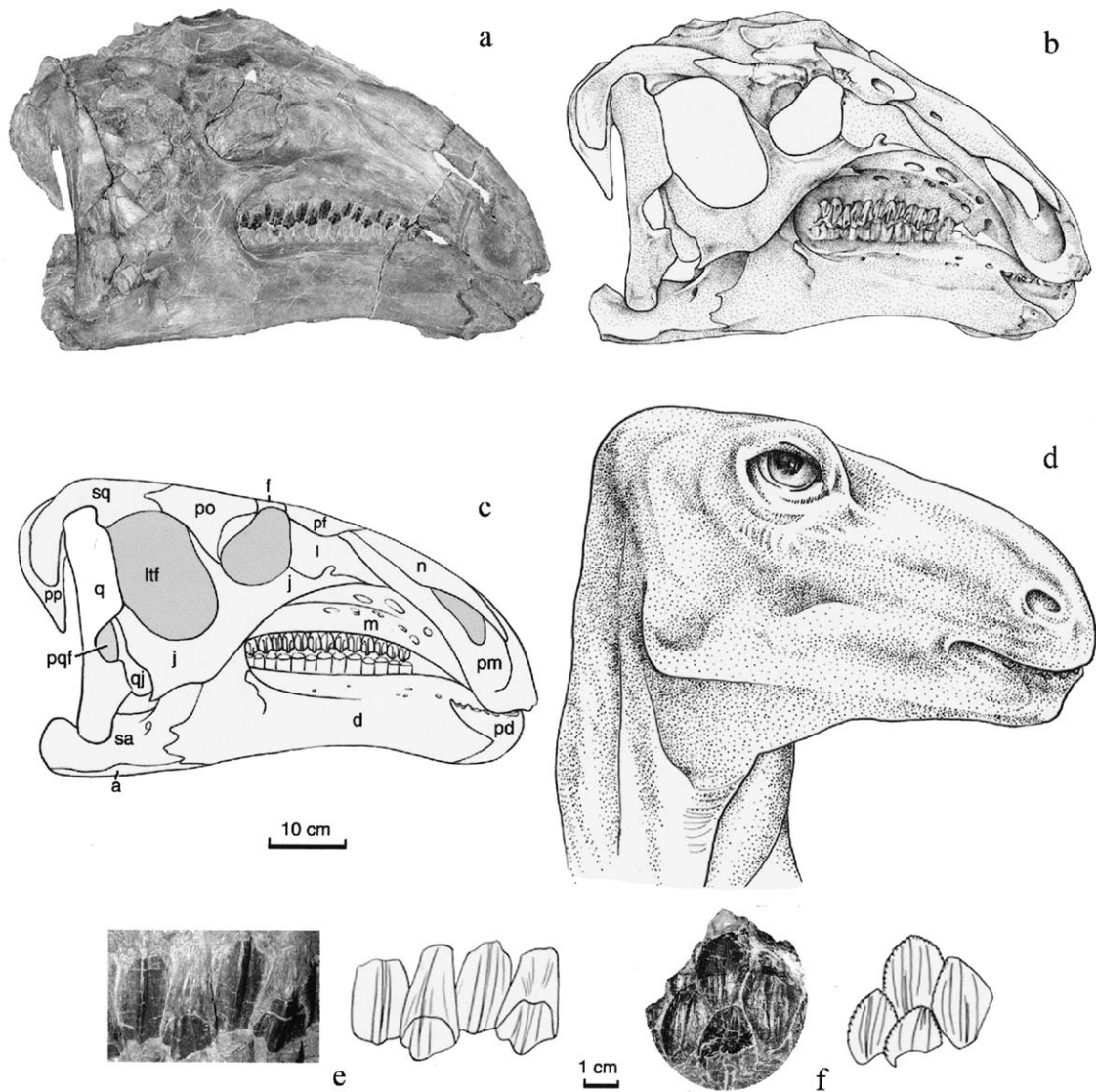


Fig. 1. *Equijubus normani* gen. et sp. nov. Skull and lower jaw in right lateral views: a, photograph; b, schematic; c, reconstruction, and d, restoration. Maxillary teeth in labial view (e), and dentary teeth in lingual view (f). Abbreviations: a, angular; d, dentary; f, frontal; j, jugal; l, lacrimal; ltf, lower temporal fenestra; m, maxilla; n, nasal; pd, predentary; pf, prefrontal; pm, premaxilla; po, postorbital; pp, paroccipital process; pqf, paraquadratic foramen; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal.

2. Systematic paleontology

Superorder: Dinosauria Owen, 1842

Order: Ornithischia Seeley, 1888

Suborder: Ornithopoda Marsh, 1881

Infraorder: Iguanodontia Dollo, 1888 (emended Norman, 1998)

Superfamily: Hadrosauroidea Cope, 1869 (emended Sereno, 1986)

Genus *Equijubus* gen. nov.

Type species. *Equijubus normani* sp. nov.

Etymology. Latin *Equus*, horse and *juba*, mane. Horse Mane is what 'Ma Zong' means in Chinese, and Ma Zong Mountain is where the fossil was discovered.

Diagnosis. As for the type and only species.

Equijubus normani sp. nov.

Fig. 1, 2

Holotype. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V 12534, a complete skull (57 cm in length, laterally compressed) with articulated lower jaw, plus incomplete postcranium.

Etymology. In honor of Dr David B. Norman for his work on ornithopod dinosaurs.

Locality and horizon. Gongpoquan Basin, Mazongshan area, Gansu Province, China. Middle Grey Unit of Xinminbao Group (Tang et al., 2001; late Early Cretaceous).

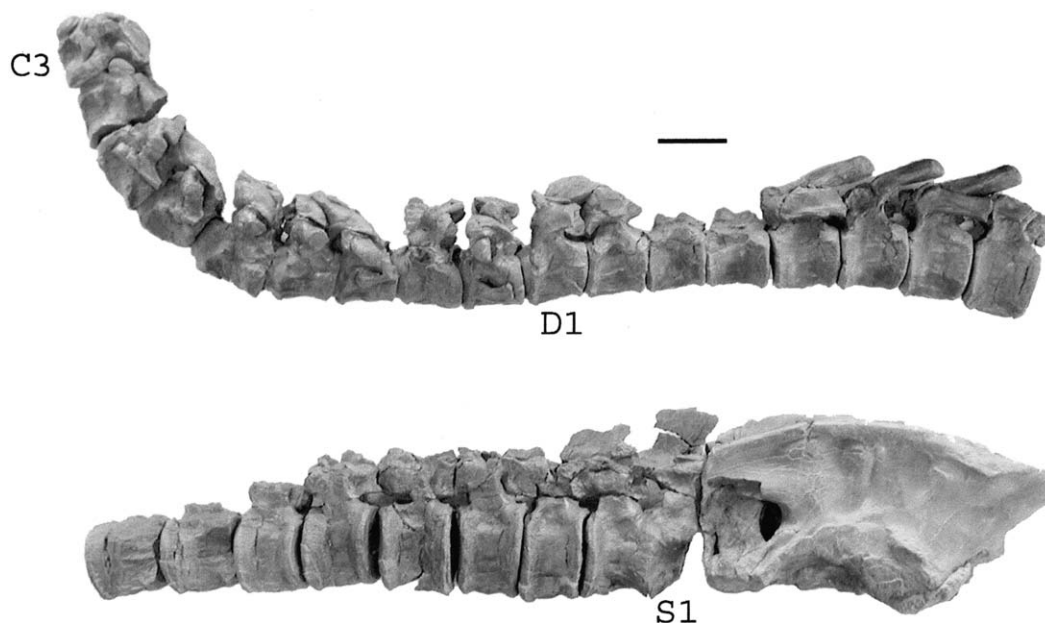


Fig. 2. Vertebral column (except for atlas, axis, and caudals) of *Equijubus normani* gen. et sp. nov. Scale bar represents 10 cm.

Diagnosis. *Equijubus normani* is characterized by a unique, finger-like process extending dorsally from the rostral process of the jugal to the lacrimal, and a very large lower temporal fenestra. Distinguished from non-hadrosauroid iguanodontians in having a long lacrimal with a rostroventral process positioned above the dorsal margin of the maxilla. Distinguished from other hadrosauroids in lacking the median primary ridge on the crown of the dentary teeth.

2.1. Description

Skull. *Equijubus* has several derived features in the premaxilla and lacrimal that are diagnostic of hadrosauroids, but absent in iguanodontids (Norman, 1998) (Fig. 1a–d). The oral portion of the premaxilla deflects ventrally below the dentary tooth row, with a ventrally curved margin, unlike the slightly deflected (except for *Altirhinus*) and straight ventral margin in other iguanodontians. The lacrimal is elongated, with its ventral border situated above the dorsal edge of the maxilla. The lacrimal also possesses a prominent, long rostroventral process wedged between the caudodorsal process of the premaxilla and the dorsal margin of the maxilla. In non-hadrosauroid iguanodontians, however, the lacrimal is block-like in lateral view, without a rostroventral process, and with its ventral edge placed ventral to the level of the dorsal margin of the maxilla.

The maxilla of *Equijubus* is similar to that of other hadrosauroids, and lacks the key features diagnostic for iguanodontids. It is shaped like an isosceles triangle in lateral view, with the ventral border measuring 30 cm long. Its rostral 7 cm is edentulous, and tapers into a

process that inserts medial to the oral portion of the premaxilla. The tooth-bearing edge of the maxilla is slightly arched and possesses 23 teeth. Neither lacrimal nor jugal process exists in *Equijubus*, which has locked the elongated maxilla to the lacrimal and the jugal, respectively in iguanodontids (Norman, 1998).

The jugal of *Equijubus* is unique among iguanodontians in having a very long, thin rostral process that wedges between the lacrimal and the maxilla. Unlike the condition of other iguanodontians, a small, finger-like projection protrudes dorsally from the middle of this process and overlaps the lacrimal. The caudal portion of the jugal borders a large lower temporal fenestra, which is twice the size of the orbit.

Characteristics of the bones in the skull roof and cheek are similar to the plesiomorphic conditions of iguanodontians. The nasal is slender, 37 cm long, and gently curves backwards without dorsal enlargement. The prefrontal overlaps the lacrimal, and has a small contact with the lower caudodorsal process of the premaxilla. A small part of the frontal borders on the dorsal margin of the orbit. The parietal forms the inner margin of the upper temporal fenestra. The postorbital has a triangular outline, with a small, laterally directed cone in the middle. The squamosal links the postorbital, quadrate, and paraoccipital process by means of three processes. The quadrate is stout, with a transversely expanded ventral head. The quadratojugal is a thin sheet of bone that borders the paraquadratic foramen rostrally.

The predentary possesses two lateral processes and a bifurcated ventral process. Its dorsal margin is denticulate, with the most prominent cusp directly on the

midline. The dentary is the most robust bone of the lower jaw. Its rostral end tapers to a point and underlaps the prementary. A 6-cm diastema separates the prementary and the first dentary tooth. The coronoid process (12 cm high) is mainly formed by the caudal portion of the dentary, and projects vertically into the gap between the maxilla and the jugal. A foramen pierces the rostro-dorsal surface of the surangular. The angular is visible on the lateral surface of the lower jaw.

The teeth of *Equijubus* have retained some plesiomorphic features of non-hadrosauroid iguanodontians. The labial surface of the crown of each maxillary tooth has a prominent primary ridge that is slightly offset distally from the midline (Fig. 1e). Mesial to the primary ridge, two or three accessory ridges rise from the base of the crown, running either parallel to one another or converging before reaching the cutting edge. There are also one or two weak ridges distal to the primary ridge. Each dentary tooth has six or seven weak ridges but lacks a prominent primary ridge on the enamelled lingual surface of the crown (Fig. 1f). There are two rows of replacement teeth on the dentary, although the second one is rudimentary. The maxillary and dentary teeth are of almost equal size in *Equijubus*, a primitive feature. By contrast, the more derived hadrosauroids (*Probaenodon*, *Bactrosaurus*, +Hadrosauridae) have smaller (but more numerous) maxillary teeth than the larger (but fewer) dentary teeth.

Axial skeleton. An articulated series of 31 vertebrae, which includes nine cervicals, 16 dorsals, and six sacrals, was recovered (Fig. 2). The centra are well preserved, while the neural arches and spines are not, especially the dorsals.

Nine cervical vertebrae (3–11) are preserved. The centrum of cervical 3 is strongly opisthocoelous, with a well-developed, 2.5-cm-long, cranial ball. The transverse width of this ball is larger than its dorsoventral height. In lateral view, the centrum is compressed ventrally to form a thin keel, which becomes broader caudally. Dorsal to this keel, the centrum surface is concave for its lower half, and develops a horizontal ridge on the upper half. The parapophysis is situated on the cranial end of this ridge. The neural arch is anchored along the dorso-lateral edge of the centrum. The diapophysis projects laterally about 2 cm right above the parapophysis. Cranial to the diapophysis, the prezygapophysis projects cranio-laterally. There is a depression on the lateral surface of the neural arch caudal to the diapophysis, and cranio-ventral to the well-developed postzygapophysis. The postzygapophysis begins at the caudodorsal corner of the neural arch, and curves upwards and backwards beyond the caudal margin of the centrum. The neural spine is low and short; its caudal portion broadens transversely, and covers the cranial part of the postzygapophysis.

The rest of the cervicals show the general features of cervical 3, but also show some changes. The right prezygapophyseal articular facet of cervical 4 is well preserved; it faces dorsomedially, and is oval in shape, 3.7 cm long craniocaudally and 2.5 cm wide. There is an obvious increase in the centrum size from cervical 4 to 5, and the centrum heights of its cranial and caudal surfaces become roughly the same in cervical 5, unlike the shorter cranial surface height in the cranial ones. The diapophysis is more robust and dorsally placed with a narrower divergence in between in cervical 5 compared to that of cervical 3, and is situated caudal to the parapophysis. The postzygapophyses diverge from above the middle of the centrum, hook backwards and end well into the middle range of the next vertebra, with the articular facet facing ventrally, laterally, and caudally. The neural spine is low and short, with a rudimentary caudal expansion over the cranial part of the postzygapophyses as in cervical 3. In cervical 6, the cranial ball directs more cranio-dorsally than cranially in the previous ones. Cervicals 7–9 are fused, and the diapophyses in cervicals 8 and 9 are long. In cervicals 10 and 11, the neural arches are narrow craniocaudally.

There are 16 dorsal vertebrae, with the last one fused to the first sacral vertebra. The first two dorsals are fused to each other. Their parapophyses have moved onto the neural arches; however, their centra still possess the cranial balls. The hooked postzygapophyses are much reduced in length. Only the centra of dorsals 3 and 4 are preserved, and they are amphiplatyan, with slightly concave cranial surfaces. In dorsals 5–8, the parapophyses and diapophyses have connected to each other, and together form a large circle. The bases of the neural spines become wide transversely. Only the centra of dorsals 9–11 are preserved, and their lengths are roughly the same as the height, unlike either of the cranial ones, which are longer than high, or the caudal ones, which are higher than long. In cervicals 12–15, the postzygapophyses are much reduced, with the articular facets facing ventrally. The bases of the neural spines are compressed craniocaudally, and high, with the caudal edges near the following vertebra. Although no complete neural spine is preserved, it seems to be a tall, thin plate based on some fragmentary materials. The last dorsal is fused to the first sacral.

Six sacral vertebrae are identified, and they are obscured by the ilia in lateral view, except for the first two. The first sacral keeps the similar shape as the cranial dorsals, but with an enlarged diapophysis. In ventral view, the centra of the sacrals have relatively flat ventral surfaces, with enlarged ends and restricted middles. The bases of the neural spines are fused together.

3. Discussion

The discovery of *Equijubus*, and its basal position in hadrosauroid phylogeny, elucidates the phylogenetic

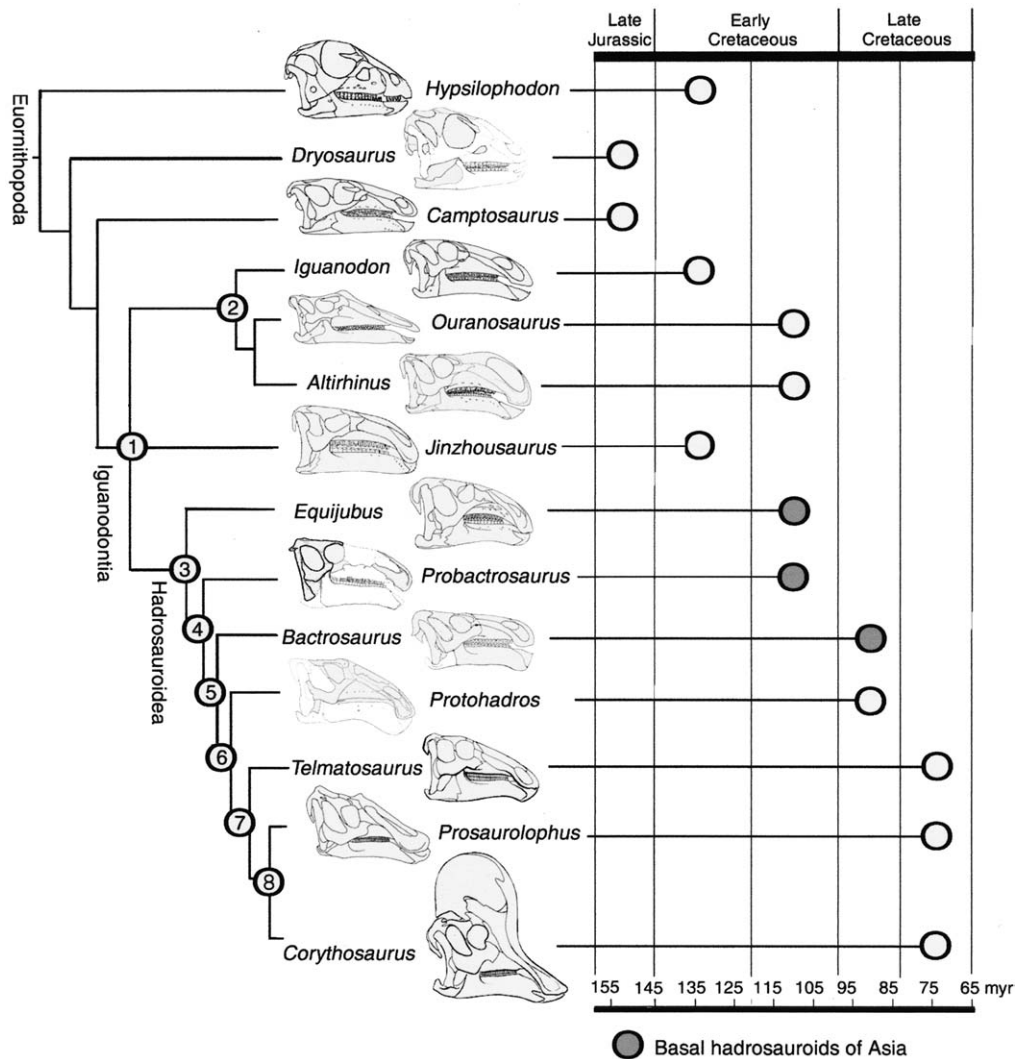


Fig. 3. Phylogenetic relationships of *Equijubus normani* gen. et sp. nov. The topology is based on the strict consensus of two equally parsimonious and shortest trees from PAUP Branch-and-Bound search for 66 characters of 15 comparative taxa, with all multi-state characters unordered. The 50% majority consensus tree also has identical topology as the strict consensus; see Table 1, Table 2 for character list and data matrix, respectively). Node 1, Iguanodontia (defined by Norman, 1998; Node 2, Iguanodontidae (defined by Norman, 1998 and including *Ouranosaurus*); Node 3, Hadrosauroidia (defined by Godefroit et al., 1998 and Sereno, 1999, modified to include *Equijubus normani*); Nodes 4–7 represent successive phylogenetic hierarchies of several ‘hadrosauroid’ stem taxa; Node 8, crown group of Hadrosauridae. The highly mobile maxilla and elaborate dental batteries of the Late Cretaceous hadrosauroids (Node 8) have an intermediate and precursor condition in the stem taxa of hadrosauroids (Nodes 3–7), indicating a step-wise pattern of phylogenetic evolution. Stratigraphical distributions follow Norman and Weishampel (1990), Sues and Norman (1990), and Weishampel and Horner (1990), and are based on species used in this morphological analysis, although the stratigraphical distribution of genera and/or families for these species can be different.

transformations in the origin of the feeding specialization of Late Cretaceous hadrosauroids. The highly elaborated feeding structures seen in the Late Cretaceous Hadrosauridae are assembled gradually in clearly defined transformation series (Fig. 3). Derived hadrosaurian features, such as the ventrally deflected and curved oral margin of the premaxilla and the long rostroventral process of the lacrimal above the maxilla, incipiently occurred in the common ancestor of *Equijubus* and all other hadrosauroids (Fig. 3, Node 3). These apomorphies of the upper jaw evolved prior to the origin of the derived hadrosaurian dental characters

in *Bactrosaurus* of a younger geological age (Godefroit et al., 1998) and other, more derived, hadrosauroids, such as the much better developed second row of replacement teeth, the loss of the accessory ridges on the crowns of maxillary teeth, and the shifting of the primary ridge on the maxillary tooth crown to the midline (Fig. 3, Node 5). The simplified crowns allowed the teeth to interlock, resulting in the more elaborate structure of the dental battery. In a yet more derived clade inclusive of *Protohadros* (Fig. 3, Node 6), the tooth number increased to more than 29 in correlation with the miniaturization of the teeth. In the clade composed of

Table 1
Character list

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- 1 Skull height across the quadrate, relative to basal skull length: between half to two-thirds (0); less than half (1).
 - 2 Preorbital length/basal skull length: short, about half (0) half to two-thirds (1); long, more than two-thirds (2).
 - 3 External naris enlargement: absent or incipient (0); relatively large, 20–40% of basal skull length (1); extremely large, >40% of basal skull length (2).
 - 4 Antorbital fenestra, lateral exposure: present (0); absent (1).
 - 5 Paraquadratic foramen between quadratojugal and quadrate: absent (0); present (1).
 - 6 Surangular foramen: present (0); absent (1).
 - 7 Premaxilla oral part, lateral expansion: absent or incipient (0); moderately developed (1); well developed (2).
 - 8 Premaxilla oral part, ventral inflection: absent (0); incipient (1); below dentary tooth row (2).
 - 9 Premaxilla oral part, ventral margin form: straight (0); ventrally curved (1).
 - 10 Premaxilla oral part, ventral margin denticulation: absent (0); present (1).
 - 11 Premaxilla oral part, double layered lateral expansion: absent (0); present (1).
 - 12 Maxilla, length ratio between rostral/caudal portions: about the same length (1); relatively longer rostral portion, but <twice the length of the caudal portion (1); extremely long rostral portion, about twice the length of the caudal portion (2).
 - 13 Maxilla, dorsal process, relative position to lacrimal ventral level: above (0); below (1).
 - 14 Maxilla, finger-like lacrimal process: absent (0); present (1).
 - 15 Maxilla, jugal process: absent (0); present (1).
 - 16 Lacrimal, shape: block-shaped (0); long, with a rostroventral process (1).
 - 17 Supraorbital: free articulation to orbit rim (0); fusion or loss to orbit rim (1).
 - 18 Solid crest in supraorbital region: absent (0); present (1).
 - 19 Jugal, rostral end, dorsoventral expansion: absent (0); present (1).
 - 20 Jugal-ectopterygoid contact: present (0); absent (1).
 - 21 Quadratojugal, caudal reduction in lateral view: not developed (0); reduced to tear drop shape (1); reduced to rostrocaudally short sheet (2).
 - 22 Quadrate, mandibular condyle, transverse width: wide (0); narrow (1).
 - 23 Supraoccipital contribution to foramen magnum: present (0); absent (1).
 - 24 Occipital condyle articular surface, inclination: rostroventrally (0); vertically (1).
 - 25 Basipterygoid process, length: short (0); long (1).
 - 26 Mandibular diastema: absent (0); present (1).
 - 27 Coronoid process, composition: about equal from dentary and surangular (0); dentary dominated (1).
 - 28 Coronoid process, projection: vertically (0); inclines rostrally (1).
 - 29 Dentary tooth row distal end position, relative to apex of the coronoid process: rostral(0); ventral (1); caudal (2).
 - 30 Angular, lateral exposure: present (0); absent (1).
 - 31 Tooth count per tooth row: fewer than 20 (0); 20–29 (1); more than 29 (2).
 - 32 Inter-crown spaces: present (0); absent (1).

Table 1 (continued)

33	Number of replacement teeth per dentary tooth family: one (0); two (1); three or more (2).
34	Relative size of maxillary and dentary teeth: about the same (0); larger dentary teeth (1)
35	Maxillary crown, prominent primary ridge on the labial surface: absent (0); present (1)
36	Maxillary crown, position of primary ridge: offset the midline (0); median (1).
37	Maxillary crown, accessory ridges: present (0); absent (1).
38	Dentary crown, ridges: multiple ridges without a dominant one (0); two subequal ridges (1); one prominent primary ridge (2).
39	Dentary crown, position of primary ridge: offset the midline (0); median (1).
40	Dentary tooth, angle between axis of root and crown: large, more than 130 degrees (0); small (1).
41	Postaxial cervicals, neural spine height: prominent (0); rudimentary (1).
42	Postaxial cervicals, form of postzygapophyses: weakly arched (0); strongly arched (1).
43	Sacral number: five (0); six to seven (1); eight or more (2).
44	Caudal neural spines height, compared to respective chevrons: shorter (0); longer (1).
45	Sternal ventrolateral process: absent (0); present (1).
46	Carpals and metacarpal I, articulation: free (0); co-ossified (1).
47	Metacarpal I, length, compared to metacarpal II: more than 50% (0); less than 50% (1).
48	Metacarpal II length, compared to metacarpal III: subequal (0); 70–80% (1).
49	Metacarpals II–IV, configuration: spreading (0); appressed, ligament-bound (1).
50	Metacarpal IV, length, compared to metacarpal III: 60–70% (0); subequal (1).
51	Manual digit I, orientation, angle from the axis of digit III: 15–25 degrees (0); more than 45 degrees (1).
52	Manual digit I, phalanx 1, shape: longer than broad (0); broader than long (1).
53	Manual digit I, ungual, shape: claw-shaped (0); subconical (1).
54	Manual digit I, ungual, length, compared to that of manual digit II: shorter (0); longer (1).
55	Manual digits II–IV, phalanx 1 length: compared to phalanx 2 length: less than twice (0); more than twice (1).
56	Manual digits II and III, ungual shape: claw-shaped (0); hoof-shaped (1).
57	Manual digit II, ungual, shape, compared to that of manual digit III: broader (0); narrower (1).
58	Manual digit V, phalangeal number: two (0); three (1).
59	Manual digit V, phalanx 1, length, compared to length of metacarpal V: less than 50% (0); subequal (1).
60	Iliac preacetabular process, length, compared to ilium length: less than 50% (0); more than 50% (1).
61	Iliac preacetabular process, length, compared to postacetabular process: subequal (0); longer (1).
62	Iliac preacetabular process, depth of distal end, compared to that of proximal end: subequal (0); greater (1).
63	Iliac peduncle of pubis: absent (0); present (1).
64	Prepubic process, depth of distal end, compared to its minimum depth: subequal (0); 25% greater (1); 50% greater (2).
65	Postpubic process, length: about the same of ischium (1); about half the length of ischium (2).
66	Femur, intercondylar extensor groove: moderately developed (0); very deep to form a tunnel (1).

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