ORIGINAL PAPER

The first ceratopsian dinosaur from South Korea

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Abstract In 2008, a new basal neoceratopsian was discovered in the Tando beds (Albian) of Tando Basin in South Korea. It represents the first ceratopsian dinosaur in the Korean peninsula and is assigned to *Koreaceratops hwaseongensis* gen. et sp. nov. Autapomorphies of *Koreaceratops* include very tall neural spines over five times higher than the associated centra in the distal caudals, and a unique astragalus divided into two fossae by a prominent craniocaudal ridge on the proximal surface. A phylogenetic analysis indicates that *Koreaceratops* is positioned between *Archaeoceratops* and all more derived neoceratopsians, and the elongation of caudal neural spines was an important derived character in non-ceratopsid neoceratopsians. The very tall caudal neural spines in *Koreaceratops*, *Montanoceratops*, *Udanoceratops*, *Protoceratops*, and *Bagaceratops* appear to be homoplasious, suggesting an independent adaptation, possibly for swimming. Skeletal evidence suggests that obligate quadrupedalism occurred gradually in neoceratopsians progressing from bipedal through facultative quadrupedalism, to complete quadrupedalism in Coronosauria.

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Introduction

Ceratopsia (horned-dinosaurs) consists of numerous basal taxa and Ceratopsidae which are most easily recognized by presence of the rostral bone (You and Dodson 2004). While ceratopsids comprise large-bodied, quadrupedal, herbivorous ornithischians typified by elongate postorbital brown horns and expansive shield-like frills that may have elaborate ornamentation, basal ceratopsians are small, bipedal or quadrupedal forms (Dodson et al. 2004). Ceratopsians appear to have originated in Asia with the earliest basal ceratopsian being *Yinlong downsi* (Xu et al. 2006) from the early Late Jurassic of China. The basalmost neoceratopsians are confined to the Late Jurassic and Early Cretaceous of China, with some psittacosaurids also being known from western Siberia, Mongolia, and possibly Thailand (Sereno 2010). By the Late Cretaceous, basal neoceratopsians became common in North America and more widely distributed in Asia, especially in the Gobi region that has produced nearly all of the Asian genera (Chinnery-Allgeier and Kirkland 2010). Ceratopsids were confined to the Late Cretaceous (Santonian~Maastrichtian) of North America until the discovery of a centrosaurine *Sinoceratops zhuchengensis* from China (Xu et al. 2010). The putative ceratopsid, *Turanoceratops*, is also known from the Turonian of Uzbekistan (Farke et al. 2009; Ryan 2009; Sues and Averianov 2009a, b).

In 2008, a new basal ceratopsian was discovered in the Tando beds (Lower Cretaceous) of Tando Basin in Korea (Fig. 1). It represents the first ceratopsian dinosaur
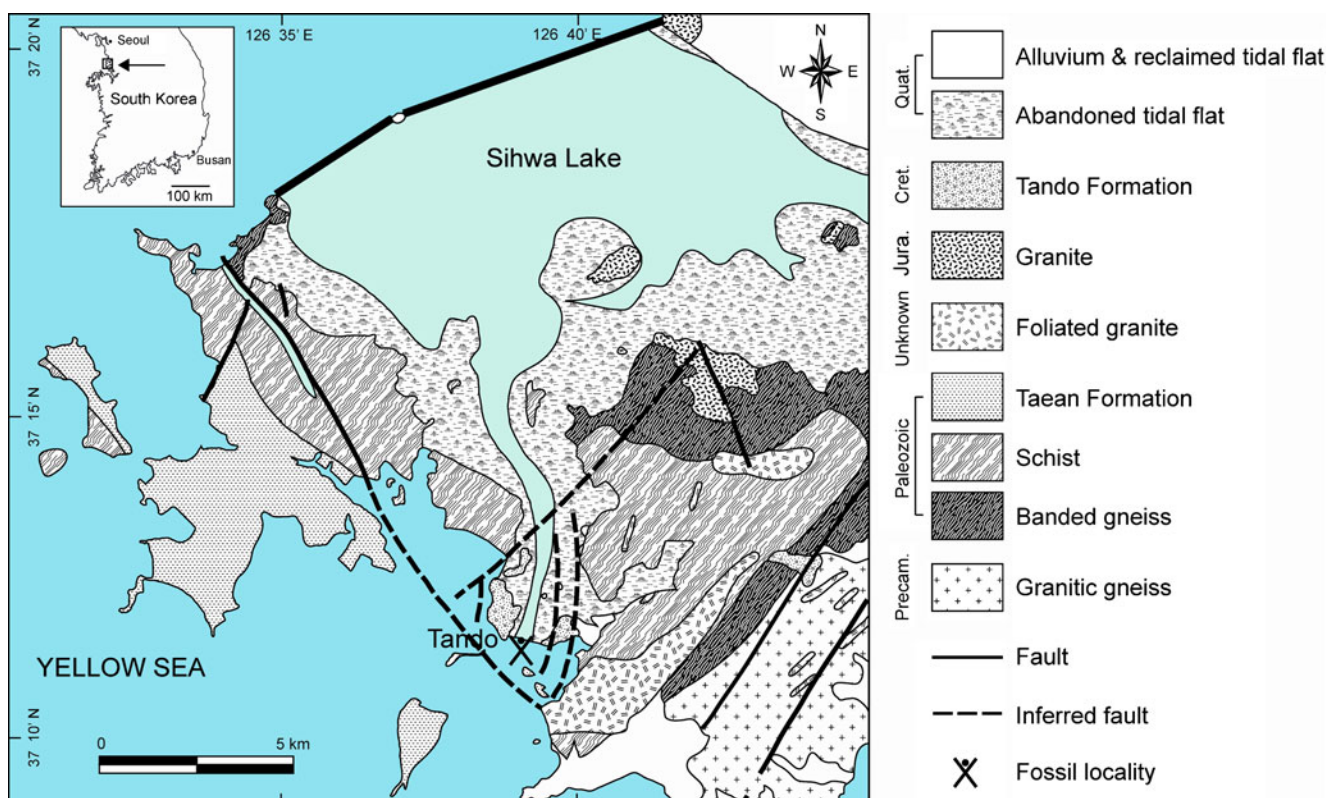
Fig. 1 Regional geologic map in the vicinity of the Tando Basin (modified after Park and Kim 1972; Kim et al. 2009). The Tando beds are uncomfortably underlain by the basement of Precambrian metamorphic and Mesozoic plutonic rocks, deposited mainly in the fault-bounded basin

from the Korean peninsula. This new basal ceratopsian is not only an important contribution to the growing database of basal ceratopsians in Asia, but it is also an important datum for the paleogeographic distribution of this group since it represents the easternmost occurrence of the group in Eurasia (contra Lucas 2006; see Kobayashi 2006). It also comes from a time period (Albian) with a very limited fossil record for basal neoceratopsians. The Korean ceratopsian is of particular interest because it has very long caudal neural spines which are comparable to those of some Late Cretaceous basal ceratopsian taxa such as *Protoceratops*, *Bagaceratops*, *Udanoceratops*, and *Montanoceratops*. The purpose of this paper is to describe the new basal ceratopsian from the Tando beds, Hwaseong City in Korea and to compare it with other basal ceratopsians to establish its phylogenetic position.

Systematic paleontology

Dinosauria Owen 1842
Ornithischia Seeley 1888
Ceratopsia Marsh 1890
Neoceratopsia Sereno 1986
Koreaceratops hwaseongensis, gen. et sp. nov.

Etymology The genus and species are named after Korea and Hwaseong City, respectively, which yielded the holotype.

Holotype KIGAM VP (Korea Institute of Geoscience and Mineral Resources, Vertebrate Paleontology, Daejeon) 200801, a nearly complete tail with both ischia, partial distal hind limbs and feet (Figs. 2 and 3).

Fig. 2 *K. hwaseongensis*, gen. et sp. nov., from the Tando beds (Albian) of Tando Basin in South Korea (KIGAM VP 200801, holotype) in ventral view. The proximal tibiae and fibulae are sharply cut off at the edge of the block
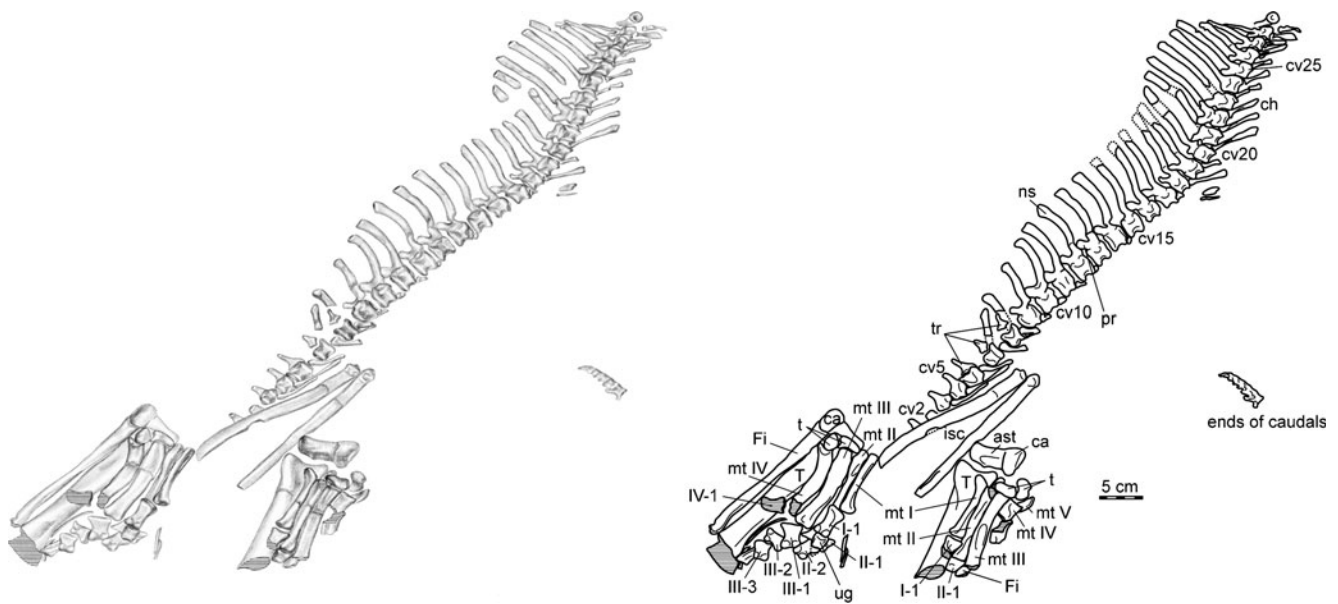
Fig. 3 Illustrations of *K. hwaseongensis*, gen. et sp. nov., with anatomical abbreviations: *ast* astragalus, *ca* calcaneum, *cv* caudal vertebra, *Fi* fibula, *isc* ischium, *mt* metatarsal, *ns* neural spine, *pr* prezygapophysis, *T* tibia, *t* tarsal, *tr* transverse process, *ug* ungual. *Cross-hatch pattern* indicates broken edge of bone and partial restorations of neural spines are shown with *dotted lines*

Type locality and geological setting The Tando Basin is a very small basin (approximately 25 km², located in mid-west Korea (Fig. 1). This terrestrial Cretaceous sedimentary basin was found in 1972 (Park and Kim 1972) and officially named as the Tando Basin by Park et al. (2000). The basin is mainly filled with clastic sediments, which consists of predominantly purple, fine-grained sandstones and siltstones, and thin sandstones with thick conglomeratic sandstones in the lower part, and well-bedded tuffaceous rocks and cherty mudstones in the upper part. Although we regard these deposits as deserving of formational status, they are referred to here as the Tando beds, pending a full description and establishment of a type section. The Tando beds crop out on several small islands in the basin such as Tando, Buldo, Ttakseum, Goryeom, and Seoksan islands.

KIGAM VP 200801 was found in a block of rock in the rock-filled Tando embankment dam between the Tando dock and the Jeongok harbor by a public official of Hwaseong City in 2008. The block (80 cm×60 cm× 80 cm) containing the bones is composed of reddish, fine-grained sandstone (Fig. 2). The Tando embankment dam was built in 1994 with rocks taken both from the Tando and Buldo quarries. Based on the lithology of rocks from these abandoned quarries, it is believed that the source rock of the block containing the specimen was originally from the lower part of the Tando beds. Six ornithopod tracks were previously reported from the tuffaceous sandstone and cherty mudstone in the upper layers of the Tando beds (Choe et al. 2001). Fossil palynomorphs for age determination could not be acquired because of the oxidation and thermal alternation of the sediments by volcanic activities in this area (Yi et al. 2004). K–Ar plagioclase and biotite age of three andesitic tuff samples from the upper section of the Tando beds is 103±0.5 Ma indicating that the Tando beds are late Early Cretaceous in age (Albian).

Diagnosis Very tall neural spines over five times higher than the associated centra in the distal portion of the caudal vertebrae except for caudalmost caudals; surface of astragalus capping the distal end of the tibia divided into two fossae by a prominent craniocaudal ridge; triangular-shaped calcaneum is 1.5 times longer craniocaudally than the astragalus in proximal view.

Description KIGAM VP 200801 consists of the nearly articulated, partial hind limbs and tail of a small basal neoceratopsian. The proximal tibiae and fibulae are sharply cut off at the edge of the block (Fig. 2), suggesting that the rest of the skeleton could have been present before the block was broken up in the quarry, but this cannot now be determined. Preserved elements are the caudal vertebrae, ischia, tibiae, fibulae, tarsals, metatarsals, and phalanges (Fig. 3) and the measurements of each bone are given in Online Resource 1.

The specimen preserves a nearly complete tail of 36 vertebrae. Possibly four or five vertebrae are missing from the posterior end of the caudal series, but the delicate terminal distal caudals are preserved detached from the rest of the tail. The estimated length of the tail is approximately 813 mm. The articular surfaces of the centra of the caudal vertebrae are sub-rounded, decreasing in all dimensions caudally. They are spool-shaped in lateral view and tightly

articulated to each other except for the detached distal end. Each centrum of the main portion of the tail has two well-developed chevron facets on the caudoventral margin, and a slight depression on the cranial surface of the centrum. The caudalmost seven preserved caudal centra are completely fused to one another, elongate, and lack neural spines and chevrons. Transverse processes decrease in size caudally and persist until caudal 11. In dorsal view, each transverse process is triangular in shape with a broad, convex base along the centroneurapophysial suture. The proximal eight transverse processes are not fused with the centrum. The length of the best preserved transverse process from caudal 5 is 23.0 mm. The neural spines on the first eight caudals are incomplete or broken. In general, the neural spines are very tall and slightly inclined caudally, and concave cranially in lateral view. Their cross-sections are subrectangular and they are very flat laterally. The neural spines from caudal 9 to caudal 14 are well preserved and slightly flared craniocaudally at the distal end. The neural spines of these caudals increase caudally from 52.4 to 85.8 mm in length. The total height of caudal 14, including the neural spine, is 128.2 mm. The distal ends of the neural spines beyond that point are broken until caudal 20 in which the neural spine is 97.3 mm in length. The lengths of the spines increase continuously to caudal 22, where the spine reaches the maximum length of 98.9 mm (measured from a point above its base) with a total height of 134.5 mm. This neural spine is approximately 5.6 times as high as the vertebral centrum. From this point, the lengths of neural the spines decrease abruptly to caudal 28. Therefore, the tallest neural spines occur in the distal tail rather than in the middle. The tip of the tail (last seven caudals) lacks neural spines. Neural arch bases and articular processes are evident as far caudally as the tip of the tail except for last six caudals. Pre- and post-zygapophyses form lobe-like projections craniodorsally and caudodorsally with approximately equal height, respectively. Prezygapophyses are slightly larger and longer than the post-zygapophyses. The latter are more inclined to the dorsal than the former, which are inclined at approximately 60° to the horizontal. The prezygapophyses project beyond the cranial margin of the centrum and articulate laterally with the post-zygapophyses of the preceding caudal. Preserved chevrons persist until caudal 28, but almost half of these are missing or incomplete. All chevrons are oriented caudoventrally and intersect the axis of the tail at a 45° angle. Well-preserved chevrons are rod-like and straight in lateral view. In cranial and caudal view, they are triangular in shape with a triangular foramen for the hemal artery. The articular surface of the hemal arches becomes progressively smaller along the caudal series while the distal portion becomes slightly expanded craniocaudally and flattened laterally. Chevrons are consistent in length until caudal 22, but rapidly shorten beyond this point.

Both ischial shafts are preserved, although lacking proximal ends. Each shaft is 195 mm long, as preserved, and narrow and sub-oval in cross-section. Although they diverge from the midline proximally, each shaft is essentially straight, contacting with each other along their distal surfaces. The distal ends of both shafts are swollen, with a rugose surface.

Unfortunately, the proximal ends of both lower hind limbs are not preserved so their exact lengths cannot be determined. The shaft of the tibia is cylindrical and the distal end flares mediolaterally. The width of the distal end is 61 mm and its craniocaudal length is 17 mm. The fibular, calcanear, and astragalar articulations are distinct. The inner malleolus is wide and flared to articulate with the concave surface of the astragalus. The outer malleolus bears a narrow cranial flange forming part of the articular surface for the distal end of the fibula. Thus, the astragalar facet is both higher and wider than the calcanear facet. The distal surface of the tibia between the two malleoli is concave and receives the prominent craniocaudal ridge on the inner surface of the astragalus. The distal end of tibia must be rotated relative to the proximal end, but the extent of this cannot be determined. The preserved left and right tibiae are 222 and 152 mm long, respectively.

As for all ceratopsians, the fibula is much more gracile than the tibia. The proximal portion is slightly curved and concave on the medial surface, but the midshaft is oval in cross-section. Below the midshaft, a raised edge is developed craniolaterally. The distal end of the fibula is positioned directly dorsal to the calcaneum. The anterior surface of this distal end is slightly concave dorsoventrally while the posterior surface against the tibia is flat. The ventral portion of the distal end is convex to fit into the triangular fossa of the calcaneum (Fig. 4c).

The astragali and calcanei are perfectly preserved in both feet (Fig. 4). The astragalus is tightly fused to the calcaneum laterally. The astragalus consists of a rhomboidal body and an ascending process overlapping the cranial surface of the tibia. The astragalar body is slightly constricted in the middle, forming a smooth, cylindrical surface for the intertarsal articulation distally. It bears lateral and medial expansions. Both expansions are hemispherical in shape, and the medial expansion is thicker than its shallow lateral counterpart, forming a wedge in caudal view. In proximal view a prominent craniocaudal ridge divides the astragalus into a larger medial, and smaller lateral, fossae into which the inner and outer malleoli of the tibia insert, respectively. The outer malleolus of the tibia also extends onto the caudolateral margin of the calcaneum. The astragalus measures 37.5 mm in width, 65% of the width of the distal tibia. The cranial ascending process is wide, low, and bluntly squared off proximally. In cranial view, the height of the ascending process is less than the height of the calcaneum. It does not completely cover the inner malleolus of the tibia, so that the tibia is widely exposed craniomedially where the
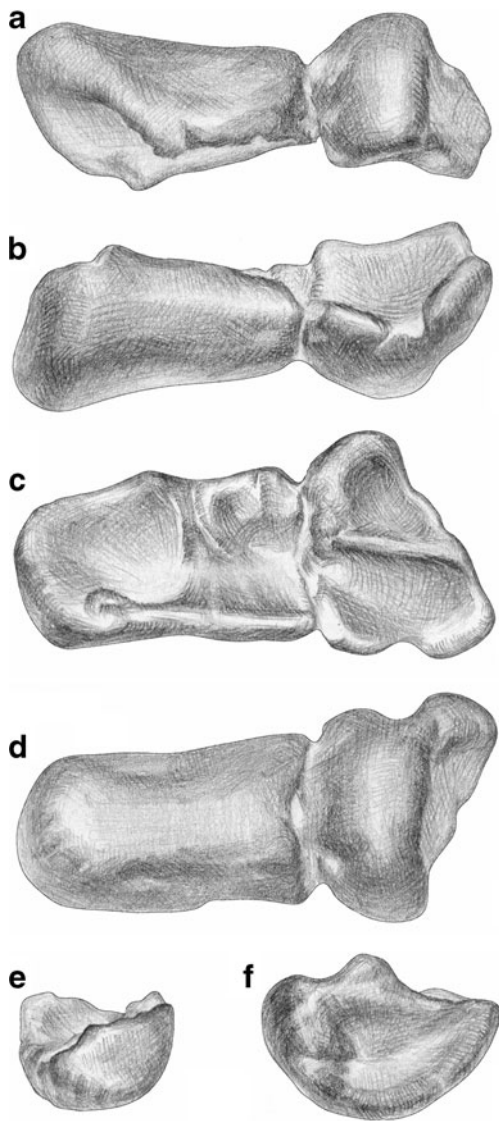
Fig. 4 Left astragalus and calcaneum of *K. hwaseongensis*, gen. et sp. nov. **a** cranial view; **b** distal view; **c** proximal view; **d** ventral view; **e** medial view; **f** lateral view

process is indented proximal to the astragalus body. A broad and shallow depression is developed at the junction of the body and ascending process making the cranial surface of astragalus flatter than the caudal surface.

The calcaneum is firmly fused to the astragalus medially. It is distinctively expanded proximodistally and craniocaudally, making a larger body configuration than the astragalus. In proximal view, it is triangular in shape with two fossae which are completely separated by a sharp ridge. The larger caudal fossa provides a broad and shallow surface for stabilizing the strongly developed outer malleolus of the tibia. This fossa is also open caudally, but its cranial surface is nearly vertical and has a sharp ridge to firmly contact the tibial facet. The upper, smaller fossa of the calcaneum provides a concavity for the distal end of the

fibula. The cranial portion of this fossa is thickened to support the downward force of the fibula. In distal view, the calcaneum contacts the astragalar body by a trochleated joint, but the constriction along astragalocalcaneal suture is strong and offset above the level of the astragalus. In lateral view, the calcaneum is semicircular, with a convex distal outline and two concave proximal margins. Its diameter is 32.5 mm, exceeding the medial diameter of the astragalus (23.0 mm).

Two distal tarsals are preserved in both feet. The medial and lateral tarsals contact the proximal end of metatarsals III and IV, respectively. The medial tarsal is flat and larger (24 mm, left foot; 27 mm, right foot) than the lateral (16 and 17 mm, respectively). The proximal end of the medial tarsal is sub-rounded mediolaterally while the lateral is oval in shape. Each tarsal is assumed to be in situ since they occur in the same position on both feet.

The elongate and slender metatarsals of both feet are preserved, exposing the plantar surfaces. The left metatarsals are complete except for the damaged distal end of mt IV. Metatarsals I and II are complete in the right foot, but the distal end of mt III is broken and only the proximal portion is preserved for mt IV. A small flat splint is attached to the proximal end of mt IV laterally, representing mt V. Among the four functional metatarsals, mt III is the longest and stoutest with the shortest being mt I. Metatarsal I measures 73.2 mm in length, 68% of the length of mt III (107.8 mm) in the left foot. The relative length between mt II and mt IV is not certain because mt IV are incomplete in both feet. The proximal end of mt I is expanded craniomedially and convex proximally. Its lateral surface is also convex, while the medial surface is flat. The distal end is subtriangular in cross-section with two well-formed distal articular condyles, of which the lateral is more prominent than the medial. The shaft is thin and compressed mediolaterally between both expanded ends. The completely exposed mt II is 97.6 mm long in the right foot, which is 10 mm shorter than the mt III in the left foot. In proximal view, the proximal end is elongate craniocaudally. In caudal view, it is convex proximally, and its lateral surface is slightly convex while the medial surface is slightly concave to fit against the lateral surface of mt I. The shaft is compressed mediolaterally. The distal surface is a crescentic in cross-section with two condyles, of which the lateral is slightly more developed than the medial. Metatarsal III is slightly curved laterally from the mid shaft. The proximal end is wide and rectangular in cross-section, and contoured to fit against distal tarsal 1. Its medial surface is slightly concave to fit into the lateral surface of mt II, while the lateral is convex. The shaft is not compressed, remaining wide until the distal end, which is subrectrangular in cross-section with two moderately sized condyles that are almost symmetrical in distal view. The distal half of mt IV diverges laterally. Its proximal end is

concave in proximal view which fits into a rounded tarsal 2. The shaft is somewhat triangular in outline with a sharp lateral margin formed by the junction of the gently convex cranial and concave caudal surfaces. Metatarsal V is reduced to a splint which is preserved in the right foot. It is a flat triangular bone in lateral view. Its proximal end is craniocaudally expanded and articulated with the craniolateral surface of mt IV.

A total of ten phalanges are preserved including one ungual. In the right foot, a phalange is articulated with the distal end of mt I and mt II, respectively, but only a proximal portion is preserved in both. In the left foot, eight phalanges are preserved, but most distal phalanx is missing. Therefore, it is not possible to determine the exact phalangeal formula, except for digit I. The phalanges are slightly displaced, but their positions can be determined based on their relative size and morphologies (Fig. 3). Although the relative length and width of these phalanges varies, their general morphology (except for the unguals) is very similar to each other. In ventral view, the proximal ends of the first phalanges of each digit are somewhat slightly concave, but they are convex in the more distal phalanges. Two distal condylar heads are well developed on each phalange. The ungual of digit I from the left foot is slender and pointed, with the grooves for the claw along the lateral margins.

Phylogenetic analysis

K. hwaseongensis is a new basal neoceratopsian taxon. The currently known hypodigm for *Koreaceratops* can only be coded for 6 out of 133 characters listed in the character-taxon matrix for Ceratopsia compiled by Makovicky and Norell (2006) and Makovicky (2010) because only partial postcranial elements without a cranium are available for the specimen. The coded characters for *Koreaceratops* are 116 (1), 117 (0), 118 (1), 129 (0), 132 (0), and 133 (0). From the detailed observation on *Koreaceratops*, three new characters were added to the matrix: the height ratio of middle caudal neural spine to associated centrum (char. 134), less than or equal to 2 (0), 2.1~3 (1), 3.1~4 (2), more than 4.1 (3); the width of proximal end of the ungual relative to width of distal end of the preceding phalanx (char. 135), equal (0), wider (1); the height of the caudal neural spine is greater than the length of the chevron for any given caudal vertebra (char. 136), absent (0), present (1). To determine the phylogenetic position of *K. hwaseongensis*, a cladistic analysis was conducted using PAUP*, 4.0b10 (Swofford 1998). The branch-and-bound parsimony algorithm in PAUP* was performed for 21 taxa including two outgroups with equally weighted and unordered 136 characters as shown in Online Resource 2. *Asiaceratops* (Nessov et al. 1989) was not included in this analysis due to its questionable taxonomic status (but see Averianov and Sues 2009). The analysis resulted in four most parsimonious trees. The only difference between these four trees is the internal topologies of *Udanoceratops*, *Leptoceratops*, *Udanoceratops*, and *Prenoceratops*. Strict consensus methods were used to analyze the commonality of branching patterns between these four trees. This strict consensus tree has a length of 241 steps, a consistency index of 0.672, a rescaled consistency index of 0.527, and a retention index of 0.785 (Fig. 5).

Fig. 5 Strict consensus of four most parsimonious trees resulting from analysis of the 136 characters, 21 taxa matrix (TL=241, CI=0.672, RC=0.527, RC = 0.785). *Numbers* next to nodes indicate synapomorphies
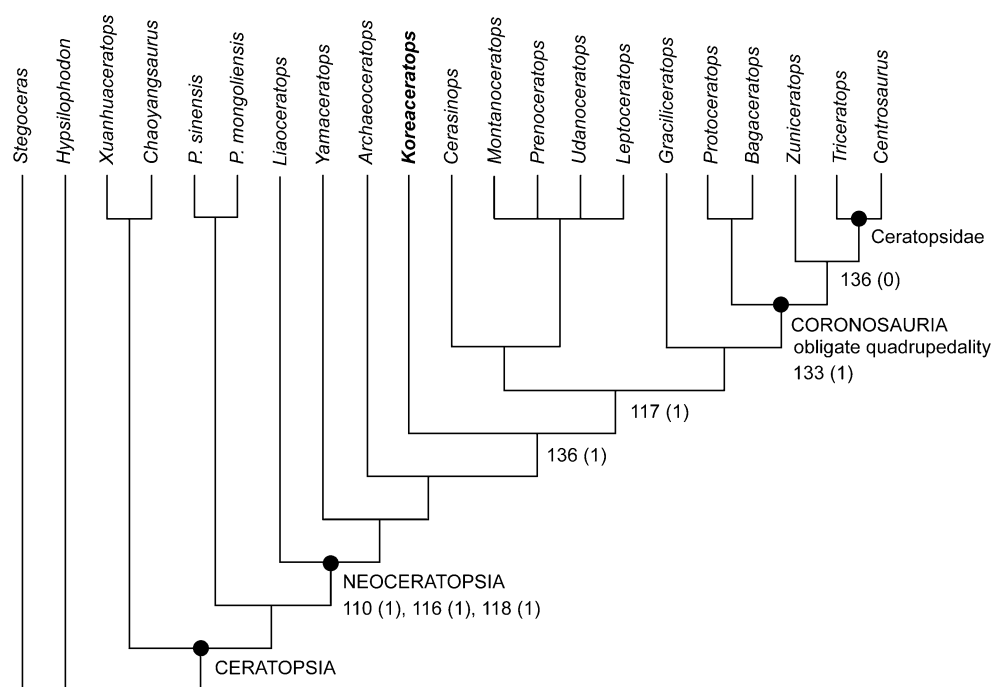
In this analysis, *Koreaceratops* occupies a phylogenetic position as a basal neoceratopsian intermediate between *Archaeoceratops* (Dong and Azuma 1997; You and Dodson 2003) and *Cerasinops* (Chinnery and Horner 2007)+more derived ceratopsians. *Liaoceratops, Yamaceratops, Archaeoceratops,* and *Koreaceratops* are successive outgroups to *Cerasinops*+more derived ceratopsians. Only one unambiguous synapomorphy (char. 136) unites *Koreaceratops* with higher neoceratopsians, but it is secondarily lost in the Ceratopsoidea (*Zuniceratops*+Ceratopsidae, sensu Sereno 2000). One unambiguous synapomorphy of the clade comprising *Cerasinops* and the Leptoceratopsidae (sensu stricto, Makovicky 2001), *Graciliceratops* and more derived neoceratopsians, but not in *Koreaceratops,* is that neural spines and chevrons persist virtually to the end of tail (char. 117; note that the end of tail is not preserved in *Cerasinops*). This character was also recognized by Sereno (2000), but its function in neoceratopsians is not known.

Discussion

Synapomorphies of Ceratopsia are mainly recognized from cranial elements which include the presence of the rostral, broad pointed jugals, vaulted premaxillary palate, and broad base of the ventral process of the predentary supporting the dentary symphysis (Sereno 2000). Few, if any postcranial synapomorphies have been identified. Although cranial synapomorphies cannot be determined for KIGAM VP 200801, the referral of this specimen to a neoceratopsian can be made by comparison of its preserved skeletal elements to other members of this clade that excludes it from being a more derived ceratopsid, or any other member of Ceratopsia, including Psittacosauridae. The foot of *Koreaceratops* is gracile and long, having constricted metatarsus and elongate phalanges. It is different from ceratopsid foot which is short and uncompressed, all phalanges wider than long (char. 132, a synapomorphy of the Ceratopsidae). *Koreaceratops* is not a psittacosaurid because the chevrons of the latter are always longer than the respective neural spines (You and Dodson 2004).

Koreaceratops is a new basal neoceratopsian and it is the first to be recovered from Korea. It represents the easternmost occurrence of this clade in Eurasia and is the oldest neoceratopsian expressing the deep tail profile, predating *Udanoceratops* by approximately 20 Ma. With the late Albian age, it helps to fill in a time gap (Late Albian to Early Santonian) in which few ceratopsian fossils are known (notably the basal neoceratopsian *Asiaceratops* from the Cenomanian of Uzbekistan (Averianov and Sues 2009; Nessov et al. 1989), and the putative ceratopsid *Turanoceratops* (Farke et al. 2009; Nessov et al. 1989; Sues and Averianov 2009a, b) from Uzbekistan).

Koreaceratops is diagnosed based on two autapomorphies, the shape of the astragalus and the very tall caudal neural spines. Although similar spines are known for four other basal neoceratopsians (*Bagaceratops, Montanoceratops, Protoceratops,* and *Udanoceratops*), none have the combination of length and caudal position seen in *Koreaceratops*. *Montanoceratops* from the early Maastrichtian of Montana (Sternberg 1951) and Alberta (Ryan and Currie 1998) has a complete tail which is leaf-shaped. Its tallest neural spine (caudal 15) occurs in the middle of the tail, unlike the more distal position in *Koreaceratops*, and is only approximately four times as high as its vertebral centrum. Additionally, the lateral portion of the astragalus of *Montanoceratops* is expanded proximally (Chinnery and Weishampel 1998), a feature not shared with *Koreaceratops*.

Udanoceratops tschizhovi from the Djadokhta Formation, Mongolia (Kurzanov 1992) also has long neural spines in the middle caudals, but these are only three times as long as the vertebral centrum and therefore shorter than the longer, more distally placed spines of *Koreaceratops*. The unguals of *Udanoceratops* are flat and wide, forming an "ungulohoof shape" (sensu Tereschenko 2008, Fig. 5c), and thus differs from the slender and pointed ungual of *Koreaceratops*.

Protoceratops andrewsi is known from multiple specimens including hatchlings to large adults (Brown and Schlaikjer 1940; Gregory and Mook 1925). The second species, *Protoceratops hellenikorhinus,* from the Bayan Mandahu Formation, China was described on the basis of a skull discovered by the Sino-Belgian Expeditions (Lambert et al. 2001). The circular or laterally flattened neural spines of the middle caudal vertebrae of *Protoceratops* are four times as long as their centra, and the unguals are short, wide, and hoof-shaped, again differing from those of *Koreaceratops*.

Bagaceratops rozhdestvenskyi (Maryańska and Osmólska 1975) from the Baruungoyot Formation (Campanian), Mongolia is very similar to *Protoceratops* in many details with its most distinctive character being the extremely high caudal neural spines which are five times as high as the vertebral centrum. This ratio of neural spines to the centrum is very similar to that seen in *Koreaceratops*, however, the foot of *Bagaceratops* differs from that of *Koreaceratops* in being relatively short and wide with hoof-shaped unguals.

Evolutionary trends in Ceratopsia

Even though *Koreaceratops* lacks the skull it can still help provide important insights into the evolutionary sequence of neoceratopsian postcranial features. Although postcranial shape differences between *Psittacosaurus,* basal neoceratopsians, and ceratopsids have been recognized by mor-

phometric analysis (Chinnery 2004), evolutionary trends within the postcranial skeleton of basal neoceratopsians have yet to be described in detail. The addition of *Koreaceratops* and three newly recognized postcranial characters to the cladistic matrix developed in Makovicky and Norell (2006) and Makovicky (2010) has allowed us to analyze a total of 30 basal neoceratopsian postcranial characters using PAUP*.

Ceratopsoidea is united by 13 synapomorphies (char. 107 (atlas intercentrum semicircular disk shaped), 110 (axial neural spine elongate and posteriorly inclined), 112 (syncervical completely coossified), 115 (outline of sacrum oval in dorsal view), 119 (clavicles present), 123 (olecranon process enlarged), 124 (less than two distal carpals), 125 (manus much closer to pes in size), 127 (postpubis short and posteriorly directed), 128 (prepubis long and flared at anterior end), 129 (ischial shaft straight posterodorsally convex), 131 (tibiofemoral ratio less than one), and 132 (foot short and uncompressed)). Most of these synapomorphies are probably closely related to a shift to larger body sizes in ceratopsids, with a proportionate increase in skeletal robustness and the requirement for the skeleton to support more weight in these derived ceratopsians; these preliminary findings could be more fully resolved with more complete material of *Zuniceratops* (Wolfe and Kirkland, 1998; Wolfe et al. 2010) which can presently only be scored for character 126.

Three unambiguous postcranial synapomorphies (char. 110 (axial neural spine tall and hatchet-shaped), 116 (caudal neural spines tall and straight), and 118 (distal chevrons rod-like)) diagnose Neoceratopsia. In more derived taxa both the axial and caudal neural spines become taller, and the distal chevrons become reduced and rod-like. One unambiguous postcranial synapomorphy (char. 136) uniting *Koreaceratops* with higher neoceratopsians is the caudal neural spines that are much longer than the chevrons. This feature is further exaggerated in some neoceratopsians such as *Koreaceratops*, *Montanoceratops*, *Udanoceratops*, *Protoceratops*, and *Bagaceratops* that display height ratios of the middle neural spine to the caudal centrum (char. 134) of 3, 2, 1, 2, and 3, respectively. This feature becomes lost secondarily in Ceratopsidae, suggesting that elongation of caudal neural spines may have evolved as a functionally integrated module in non-ceratopsid neoceratopsians more derived than *Archaeoceratops*.

Koreaceratops is notable for having a claw-like ungual, a character it shares with *Cerasinops* and *Graciliceratops*. Sereno (2000) included *Graciliceratops* in Coronosauria, but Makovicky (2002) regarded it as a metaspecies, although he did note that it retains claw-like pedal unguals, unlike any other coronosaur (Makovicky and Norell 2006). In the most parsimonious trees of this cladistic analysis (Fig. 5), rounded, hoof-like pedal unguals (char. 133) are an

unambiguous postcranial synapomorphy of Coronosauria. Increasing size and body weight with a proportional shortening of the tail and limbs occurred in the evolution of ceratopsian dinosaurs. Consequently, this trend was also accompanied by the transition of foot morphology from gracile to robust form. Metatarsals became relatively shorter and wider than seen in more basal forms, while phalanges, including unguals, also became shorter and thicker. The width of the proximal end of the ungual relative to preceding phalanx became larger (char. 135) in *Udanoceratops*, *Graciliceratops*, and Coronosauria. Tereschenko (2008) divided ungual shapes into claw-shape, ungulohoof-shape, and hoof-shape based on the ratio of length of ungual to width of its proximal end, with the hoof-shaped unguals typical of *Protoceratops*, *Bagaceratops*, and Ceratopsidae being a synapomorphy of Coronosauria. These hoof-shaped unguals are short, wide, flat, and slightly pointed, and have a ratio of length to width that is less than 1.5. Narrow and long claw-shaped unguals are present in non-coronosaurian basal ceratopsians and have ratios of length to width of usually more than 2.0. The "ungulohoof-shaped" ungual of *Udanoceratops* is intermediate in form being long, flat, and slightly pointed, with ratios of length to width of between 1.5 and 2.0.

Although there is a consensus that ceratopsids were a habitual quadrupeds (Dodson et al. 2004), terrestrial locomotion of non-ceratopsid neoceratopsians is still being debated by researchers (Dodson and Farlow 1997; Paul and Christiansen 2000; Rega et al. 2010; Thompson and Holmes 2007). Coombs (1978) first mentioned that *Leptoceratops* and *Protoceratops* were at least facultative quadrupeds based on their forelimb and hind limb proportions. This argument was supported by Senter (2007) with a study of the forelimb morphology and range of motion, but Tereschenko (2008) believed that they were obligate quadrupeds. Senter (2007) pointed out the differences in palm orientation between *Leptoceratops* and *Protoceratops* and related these to modes of locomotion. In *Protoceratops* the palms face posteriorly for typical quadrupedal locomotion, while the fingers of the medially faced palms of *Leptoceratops* would need to be reoriented for walking. In addition, the trunk of *Protoceratops* is relatively longer than *Leptoceratops*, suggesting that the former had a body plan more suitable than the latter for quadrupedal locomotion (Galton 1970; Senter 2007). The development of hoof-shaped unguals, typical of many large extant herbivorous quadrupeds and a synapomorphy of Coronosauria, also seems to be in accord with acquisition of quadrupdalism in Coronosauria.

The ratio of the skull and hind limb+foot length of ceratopsian dinosaurs seems to be related to their mode of locomotion, and implies that the development of large skulls may have, in part, required a shift to a quadrupedal

lifestyle in the most derived ceratopsians. The ratio in Coronosauria is more than 0.7, while the less-derived *Psittacosaurus* (recognized as being bipedal) and *Cerasinops* have ratios of less than 0.4. The ratios for *Montanoceratops*, *Prenoceratops*, and *Leptoceratops* range from 0.60 to 0.65, indicating that these ceratopsians are intermediate between the former two groups. Based on its phylogenetic position, we predict that when more complete specimens of *Koreaceratops* are discovered they will have skull-hind limb+foot ratios indicative of a bipedal lifestyle.

This analysis implies that obligate quadrupedalism occurred gradually in neoceratopsians developing from bipedal (probably both *Koreaceratops* and *Cerasinops*) to facultative quadrupedal (*Graciliceratops*, Leptoceratopsidae, sensu stricto Makovicky 2001), and finally to fully quadrupedal (Coronosauria) forms through a progressive increase of body and skull size with a relative elongation in trunk length, and an increase in robustness of the hands and feet with the modification of claws into hoof-shaped unguals.

Behavioral inferences

The function of long caudal neural spines of *Protoceratops* has been speculated as being an adaptation for swimming by various authors. Gregory and Mook (1925) suggested that the taxon was aquatic because of its large feet and deep tail. Brown and Schlaikjer (1940) and Barsbold (1974) accepted this idea and suggested that *Protoceratops* was probably amphibious and a relatively good swimmer based on its laterally flattened tail with very high neural spines. Bailey (1997) disagreed and suggested that the high caudal neural spines were related to a desert mode of life to store fat and metabolic water on the side of tail. Based on paleoecology of *Protoceratops* from the Djadokhta Formation (e.g., association with ponds or lakes, Eberth 1993), and distinctive anatomical features of its tail (e.g., heterocoelous caudal vertebrae), Tereschenko (2008) concluded that tail height is an indicator of adaptation of "protoceratopoids" for swimming. He argued that *Bagaceratops* was probably the most aquatic, followed in decreasing swimming ability by *Protoceratops*, and *Udanoceratops*, with *Leptoceratops* being the most terrestrially adapted. If one accepts this argument, then the tall caudal neural spines of *Koreaceratops* suggests that it could have been a good swimmer.

Such conclusions are difficult to prove, however, given that, unlike psittacosaurs which lack deep tails but are frequently associated with lacustrine deposits, and have long been suggested to have had an aquatic component to their behavior (e.g., Ford and Martin 2010, Rozhdestvensky 1955; Suslov 1983), many deep-tailed *Protoceratops*

specimens have been recovered from eolian deposits. Additionally, other deep-tailed taxa (e.g., *Leptoceratops*, *Montanoceratops*) which are known from fluvial deposits are inferred to be the poorest swimmers of the group. It should be noted that recently, Longrich (2010) argued that *Protoceratops* may have been nocturnal, and that its deep, narrow tail may have helped it to shed excess heat during the day when the animal was active, and to burrow into sand dunes to escape the heat during the day, thus explaining the specimens that have been recovered in an upright "standing" posture (Jerzykiewicz et al. 1993). Although the tail of *Koreaceratops* does not preclude it from having good swimming abilities, the evidence for such speculation is equivocal at this time. If the local paleoecology of the region from which the specimen was recovered can be determined in the future then further speculation about its lifestyle can be made.

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