Redescription of neoceratopsian dinosaur *Archaeoceratops* and early evolution of Neoceratopsia

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Archaeoceratops oshimai Dong and Azuma, 1997 is a basal neoceratopsian from the late Early Cretaceous of Mazongshan area, Gansu Province, northwest China. Here we provide a detailed description on *Archaeoceratops oshimai* based on both the holotype, which consists of a well preserved, nearly complete skull, partial vertebral column, and partial pelvis, and the paratype, which consists of a partial vertebral column including a nearly complete tail, a partial pelvis, fragmentary hind limb bones, and a complete pes. Cladistic analysis shows that *Archaeoceratops* is the sister group to all currently known Late Cretaceous Neoceratopsia, and Late Cretaceous Neoceratopsia diverged into two clades: the Asian Protoceratopsidae and the North American Ceratopsoidea, indicating a dual evolution for the two major groups of horned dinosaurs in two landmasses of Late Cretaceous. A suite of derived features characterizes Ceratopsoidea, such as a round-shaped external naris, a long caudolateral process of the rostral bone, and ventrally curved premaxillary ventral edge.

Key words: Dinosauria, Neoceratopsia, Cretaceous, China, Gansu Province, Mazongshan area.

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Introduction

Archaeoceratops oshimai Dong and Azuma, 1997, one of the best-preserved Early Cretaceous representatives of the Neoceratopsia known so far, was recovered from the Mazongshan area of Gansu Province, northwest China by the Sino-Japanese Silk Road Dinosaur Expedition in 1992, and was the subject of a preliminary description by Dong and Azuma (1997). It is probably Albian in age (Tang et al. 2001), and is a key component to an analysis of the evolution of basal neoceratopsians (Sereno 2000; Makovicky 2001; Xu et al. 2002; You 2002). Here we provide a detailed description on the type specimens of *Archaeoceratops oshimai*, and discuss its phylogenetic significance.

Archaeoceratops oshimai is a basal neoceratopsian as demonstrated by its morphology, which is supported by cladistic analysis. Its skull has no trace of nasal and orbital horncores, and the frill is incipient. The naris is small and low, while the orbit is large. The rostral is small, and the premaxilla still possesses teeth. *Archaeoceratops oshimai* also has some peculiar autapomorphic features, such as a modest bumpy ornamentation covering much of the lateral surface of the jugal. Its ischiadic peduncle has an excavation on the lateral surface, and the shaft and proximal end of metatarsal I are strongly reduced.

The specimens described in this paper are housed at the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, abbreviated as IVPP.

Description

The holotype of *Archaeoceratops oshimai* Dong and Azuma, 1997, IVPP V 11114, consists of a well preserved, nearly complete skull and jaws, partial vertebral column, and partial pelvis. The paratype, IVPP V 11115, a somewhat smaller specimen, consists of a partial vertebral column including a nearly complete tail, a partial pelvis, fragmentary hind limb bones, and a complete pes.

Skull.—The skull of *Archaeoceratops* is preserved in three dimensions. Although slightly distorted by crushing, it is best preserved on the right side (Fig. 1). The left side of the face is collapsed in the region of the antorbital fossa. The left squamosal, quadratojugal, exoccipital and quadrate shafts are not preserved. The parietals have been destroyed by erosion, making it impossible to determine the details of the frill. The jaws are articulated, rendering aspects of the dental anatomy difficult to ascertain. The descriptions that follow are based on the right side of the skull unless otherwise stated. Cranial sutures are visible (Dong and Azuma 1997). Although the specimen may not have achieved full adult size, closure of vertebral sutures was underway, indicating the approach of adult size.

The skull measures 145 mm from the tip of the rostrum to the caudal end of the quadratojugal and 175 mm from the tip of the rostrum to the caudal end of the squamosal. It has the characteristic ceratopsian triangular morphology in dorsal

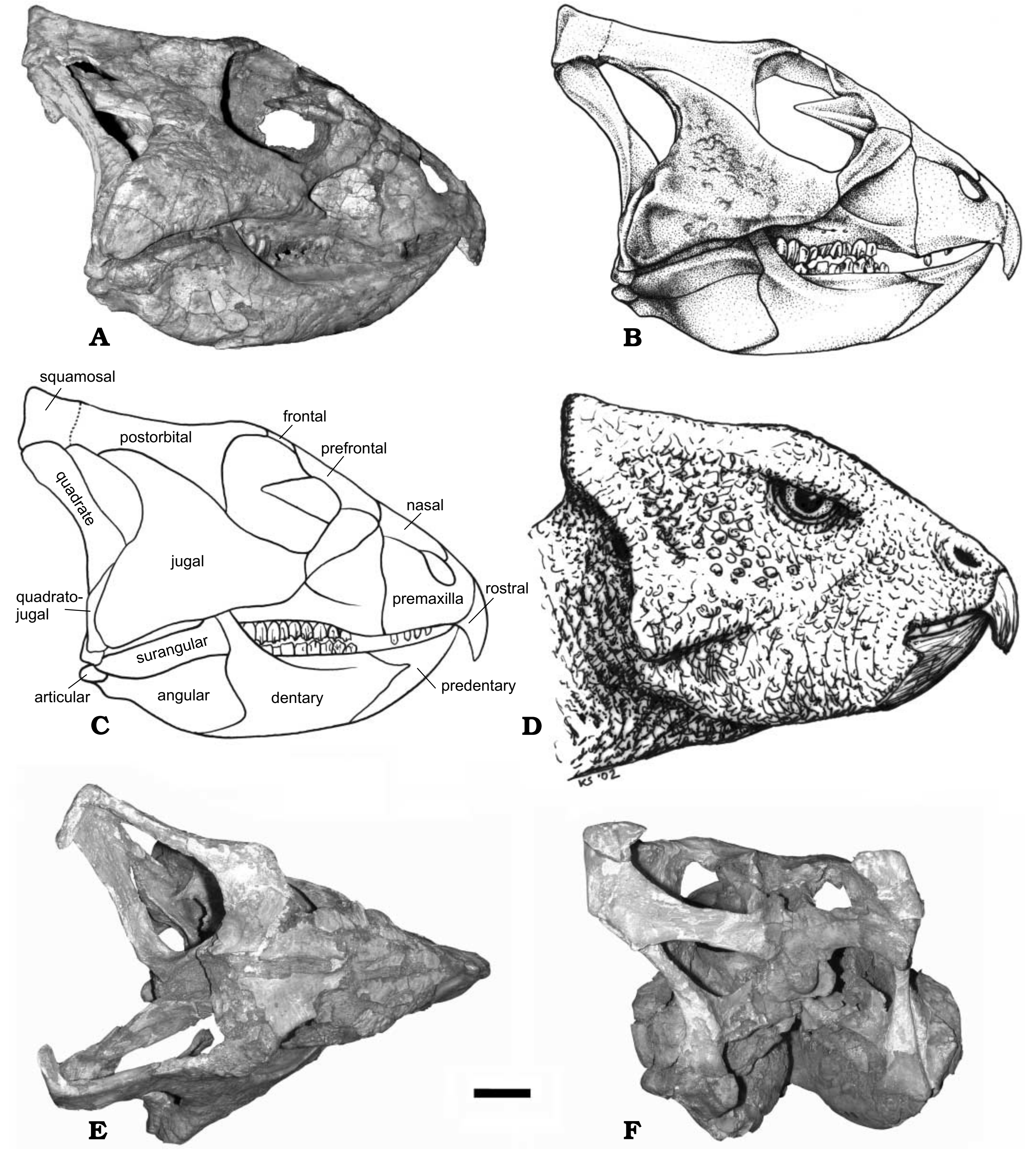

Fig. 1. *Archaeoceratops oshimai*, IVPP V 11114, holotype in right lateral (**A**–**D**), dorsal (**E**), and caudal (**F**) views of the skull. A, E, and F, photographs; B, drawing; C, interpretive outline; D, live reconstruction. Scale bar 2 cm.

view, with a narrow beak and moderately flaring jugals. The width between the jugals is about 125 mm. Skull width between the quadrates is 95 mm. There is no trace of either orbital or nasal horn cores.

The preorbital region is relatively short, and slopes strongly ventrally from the orbit to the beak. The external naris is small and elliptical, situated relatively high on the face: its dorsalmost extent is situated at the level of the bottom third of the orbit and it extends somewhat ventral to the lower border of that structure. On the right side, the naris measures 18 mm in its longest dimension. The rostral bone is rather delicate and unusually pendant, extending well below the level of the maxillary tooth row. Three peg-like teeth are prominent along the caudal half of the ventral border of the premaxilla; a socket for a fourth tooth may be present. The rostral half of the premaxilla is edentulous. The pronounced antorbital fossa attains a depth of nearly a centimeter on the right side. In typical basal neoceratopsians, the antorbital fossa is preorbital in position but in *Archaeoceratops*, consistent with the low facial region, the antorbital fossa is shifted caudally, ventral to the rostral part of the orbit. It does not have the subcircular form seen in *Protoceratops* (Brown and Schlaikjer 1940) or *Bagaceratops* (Maryańska and Osmólska 1975), but is triangular, with its apex directed caudally. The fossa deepens caudally and has sharply defined dorsal and ventral edges. No antorbital foramen is evident. The orbits are relatively enormous, occupying 25% of the linear dimension of the skull. This is comparable to the relative size of the orbit in *Psittacosaurus* (Sereno 1990) but larger than in other adult neoceratopsians. A palpebral bone is also more prominent than in any ceratopsian. The infratemporal fenestra is tall, and does not extend rostrally very much. The supratemporal fenestrae are very prominent.

The rostral is rather delicate, and is primarily vertical in orientation. It extends caudally only very little along the buccal border of the premaxilla, and its dorsal tip does not seem to meet the nasal (but see Dong and Azuma 1997). It is 31 mm high but is transversely narrow, 7 mm in width. The premaxilla is a prominent, plate-shaped element. It borders the external naris caudally and ventrally, and wraps it rostrodorsally with its caudodorsal process. Caudally, the premaxilla contacts the maxilla, and the premaxillary-maxillary suture rises more or less vertically immediately caudal to the terminal premaxillary alveolus.

The maxilla has the form of a right triangle with the apex at the ventral end of the maxillary-premaxillary suture and the hypotenuse sloping caudoventrally from the lacrimal rostrodorsally to the jugal caudoventrally. No evidence shows the participation of the maxilla in the ventral border of the orbit as illustrated in fig. 2A of Dong and Azuma (1997). The lateral aspect of the maxilla is dominated by the antorbital fossa. The rostral 2 cm of the ventral border of the maxilla is edentulous. This portion is directed caudomedially to form the rostral end of the maxillary recess. The dentigerous margin of the maxilla is strongly inset by as much as 2 cm. Approximately 12 maxillary tooth positions can be ascertained on each side; perhaps one or two more lay opposite the coronoid process. The maxilla is 59 mm long measured along the tooth row.

The lacrimal is a prominent, crescentic bone, oblique in orientation, that forms the rostroventral quarter of the orbital rim. It forms the caudodorsal rim of the antorbital fossa. It contacts the prefrontal dorsally, the jugal caudally, and the maxilla rostroventrally. The lacrimal-nasal contact is very weak. The lacrimal measures 32 mm in length and 15 mm across at its widest point dorsally.

The jugal runs between the orbit and the caudoventral corner of the skull, and forms part of the rostral border of the infratemporal fenestra. The jugal overlaps the caudal half of the maxilla and extends as far rostrally as the antorbital fossa, reaching its caudal border. It contacts the lacrimal dorsal to the antorbital fossa. Caudally it overlaps the quadratojugal, largely occluding this element in lateral view. It appears to form a large portion of the rostral border of the infratemporal fenestra. A modest ridge, which represents a caudal continuation of the maxillary shelf, extends horizontally across the jugal, such that the ventral apex lies slightly closer to the midline than does the ridge. A modest bumpy ornamentation covers much of its lateral surface. Such an ornamentation is seen on the jugals of pachycephalosaurs such as *Prenocephale* and *Stegoceras* (Maryańska 1990). The jugal measures 64 mm from the orbit to the ventral apex, and 62 mm in breadth from the antorbital fossa to the infratemporal fenestra. The epijugal is probably ossified.

The quadratojugal is prominent in occipital view, and acts as a thick, wedge-shaped spacer, tapering dorsally, between the ventral shaft of the quadrate medially and the jugal laterally. Erosion has destroyed the more delicate dorsal shaft of the quadrate and quadratojugal, so that the relationships between these two bones cannot be determined. It reaches its greatest thickness, 14 mm, about 20 mm dorsal to the quadrate condyle, thinning abruptly ventrally and more gradually dorsally. Only the ventral condyles of the quadrates are preserved. These are conventional in form and measure 20 mm in width.

The nasal is broad and flat, rather than arched (Dong and Azuma 1997). Little of the bone is seen in lateral view. It surrounds the caudal half of the external naris's dorsal margin, and contacts the premaxilla, maxilla and lacrimal on its lateral edge. Caudolaterally, it is excluded from the orbit by the prefrontal. Caudomedially, it contacts the frontal. It is narrowest between the external nares and broadest at its contact with the maxilla. It narrows caudally between the prefrontals. Sutures are not distinct, but the element is about 63 mm in length along the midline and the pair measures 32 mm in width between the maxillae.

The prefrontal occupies the rostrodorsal quarter of the orbit. It extends from the lacrimal to the frontal, and excludes the nasal from the orbit. It is about 39 mm in length and 12 mm in width. Articulating with the prefrontal is a very prominent, flat, triangular palpebral. The acute apex of the triangle projects into the center of the orbit and the hypotenuse is ventral. The long ventral edge terminates rostrally in a peg-like structure that contacts the rim of the orbit at the lacrimal-prefrontal junction, while the dorsal apex of the triangle contacts the orbital rim about 1 cm rostral to the prefrontal-frontal junction. The left palpebral measures 27 mm in length, 12 mm in width, and ranges from 5 mm in thickness at the rostral end to 2 mm at the caudal apex; the right palpebral measures 29 mm by 11 mm, and range in thickness from almost 6 mm to 3 mm.

The paired frontals occupy the major portion of the caudal skull roof (see Dong and Azuma 1997: fig. 2B). The midline suture is well defined but the sutures with the postorbital and the parietal are difficult to discern, particularly on the right side. For example, the frontal presumably continues caudally to form part of the rostral border of the supratemporal fenestra as in *Protoceratops* and other basal neoceratopsians (Dodson and Currie 1990), but this cannot be verified. The frontal appears to contribute only a small portion (about 10 mm), rather than a larger portion (Dong and Azuma 1997), of the dorsal rim of the orbit. The width across the paired frontals between the orbits is 33 mm.

The postorbital forms nearly a quarter of the orbital rim, and extends as a vertical plate caudal to the orbit to form a small part (but see Dong and Azuma 1997) of the rostral border of the infratemporal fenestra dorsal to the jugal. It is damaged caudally on the right side (absent altogether on the left side), so it is impossible to assess where it ends and the squamosal begins.

A portion of the right squamosal is preserved, providing some indication of its morphology. It seems to be a simple, vertically oriented bar dorsal to the infratemporal fenestra. Above the head of the quadrate, it makes a right-angle bend towards the midline, as in *Leptoceratops*; there is no post-quadrate extension of the squamosal as in *Protoceratops*. Only the rostral end of the parietials are preserved, which fused firmly to the frontals.

The occipital region was well described by Dong and Azuma (1997), and a brief summery is provided here. On the occipital surface, the following elements and structures are preserved: the supraoccipital, the right exoccipital, the foramen magnum, the occipital condyle, and the basioccipital tuberosities. The foramen magnum is roofed by the incompletely preserved supraoccipital. On the right side, a strap-like exoccipital runs caudolaterally from the foramen magnum to the head of the quadrate. It is 43 mm long, 14 mm high at midshaft and 29 mm high as it flares distally by the head of the quadrate. The opisthotic fuses to the rostral surface of the exoccipital laterally, but more medially is separated by as much as 5 mm, resulting in a ventrally open channel leading to the fenestra ovalis. No stapes is preserved.

The elements of the palate are not well exposed, and no further information can be provided here other than Dong and Azuma (1997).

Complete lower jaws are preserved in position. The predentary is long and horizontal in orientation. It terminates in a sharp point that fits inside the upper beak. The predentary measures 57 mm in length along the ventral midline. The dentary is robust and straight along the lower edge. The ramus of the dentary is not particularly deep (26 mm) but is robust in construction. The mandibular dentition is strongly inset, corresponding to the maxillary dentition. The toothrow passes medial to the coronoid process. The dentary attains its greatest thickness at the rostral base of the coronoid process, where it measures 25 mm. The coronoid process is obscured by the jugal, and seems to be high and strong. As in *Protoceratops*, the surangular is an important bone that contributes to the caudal half of the coronoid process and extends to the caudal end of the jaw in lateral view. It bears a strong, caudally descending lateral ridge that is congruent with the ventral edge of the jugal, and can be viewed as a bony "stop" to limit jaw adduction. The articular is situated medial to the surangular and somewhat ventral to it at the caudal end of the jaw. No retroarticular is developed. The angular and splenial bones are developed on the lateral and medial sides of the mandible, respectively, but nothing of significance can be stated about them.

Premaxillary teeth are well developed. There is one prominent tooth visible on each side. On the right side, two others are in various stages of eruption. The right tooth is cylindrical. It appears to be enameled on all aspects. It is roughly 7 mm long and 3.7 mm in diameter. The left tooth is about 5 mm long and 3.2 mm in diameter. The cheek teeth are simple in pattern, with a single functional tooth corresponding to each alveolus. Twelve maxillary teeth span a distance of 48 mm. The first two teeth are the smallest, and tooth size increases distally. The teeth possess a single, parasagittal, primary ridge with several secondary ridges on either side. Twelve teeth can be seen on the left dentary and 11 on the right. Dentary tooth crowns are low, decorated with small denticles, and present prominent, steeply inclined wear facets in lateral view. Primary ridges are not very apparent.

Axial skeleton.—The holotype of *Archaeoceratops oshimai*, IVPP V 11114, includes an articulated series of 1 cervical, 12 dorsal vertebrae and a sacrum consisting of six vertebrae. In the paratype, V 11115, there is a nearly complete caudal series of 36 vertebrae as well as three dorsal vertebrae and a sacrum. Thus it is via the sacrum that the two specimens may be compared with each other. All vertebrae in both specimens have flat central articular faces.

Cervical 10 through dorsal 8 are preserved as a single unit joined by matrix; dorsals 9 and 10 similarly form a unit, and dorsals 11 and 12 are joined with, but not fused to, the sacrum. C10 consists only of a centrum, measuring 11 mm in length, 12 mm in width and 15 mm in height. The centra of dorsals 1 to 8 are all simple spools. Neural arches are not preserved but many transverse processes remain. The diapophyseal facets are pronounced on all of the transverse processes, typically about 15 mm lateral to the neural spines, but parapophyses cannot be detected. The left transverse process on dorsal 4 measures 22 mm laterally from the base of the neural spine.

The beautiful preserved unit consisting of dorsals 11 and 12 plus the sacrum also preserves two incomplete ilia (Fig. 2). The ilium extends as far cranially as dorsal 11. The neural spines are preserved on this unit, although the cranialmost four spines are somewhat damaged. The neural spines of all eight vertebrae are expanded in the axial plane and lie close to each other but remain separated by matrix. The first four spines, of dorsals 11 and 12 and sacrals 1 and 2,

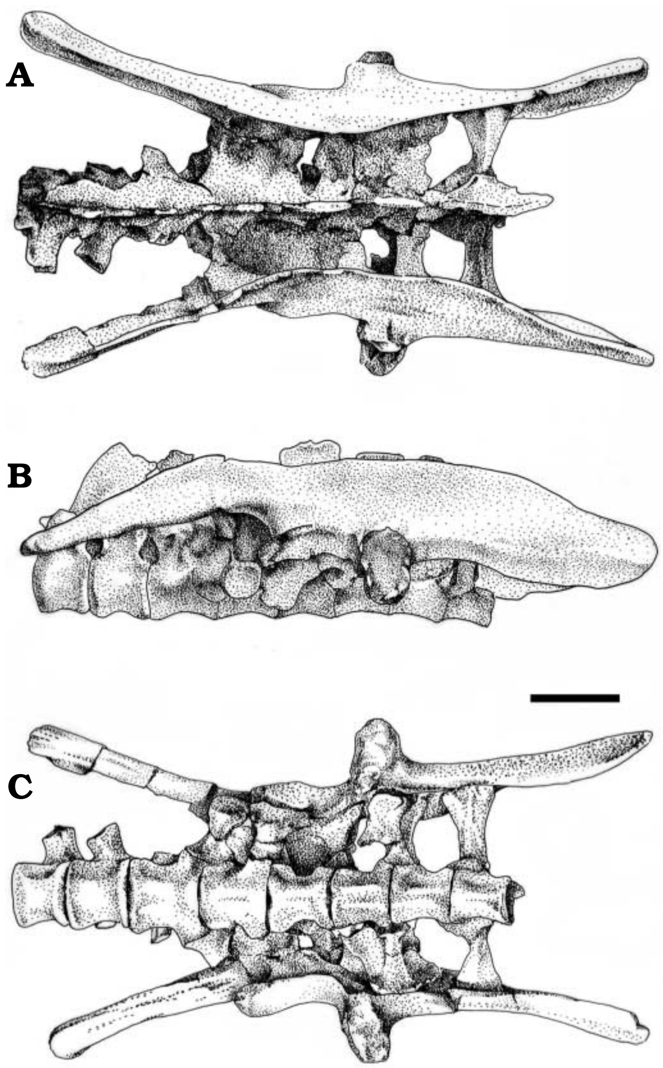

Fig. 2. Sacral vertebrae and ilia of *Archaeoceratops oshimai*, IVPP V 11114, holotype in dorsal (**A**), left lateral (**B**), and ventral (**C**) views. Scale bar 2 cm.

are mildly inclined caudally, while the spines of sacrals 3 to 6 are more erect. The tallest preserved spine is that of sacral 3, which has a total height of 45 mm from the bottom of the centrum to the top of the spine; the corresponding heights of S4, S5 and S6 are 42, 42, and 40 mm. The axial lengths of the neural spines along their distal ends are 15 mm, 17 mm, 14 mm and 12 mm for S3, S4, S5, and S6, respectively. Because the transverse processes of dorsals 11 and 12 and of sacral 1 are broken, it cannot be determined whether or not they contacted the cranial blade of ilium. The axis of the sacrum is absolutely straight. The sacral vertebrae decrease in size from the first to the sixth, with a marked decrease occurring within the body of sacral 3, and a further decrease within the body of sacral 6. The surface area of the caudal face of sacral 6 is roughly one-third the surface area of the cranial face of sacral 1. This indicates a strongly reduced tail. The ventral surface of sacral 1 is smooth, but beginning with sacral 2 there is a shallow groove on the ventral midline, most pronounced under sacral 4, and undetectable under sacral 6.

There are five pairs of sacral ribs, the first of which is borne between sacrals 1 and 2, the last between sacrals 5 and 6. Sacral ribs 1 and 2 are large, heavy and short, and the peduncles originate on the ventral portion of their associated centra. Sacral 1 has a distinctive, keystone shape in ventral view due to the oblique peduncle for the origin of sacral rib 1, whose head measures 12 mm in width. The complementary surface on the cranial end of sacral 2 is parallel to the vertebral axis and thus does not form such a prominence. Sacral rib 1 projects laterally a distance of 13 mm, and ends in a flat surface 9 mm in diameter immediately cranial to the pubic process of the ilium. It also sends a process dorsally to join the transverse process of sacral 1, which contacts the cranial blade of the ilium in front of the acetabulum. The broad, flat, irregular surface of sacral rib 2 is also located medial to the craniodorsal rim of the acetabulum. The origin of sacral ribs 3, 4 and 5 are more dorsal on their respective centra. Rib 5 is the longest and most gracile. Sacral rib 3 supports the dorsal apex of the acetabulum. Sacral rib 4 supports the region of the ischial peduncle of the acetabulum. Sacral rib 5 supports the middle of the caudal portion of the ilium. There are separate transverse processes on sacrals 2 to 5 that contact the medial surface of the ilium dorsal to the sacral ribs.

The paratype, V 11115, generally corroborates the preceding description, but due to its immaturity demonstrates some interesting further details. The centra of dorsal 10 and all subsequent dorsal and sacrals lacks their neural spines. Dorsal 10 possesses a peculiar, open groove underneath the neural canal. It runs half the length of the centrum, and measures 6.5 mm in length by 1.5 mm in breadth. By sacral 2, this feature has increased in prominence, by more than doubling in width to 3.5 mm. On S3 and S4 the groove is twinned to form a pair of grooves. On S5 and S6, the groove is once again sagittal and singular. This groove persists in the proximal caudal vertebrae at least as far as caudal 8. In this specimen, the surface area of the caudal face of sacral 6 is roughly 40% the surface area of the cranial face of sacral 1.

The paratype preserves a nearly complete tail of 36 vertebrae. Possibly one or more vertebrae are missing in the middle, but delicate distal caudals are preserved. The tail, as preserved, has a length of about 325 mm. Transverse processes persist until about caudal 15. The neural spines on the first four caudals are well developed and only slightly inclined caudally. The total height of caudal 4, including the spine, is 32 mm. Spines beyond that point are broken. Chevrons are poorly preserved. Several Y-shaped chevrons are preserved in place beneath caudals 9 to 12. The best preserved measures 15 mm in length. Chevron facets on the caudals are not evident until caudal 5 and then continue at least as far as caudal 20. Possibly one or several centra are missing between Caudals 17 and 18 as preserved, because the latter differs markedly from the former one: it is no longer spool-shaped but long and low, like a distal caudal. For example, Caudal 15 measures 9 mm in length by 8 mm in width by 8.5 mm in height, while Caudal 18 measures 9 mm by 5.5 mm by 6.5 mm. This is a striking decline in width and height, and a re-

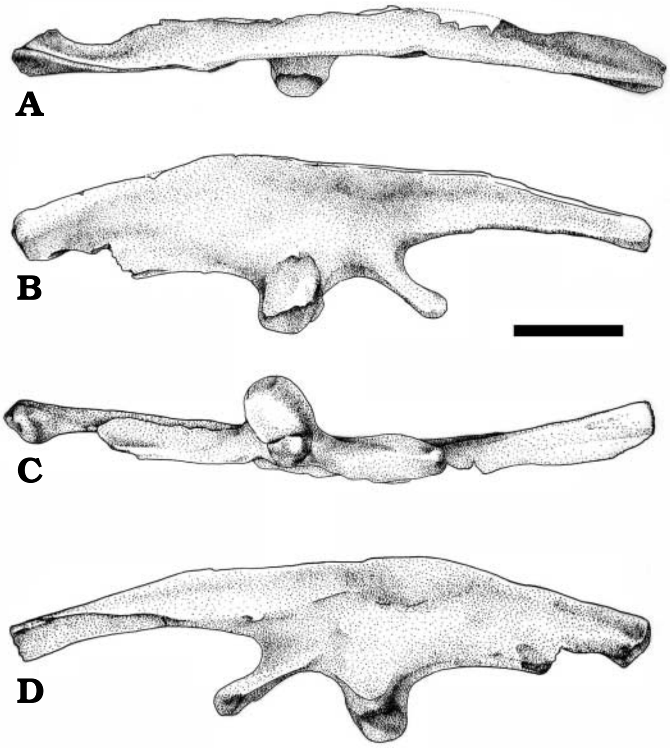

Fig. 3. Right ilium of *Archaeoceratops oshimai* IVPP V 11115, paratype in dorsal (**A**), left lateral (**B**), ventral (**C**), and medial (**D**) views. Scale bar 2 cm.

duction in volume by about 50%. Neural arch bases and articular processes are evident as far caudally as caudal 30. Beyond that point, the centra are little more than simple rods. Caudal 36 measures 5 mm in length and less than 2 mm in both breadth and height.

Pelvis.—The type specimen of *Archaeoceratops*, V 11114, includes both ilia, both pubes and a partial ischium. The paratype, V 11115, includes a right ilium (Fig. 3). In V 11114, the caudal portion of the left ilium is missing and the cranial portion of the right one is missing. The overlap between the two halves allows an estimate of 150 mm in length. V 11115 measures 127 mm in length. The description that follows is based on the holotype specimen except as noted. The ilium is long and low, with a sharp dorsal edge. The length of the preacetabular portion is about equal to the postacetabular portion, 59 mm for the former, 60 mm for the latter. The gently arched dorsal margin of the ilium has its apex over the acetabulum, and close to the midline of the sacrum (separation of dorsal margins of ilia 31 mm; separation of acetabula ventrally 53 mm). Both cranially and caudally the ilia bend laterally with an approximate separation of more than 70 mm. The cranial process of the ilium tapers cranially to a blunt point, and has a triangular cross-section with a narrow, flat surface, measuring 9 mm in width, directed ventrally. The ventral edge of the caudal process of the ilium projects slightly medially, but does not form a pronounced shelf. The acetabulum is deep dorsoventrally and arched rather than forming a semicircle. The internal diameter of the acetabulum, between the pubic and ischial peduncles, is 26 mm, while the distance between the external surfaces of the same peduncles is 38 mm. The apex of the acetabulum is 9 mm (right) to 10 mm (left) in thickness. The cranial tip of the pubic peduncle is broken on the left side, as is the first sacral rib on the right side. It appears that the latter supports the former, although the sacral rib seems much too heavy for this purpose. The second sacral rib conforms to the shape of the cranial rim of the acetabulum and may have contributed functionally to the articular surface of the hip joint. The ischiadic peduncle is much more robust than

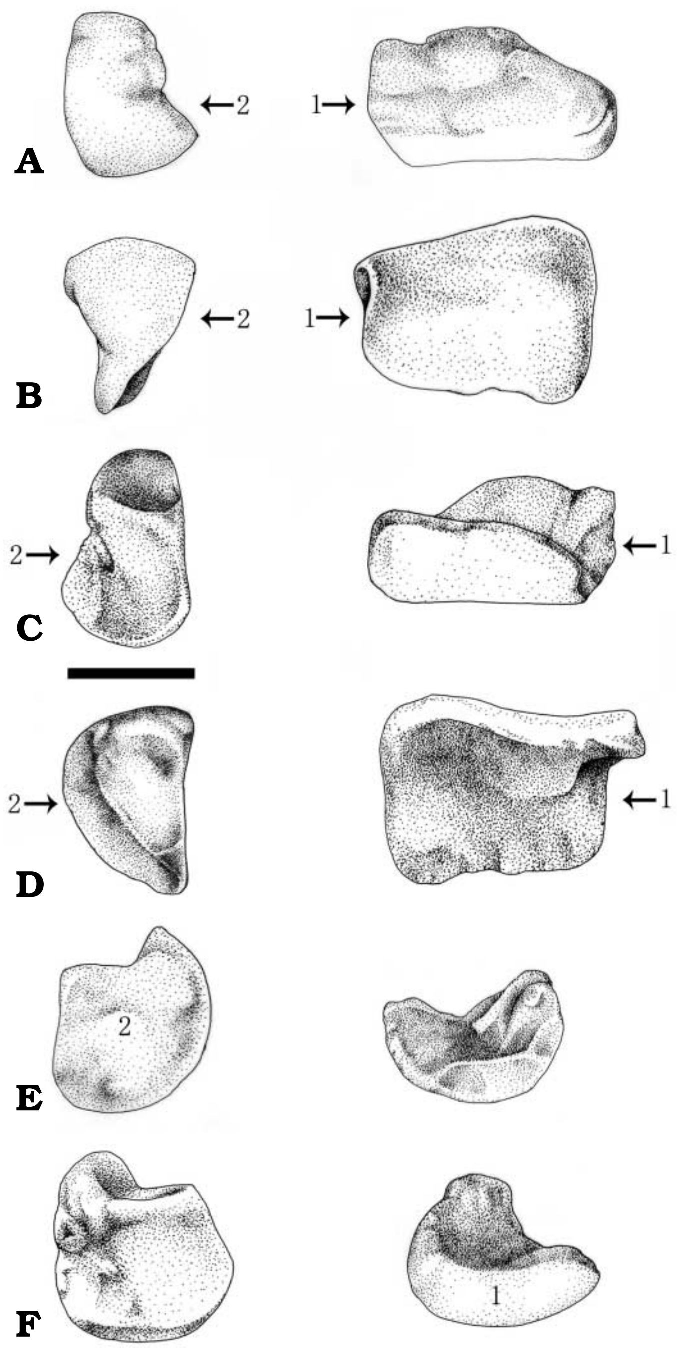

Fig. 4. Right astragalus and calcaneus of *Archaeoceratops oshimai* IVPP V 11115, paratype in cranial (**A**), distal (**B**), caudal (**C**), proximal (**D**), medial (**E**), and lateral (**F**) views. Left: calcaneus; right: astragalus. 1: Facet on astragalus for calcaneus; 2: facet on calcaneus for astragalus. Scale bar 1 cm.

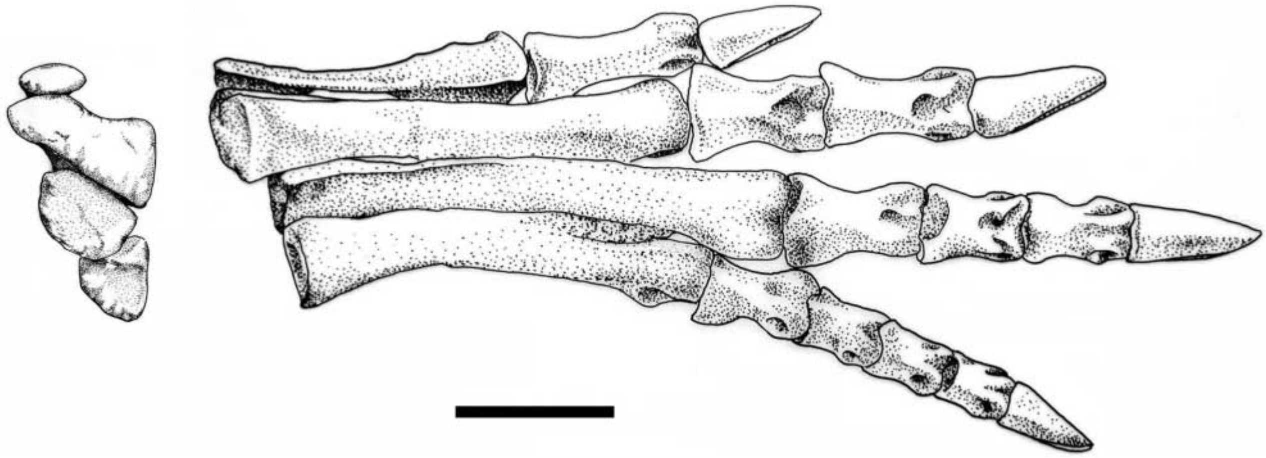

Fig. 5. Right pes of *Archaeoceratops oshimai* IVPP V 11115, paratype in dorsal view. Scale bar 2 cm.

the pubic peduncle. A large excavation of unknown significance on the lateral surface of the ischiadic peduncle displays a texture suggesting that an ossification center is missing. An identical feature is seen on the ilium of V 11115. The ischial peduncle is notched, with a weak internal shelf and a bulbous external condyle. This arrangement is more clearly seen in the paratype than in the type specimen; in either case, the feature is not seen in lateral view. Perhaps this feature is designed to stabilize the proximal end of the ischium, but unfortunately the latter is not preserved. In the holotype specimen, the scar measures 16.5 by 10 mm. The ischial peduncle measures 16 mm in width.

The pubic peduncle of V 11115 possesses, on its medial surface, a shallow scar for sacral rib 2. A prominent scar between the apex of the acetabulum and the ischial peduncle articulates with sacral rib 3, a large scar caudodorsal to the ischial peduncle is for sacral rib 4, and a scar midway on the caudal blade of the ilium correlates to sacral rib 5. In addition it shows a longitudinal ridge half way up the medial surface of the ilium for the contact of the transverse processes of the sacral rib. Near the apex of the acetabulum, this is elaborated into a circular depression, indicating elaboration of the transverse process. Another such scar is found at this level just caudal to the ischial peduncle.

Left and right pubes are preserved. Both lack the delicate postpubic process. The prepubic process appears to be complete on the right pubis. The prepubic blade appears in lateral view as a straight, thin bar, tapering from 7 mm at its base to 2.5 mm at its cranial tip. In dorsal view, it diverges laterally and then gently bends into a parasagittal plane. It is broader than high, tapering from 7 mm wide at the base of the blade to 5 mm wide at its cranial tip. Excluding the postpubic process, the right pubis measures 40 mm in length. The articular region is relatively massive, measuring 17 mm in length and 12 mm in width. A rugose medial surface 15 mm long provides primary support for the pubis against the first and second sacral ribs. There is a distinct pit on the craniodorsal surface of the peduncle for the pubic process of the ilium. The remainder of the enlarged dorsal area must serve for articulation with the ischium.

One ischial shaft, lacking the proximal end, and the distal end of the other shaft are preserved. The shaft is essentially straight except that it diverges from the midline proximally. The shaft is 106 mm long and 8 mm thick. The distal end expands to 13 by 9 mm.

Hind limb.—Preserved hind limb materials of the paratype of *A. oshimai*, V 11115, include a proximal right femur, distal right tibia and complete pes. The femur has a rather small, strongly elevated head, a low, fan-shaped greater trochanter, and a well-defined lesser trochanter. There is a shallow tendon groove on the caudal aspect of the femoral head. The femoral head measures only 10 mm in the axial plane. The proximal end of the femur is 30 mm in width. The length of the femoral fragment is 44 mm. The distal end of the tibia possesses several shallow concavities and is rather nondescript. The width of the distal end is 26 mm, and the craniocaudal length is 15 mm. There is a roughened, convex area on the lateral side of the distal end of the tibia that evidently corresponds to a congruent concavity on the calcaneum.

The astragalus and calcaneus (Fig. 4) and two probable distal tarsals are beautifully preserved. The astragalus caps the distal tibia, forming a smooth, cylindrical joint surface for the intertarsal articulation and adding 5 mm to the functional length of the crus. The astragalus shows little of the reduction that characterizes more derived neoceratopsians, including *Protoceratops*. It measures 20 mm in width, 77% of the width of the distal tibia. The cranial ascending process is wide, low and bluntly squared off dorsally. There is no caudal ascending process medially, but in caudal view the astragalus is seen as wedge that thickens medially. It shows a small facet laterally for contact with the calcaneus. The calcaneus is a small, complex bone. A broad, shallow cup, measuring 10 mm by 12 mm, stabilizes the distal tibia. A sharp ridge separates at a right angle the tibial facet from a smaller (10 mm by 6 mm), very well defined concavity for the distal end of the fibula. It also forms part of the smooth intertarsal joint surface. The lateral edge of the astragalus and medial edge of the calcaneum key to each other and form a smooth intertarsal joint surface 28 mm wide. There are two candidates for distal tarsals. The larger, perhaps medial, distal tarsal is flat and irregular, measuring 14 by 12 by 6 mm, and slightly concave on one surface. The size and concavity are consistent with the description of the medial distal tarsal of *Protoceratops* by Brown and Schlaikjer (1940). The other, perhaps lateral, distal tarsal, is a chip of bone 13 by 8 by 7 mm. The positions of these two bones can only be surmised.

A complete right metatarsus is preserved (Fig. 5). The metatarsals are long and slender. The structure is autapomorphic in that metatarsal I, though long and with a well-formed distal condyle, has a strongly reduced shaft and proximal end. The phalangeal formula is standard: 2, 3, 4, 5, 0, and the unguals are sharply pointed.

Discussion

Basal neoceratopsians represent a radiation of small dinosaurs (1 to 2.5 m long) that show at least incipient stages of many of the features that characterize the more derived Ceratopsidae. Controversy exists for the phylogeny of basal Neoceratopsia. Do they form a monophyletic group and in turn constitute the sister group to Ceratopsidae (Dodson and Currie 1990)? Or are they paraphyletic groups that led progressively to Ceratopsidae (Chinnery and Weishampel 1998; Sereno 2000; Makovicky 2001; Xu et al. 2002)? Furthermore, the interrelationships among basal neoceratopsians are not clear, if either of the above phylogenies is accepted.

Three recent cladistic analyses (Sereno 2000; Makovicky 2001; Xu et al. 2002) agree with the primitive status of *Leptoceratops*, and the close relationship between Protoceratopsidae (*sensu stricto*, Sereno 1998) and Ceratopsidae. They disagree with the placement of *Montanoceratops*, whether it is a basal Ceratopsoidea (Sereno 2000), or has a close relationship to *Leptoceratops* (Makovicky 2001; Xu et al. 2002). The detailed study of *Archaeoceratops* provides further valuable anatomical information, and permits a new cladistic analysis based on a more comprehensive data set to test previous results.

A PAUP (3.1.1) branch-and-bound search is performed for 12 taxa and 148 characters (Appendices 1 and 2). *Graciliceratops* (Sereno 2000), *Udanoceratops* (Kurzanov 1992), *Asiacerastops* (Nessov et al. 1989) and *Turanoceratops* (Nessov et al. 1989) are not included in this analysis because of their relatively poor preservations, and the goal of this analysis is trying to find the major patterns of the phylogeny of Ceratopsia. All characters are unordered and treated equally. One most parsimonious tree is found at 237 steps, with the consistency index of 0.726 and retention index of 0.781.

Cladistic analysis agrees with previous works in that *Liaoceratops* and *Archaeoceratops* are successive outgroups to Coronosauria (*sensu stricto*, Sereno 1998), and that *Protoceratop* and *Bagaceratops* are sister taxa. It also supports *Chaoyangsaurus* as the most basal Neoceratopsia (Sereno 2000), and *Montanoceratops* is the sister taxon to *Leptoceratops* (Makovicky 2001). What differs from previous topologies is that Leptoceratopsidae (*Leptoceratops* + *Montanoceratops*) (Makovicky 2001), rather than Protoceratopsidae (*Protoceratops* + *Bagaceratops*), are the sister group to Ceratopsidae. This result has profound significance for reinterpreting the paleobiogeographical pattern and evolutionary progression of horned dinosaurs (Fig. 6).

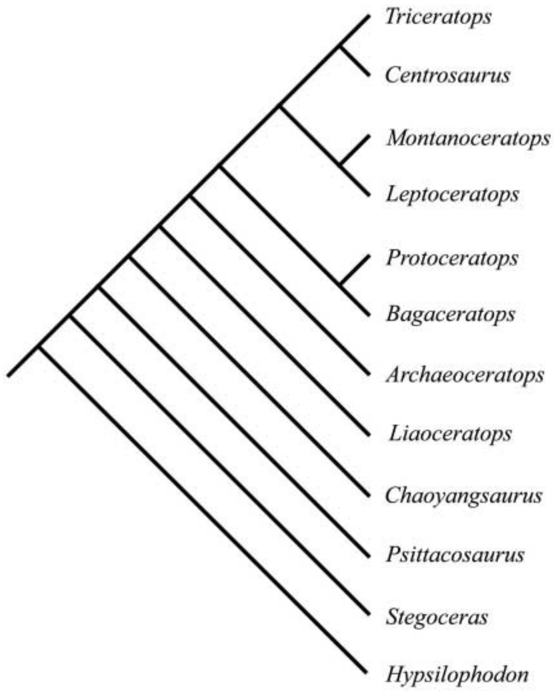

Fig. 6. The single most parsimonious tree found based on a cladistic analysis of 12 taxa and 148 characters (Appendices 1 and 2). Tree length: 237 steps. Consistency index: 0.726. Retention index: 0.781.

Chaoyangsaurus (Zhao et al. 1999) is the most basal member of Neoceratopsia (Sereno 2000), although it still lacks features typical of horned dinosaur. However, different from its closest relatives, such as dome-headed pachycephalosaurs and parrot-beaked psittacosaurs, *Chaoyangsaurus* evolved a relatively large skull, a keeled predentary with narrow caudoventral process, and a reduced retroarticular process, as in later neoceratopsians.

Liaoceratops (Xu et al. 2002) is the sister taxon to all other neoceratopsians including *Archaeoceratops* and all Late Cretaceous members. Its rostral became keeled and pointed ventrally along its rostral margin (personal observation), and developed a caudolateral process along its buccal edge. The premaxilla is longer than high. The maxillary tooth crown is ovate in lateral view. A median primary ridge exists on the labial side of the maxillary teeth. The last caudal dentary tooth is situated coincident with the apex of the pronounced coronoid process.

Archaeoceratops constitutes the sister taxon to all Late Cretaceous neoceratopsians, the Coronosauria (Sereno 1998). Its infratemporal bar is short, less than half of the supratemporal bar. The edentulous portion along the rostral maxilla margin occupies four or five tooth spaces. The epijugal exists. The quadratojugal is transversely expanded and triangular in coronal section. The predentary has a round and beveled buccal edge. The primary ridge of the maxillary tooth crown becomes prominent.

Coronosauria, the most recent common ancestor of *Protoceratops* and *Triceratops*, and all of its descendents (Sereno 1998), includes all the currently known Late Cretaceous horned dinosaurs. Member of Coronosauria have an oval, rather than triangular, antorbital fossa. The parietal is much wider than the dorsal skull roof. The basioccipital is excluded from the foramen magnum. The coronoid process of the dentary is broad and moderately deep. The dentary tooth crowns become ovate in lateral view with a median primary ridge developed on the lingual side. The atlas intercentrum is fused to the odontoid; the atlas neurapophyses are also fused to the intercentrum and odontoid. The syncervical is developed, in which elements of the atlas, axis, and several proximal cervical vertebrae fused together to support the enlarged head. Mutual contact among the sacral neural spines is present.

Coronosauris includes two clades: Protoceratopsidae (Coronosauris closer to *Protoceratops* than to *Triceratops*) and Ceratopsoidea (Coronosauris closer to *Triceratops* than to *Protoceratops*). Protoceratopsidae (*Protoceratops* + *Bagaceratops*) share the following features: the premaxilla becomes higher than long, a small nasal horn is developed; the quadratojugal is triangular in coronal section with a slender rostral prong articulating with the jugal, the caudal end of the frill is straight or wavy, the palatine has an elongate parasagittal process, the occipital condyle reduced its size, the rostral end of the predentary is rostrodorsally pointed, and the surangular has a long ventral process that overlaps the angular, and the surangular-dentary and surangular-angular sutures form an acute angle on lateral face of the mandible.

Ceratopsoidea (Leptoceratopsidae + Ceratopsidae) shares a suit of features. In the facial region, the external naris is round, the caudolateral process of the rostral is elongated, and the ventral margin of the premaxilla is convex, with the premaxilla-maxilla suture situated caudal to it. In the caudal portion of the skull, the lateral expansion of the jugal projects more ventrally than laterally, the quadratojujal is obscured in lateral view, the exoccipital is in contact with the quadrate, and the supraoccipital is in the same plane as the caudal face of the basioccipital, rather than inclined rostrally. The manus of *Leptoceratops* is stouter than that of *Protoceratops*, and is more similar to that of Ceratopsidae, with the non-ungual phalanges wider than long.

Currently, members of Protoceratopsidae are only known in Asia, while members of Ceratopsoidea only in North America. Recognition of two separate clades in Asia and North America indicates a biogeographic coherence that has not been apparent previously (You 2002). The divergence between North American Ceratopsoidea and Asian Protoceratopsidae probably occurred in early Late Cretaceous. The origin of Ceratopsidae was probably in North America, as the entire fossil record of this group and its sister group, the Leptoceratopsidae, are currently known only in North America.

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Appendix 1

Character list

The 148 characters listed below are arranged in an anatomical sequence, and 77, 20, 20, and 31 are skull, lower jaw, dental and postcranial related features, respectively. The "S" and "M", and the following numbers in parentheses refer to the characters listed by Sereno (2000), and Makovicky (2001), respectively, and some are modified. Among the 98 characters of Makovicky, and 72 characters of Sereno, 32 are shared. Ten new characters are added.

1. Skull length (rostral-quadrate)/postcranial skeleton length (S10; M1); 0: <15%, 1: 20–30%
2. Preorbital length/skull length (rostral-quadrate); 0: 50–75%; 1: 40–50%, 2: >75%
3. External naris, position (S2; M9); 0: low, adjacent to buccal margin, 1: high, separated by a flat area from the buccal margin, 2: extremely high, and caudally placed
4. External naris, shape; 0: elliptical, 1: round
5. External naris, rostrocaudal width (M12); 0: <10% skull length, 1: >10% skull length
6. Antorbital fossa (M16); 0: large, 1: reduced
7. Antorbital fossa, shape (S21); 0: subtriangular, 1: oval
8. Additional antorbital fenestra; 0: absent, 1: present
9. Orbit diameter/skull length (M18); 0: >20%, 1: <20%
10. Infratemporal fenestra, width (M27); 0: >10% skull length, 1: <10% skull length
11. Infratemporal bar length (S23); 0: long, subequal to supratemporal bar, 1: short, less than one-half supratemporal bar
12. Supratemporal fossae, relation (S32); 0: separated, 1: joined in midline
13. Supratemporal fenestra, shape (S51, S52, M29); 0: oval, 1: subtriangular
14. Frill fenestra (M39; S55); 0: absent, solid frill, 1: present
15. Rostral (M3; S1); 0: absent, 1: present
16. Rostral, rostral margin in dorsal view (M5, S11); 0: rounded, 1: keeled with point
17. Rostral, caudolateral process (S12); 0: absent, 1: rudimentary, 2: well developed, as long as high
18. Rostral rostroventral process (M4); 0: absent, 1: present
19. Premaxilla, shape in lateral view, except for the processes; 0: longer than high, 1: higher than long
20. Relative height of premaxilla to orbit (M7); 0: low, 1: deep
21. Premaxilla, ventral border; 0: flat, 1: convex
22. Premaxilla, depression rostroventral to naris (M10); 0: absent, 1: present
23. Premaxilla-maxilla suture (M8); 0: caudal to convex buccal process at front of upper jaw, 1: extend through process
24. Maxilla, edentulous maxillary/dentary margin, length (S16; M55); 0: 2 tooth spaces, 1: 4 or 5 tooth spaces
25. Dentigerous margin of maxilla (M15); 0: straight, 1: ventrally convex
26. Nasal horn (M11; S50); 0: absent, 1: small, 2: large
27. Nasal horn, position (S65); 0: caudal to caudal margin of external nares, 1: dorsal to caudal margin of external nares
28. Palpebral, articulation (M17); 0: free articulation with lacrimal, 1: fused to orbital margin
29. Jugal lateral expansion (S3; M2); 0: absent, 1: slightly developed, 2: well developed, jugal horn
30. Jugal lateral expansion, position; 0: from midsection, 1: from caudal end
31. Jugal lateral expansion, direction (M22); 0: laterally, 1: lateroventrally (ventral to M tooth row)
32. Jugal infraorbital ramus, relative dorsoventral width, compared to infratemporal ramus (S5); 0: less than, 1: subequal to more than
33. Jugal-lacrimal contact (M21); 0: reduced, 1: expanded
34. Jugal (jugal-epijugal) crest (S4); 0: absent, 1: present
35. Jugal/epijugal crest, development (S24); 0: low, 1: pronounced
36. Epijugal (M19; S31); 0: absent, 1: present
37. Epijugal, position (M20); 0: along dorsal edge of horn (epijugal trapezoidal), 1: capping end of horn (epijugal conical)
38. Quadratojugal, shape (M30); 0: mediolaterally flattened, 1: transversely expanded and triangular in coronal section, 2: triangular in coronal section, but with slender rostral prong articulating with jugal
39. Quadratojugal, exposure in lateral view; 0: large, 1: reduced, still visible in lateral view, 2: invisible laterally
40. Postorbital, shape (M24); 0: inverted and L-shaped, 1: triangular and platelike
41. Postorbital, dorsal part (M25); 0: rounded and overhanging lateral edge of supratemporal fenestra, 1: with concave dorsal shelf bordering supratemporal fenestra
42. Postorbital, contribution to upper bar of infratemporal fenestra (M26; S30); 0: participate in margin, 1: much reduced or excluded from margin, 2: J-SQ contact very wide and PO situated far from fenestra
43. Postorbital and supratemporal bars, maximum width (S22); 0: narrow, bar-shaped, 1: broad, strap-shaped, 2: very broad, plate-shaped
44. Postorbital horn (S72; M23); 0: absent, 1: present
45. Parietal-frontal contact (M37); 0: flat, 1: depressed, 2: frontal fontanelle
46. Sagittal crest, height (S60); 0: low and rounded, 1: blade-shaped
47. Parietal-squamosal shelf (partial of M38; partial of S54); 0: absent, 1: present
48. Parietal-squamosal shelf, composition (S33); 0: P-SQ equal, 1: SQ dominate, 2: P dominant
49. Parietal-squamosal frill, length (M38; partial S54); 0: frill <70% of basal skull length, 1: parietal frill >70% of basal length of skull
50. Parietal shelf, inclination (S34); : horizontal, 1: caudodorsally
51. Parietal, width (S53); 0: subequal to dorsal skull roof, 1: much wider than dorsal skull roof
52. Squamosal, shape (M28; S59); 0: subtriangular in lateral view, 1: T-shaped, with postquadratic process
53. Squamosal, postquadratic caudoventral process; 0: absent, 1: present
54. Frill caudal margin; 0: straight or wavy, 1: round and convex
55. Epioccipital ossification/frill scallops (M40); 0: absent, 1: present
56. Quadrate shaft (M31); 0: rostrally convex in lateral view, 1: straight
57. Quadrate shaft, rostrocaudal width (S25); 0: broad, 1: narrow
58. Palatal extension of premaxillae, form (M6; S6); 0: flat, 1: vaulted dorsally
59. Position of choana on palate (M13); 0: rostral to maxillary tooth row, 1: level with maxillary tooth row
60. Palatal extensions of maxillae (M14); 0: separated by vomers at rostral border for the internal choanae, 1: contact each other rostral to choanae
61. Palatine, elongate parasagittal process (M32); 0: absent, 1: present
62. Ectopterygoid in palatal view (M33); 0: exposed, 1: reduced or concealed
63. Ectopterygoid-jugal-maxilla contact (M34); 0: Ectopterygoid-J contacts, 1: ectopterygoid reduced and restricted to contact with M
64. Ventral ridge on mandibular process of pterygoid defining eustachian canal (M35); 0: absent, 1: present
65. Pterygoid-maxilla contact at caudal end of tooth row (M36); 0: absent, 1: present
66. Basioccipital, contribution to foramen magnum (M41; S35); 0: present, 1: absent, exoccipital form less than one third of occipital

condyle, 2: absent, exoccipitals form about half and more of occipital condyle
67. Basioccipital, contribution to basal tubera (M42); 0: exclude by basisphenoid and limited to occipital midline, 1: basioccipital tubera
68. Basipterygoid process, orientation (M43); 0: rostral, 1: ventral, 2: caudoventral
69. Basal tubera-basioccipital relation (M44); 0: Basal tubera flat, in plane with basipterygoid plate, 1: everted caudolaterally, forming lip beneath occipital condyle
70. Notch between caudoventral edge of basisphenoid and base of basipterygoid process (M45); 0: deep, 1: notch shallow and base of basipterygoid process close to basioccipital tubera
71. Exoccipital (M46); 0: with three exits for cranial nerves X–XII near occipital condyle, 1: with two exits
72. Exoccipital-quadrate relation (M47); 0: separated by ventral flange of SQ, 1: in contact
73. Paroccipital process, proportions (M48; S61); 0: height about half length, 1: significantly narrower
74. Supraoccipital, contribution to foramen magnum (M49); 0: participate, 1: excluded by exoccipitals
75. Supraoccipital, inclination (M50); 0: incline rostrally relative to basioccipital, 1: in the same plane as caudal face of basioccipital
76. Supraoccipital, shape (M51); 0: tall, triangular, 1: wider than tall, trapezoid, 2: square
77. Occipital condyle, size (S62); 0: large, 1: small
78. Predentary length/dentary length (M52); 0: less than two-thirds, 1: equal or more than two-thirds
79. Predentary buccal margin (M53; S26); 0: sharp, 1: with a rounded, beveled edge, 2: with grooved, triturating edge
80. Predentary dorsal margin, inclination (S63); 0: horizontal, 1: rostrodorsally inclined
81. Predentary rostral margin (S13); 0: round, 1: keeled with point
82. Predentary surface between dentaries (S36); 0: absent, 1: present
83. Predentary ventral process width of base/maximum transverse width of predentary (S7); 0: less than half, 1: equal or more than half
84. Predentary caudoventral process, shape (S14); 0: broader distally, 1: narrower distally
85. Dentary, large pit at rostral end (M54); 0: absent, 1: present
86. Dentary ramus, position of maximum dorsoventral width (S66); 0: caudal, 1: rostral
87. Dentary ventral margin, form (S47; M56); 0: straight, 1: curved
88. Dentary-prearticular contact (M57); 0: absent, 1: present
89. Dentary coronoid process, width and depth (S27); 0: narrow dentary process, low coronoid process, 1: broad dentary process, moderately deep coronoid process, 2: broad dentary process with distal expansion, very deep coronoid process
90. Coronoid, shape (S37; M58); 0: strap-shaped, 1: lobe-shaped
91. Angular ventral margin, form (S48); 0: rostral portion convex, 1: nearly all of ventral margin convex
92. Distinct lateral ridge or shelf overhanging angular (M60); 0: absent, 1: present
93. Surangular eminence (S38); 0: absent, 1: present
94. Angular-surangular-dentary contact (M61); 0: triradiate, 1: SA with a long ventral process overlapping AN, and D-SA and AN-SA sutures form acute angle on lateral face of mandible
95. Retroarticular process length (S15); 0: long, 1: very short or absent
96. Splenial symphysis (S39); 0: absent, 1: present
97. Splenial, caudal end (M62); 0: simple or with shallow dent, 1: with bifid overlap of angular
98. Premaxillary teeth (S46); 0: present, 1: absent
99. Premaxillary tooth number (S8; M6); 0: 3 or more, 1: 2
100. Premaxillary teeth, crown shape (S9); 0: recurved, transversely flattened, 1: straight, subcylindrical
101. Cheek teeth (M65; S19); 0: spaced, 1: loosely oppressed with determinate eruption and replacement pattern
102. Teeth occlusion (M66; S70); 0: at an oblique angle, 1: at a vertical angle, 2: at a vertical angle but dentary teeth have a horizontal shelf on the labial face
103. Tooth crown, shape (M74; S28); 0: radiate or pennate in lateral view, 1: maxillary crowns ovate in lateral view, 2: both maxillary and dentary teeth ovate in lateral view
104. Cheek teeth, root-crown connection (M73; partial S29); 0: cheek teeth cylindrical roots, 1: roots with anterior and posterior grooves along root
105. Dentary tooth, crown (M71; partial S29); 0: with continuous, smooth root-crown transition, 1: bulbous expansion at root-crown transition on labial side of tooth
106. Base of primary ridge on maxillary teeth (M68); 0: confluent with the cingulum, 1: set back from cingulum, which forms a continuous ridge at the crown base
107. Maxillary/dentary teeth, enamel distribution (M70; S49); 0: both sides of crowns, 1: restrict to lateral/medial sides in M/D teeth, respectively
108. Teeth median primary ridge (M67); 0: absent, 1: only on maxillary teeth, 2: on both maxillary and dentary teeth
109. Maxillary/dentary teeth, primary ridge, position (S18); 0: near midline, 1: offset, caudally and rostrally, respectively
110. Maxillary teeth, primary ridge, development (S17); 0: low, 1: prominent
111. Dentary teeth, primary ridge, development (S64); 0: low, 1: prominent
112. Maxillary (lateral view)/ dentary (medial view) crowns, secondary ridge (S71); 0: present, 1: rudimentary or absent
113. Maxillary/dentary teeth, root, form (S69, M64); 0: single, 1: double
114. Tooth row (M69); 0: double, with only one replacement tooth present at a time, 1: battery like with multiple 3 rows of replacement teeth
115. Number of alveoli in dentary (M72); 0: less than 20, 1: more than 20
116. Dentary tooth row, position of last tooth, relative to apex of coronoid process (S20, M59); 0: rostral to, 1: coincident with, 2: caudal to
117. Hypocentrum (S56); 0: absent, 1: present
118. Hypocentrum shape (S67); 0: wedge-shaped, 1: U-shaped, 2: ring-shaped(hemispherical occipital condyle)
119. Atlas intercentrum (M75); 0: semicircular, 1: disc-shaped
120. Atlas intercentrum (M76); 0: not fused to odontoid, 1: fused to odontoid
121. Atlas neuropophyses (M77); 0: free, 1: fused to intercentrum/odontoid
122. Axial neural spine (M78; S40); 0: low, 1: tall and hatchet-shaped, 2: elongate and caudally inclined
123. Syncervical (M79; S41); 0: absent, 1: partially fused(centra but not arches), 2: completely coossified
124. Cervicals 3–4, neural spine height, compared to axial's, much shorter (S42); 0: much shorter, 1: subequal
125. Mid cervicals (C5–C7) neural spines, height (S68); 0: low, 1: as high as dorsal neural spines
126. Dorsal vertebrae (M80); 0: with flat articular zygapophysial, 1: tongue and groove articulations on zygapophyses
127. Outline of sacral (M82); 0: rectangle or hourglass in dorsal view, 1: oval in dorsal view
128. Sacral neural spines, mutual contact (S58); 0: absent, 1: present
129. Sacral number (S57; M81); 0: 5 or less, 1: 6, 2: more than 6
130. Caudal neural spine (M83; S45); 0: short or inclined, 1: tall and straight
131. Mid and distal caudals, neural spine cross-section (S44); 0: subrectangular, 1: oval
132. Distal chevrons (M84); 0: lobate expanded shape, 1: rodlike

133. Distalmost caudals, neural spines and chevrons (S43); 0: absent, 1: present
134. Clavicles (M85); 0: absent, 1: present and robust
135. Scapula in sagittal view (M86); 0: distinctly curved, 1: relatively flat
136. Scapular blade (M87); 0: at acute angle relative to glenoid, 1: almost perpendicular to glenoid
137. Olecranon process (M88); 0: relatively small, 1: enlarged (one-third of ulnar length)
138. Number of distal carpals (M89); 0: more than 2, 1: less than 2
139. Manus/pes (M90); 0: manus much smaller than pes, 1: close to pes in size
140. Manus phalanges; 0: slender, 1: wider than long
141. Shaft of postpubis in cross section (M91); 0: round, 1: mediolaterally flattened, bladelike
142. Postpubic process (M92); 0: long and ventrally oriented, 1: short and posteriorly directed
143. Prepubic process (M93); 0: short and rod-shaped, 1: long and flared at anterior end
144. Ischial shaft (M94); 0: straight, 1: curved, caudodorsally convex
145. Femoral fourth trochanter (M95); 0: large and pendant, 1: reduced
146. Tibio-femoral ratio (M96); 0: more than one, 1: less than 1
147. Foot (M97); 0: gracile with long, constricted metatarsus, elongate phalanges, 1: short and uncompressed, stubby phalanges
148. Pedal unguals (M98); 0: pointed, 1: moderately rounded, hooflike

Appendix 2

Data matrix

Taxon	1111111111222222222233333333334444444444555555555 1234567890123456789012345678901234567890123456789012345678
Hypsilophodon	0000000000000?0???0000?000?00??00000?00000000000??000??000
Stegoceras	000001?001000?0???1000?000?111101000??1??0100011?0000??000
Psittacosaurus	012101?000000?10001100?000?020010100?010000000010?0000??001
Chaoyangsaurus	11??????000???10001?00?00???1001?100?01??????????????????1
Liaoceratops	?010000000000?1?1101001000?0210100?0?011011001120100010111
Archaeoceratops	1110000000110?111101001100?0210101110111?110??1?00000??111
Bagaceratops	1010?011001111111111001101002101011112110110?112?011000111
Protoceratops	12100010001111111111001101002101011112110110?1121111000111
Leptoceratops	10110010001100112101100110?0211101110121111001120100010111
Montanoceratops	1?1??010???????????1????0??0?????11101?11?100112?110???11?
Centrosaurus	120111?0111111112101110102112111111111210221201211111111111
Triceratops	120111?0111110112101110102112111111111210221201211111111111

Taxon	11111111111111111 5666666666677777777778888888888999999999900000000001111111 9012345678901234567890123456789012345678901234567890123456
Hypsilophodon	0000000000002?1000000000000001000000000000000000000000000 0
Stegoceras	10?00200000000000000001??0000000000?0?0000000000000000000000
Psittacosaurus	11010010100010100100000010000000000000?1??0000000000000000
Chaoyangsaurus	?????0001?0????????00?1?11100?0?00??10?0110000000000000000
Liaoceratops	01?00?0011010?1001?0011??10000?000101?100100100001?00?0?01
Archaeoceratops	???????01101?01001?0101??1?00?0?01??10?001001??0?111000?01
Bagaceratops	11100111110110100111111?1100011?01111?11??0021001211000001
Protoceratops	0110011111011010011111111100111101111110110021001211000001
Leptoceratops	0100?1111?1011101001101111101111101011 01??022111021100000 1
Montanoceratops	0??????112101??0101???1111?001110?1?110???022111?211000001
Centrosaurus	11?111121101210112002011110101210?001001??1121001211111112
Triceratops	110111121101210112002011110101210?001001??11?1001211111112

Taxon	11111111111111111111111111111111 11122222222223333333333444444444 78901234567890123456789012345678
Hypsilophodon	0?0000000000000?0000000000000000
Stegoceras	0???0????1?00?0?0?000?00???01000
Psittacosaurus	0?0000000000000?1100000000000000
Chaoyangsaurus	??000000????????????????????????
Liaoceratops	????????????????????????????????
Archaeoceratops	??000?0??100100???????????00??00
Bagaceratops	?????????????????????????0??????
Protoceratops	10011111010121111011000010000001
Leptoceratops	0?010011000011111011000100000000
Montanoceratops	10011111010121111011?00?00000000
Centrosaurus	12111122110112001110111111111111
Triceratops	12111122110112001110111111111111