

NIPPONOSAURUS SACHALINENSIS (DINOSAURIA; ORNITHOPODA): ANATOMY AND SYSTEMATIC POSITION WITHIN HADROSAURIDAE

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ABSTRACT—The hadrosaurid *Nipponosaurus sachalinensis* Nagao, 1936, was the first dinosaur discovered in Japan. Here we establish its ontogenetic stage, diagnostic characters, and systematic position by redescribing and phylogenetically analyzing the type and sole specimen of *Nipponosaurus*. The unfused neurocentral sutures of all vertebrae suggest that the type specimen of *Nipponosaurus* is subadult. Furthermore, it can be diagnosed by the following characters: (1) the coronoid process of the surangular is robust, (2) the neural spine of the axis is only slightly developed, and (3) the lateral margin of the first phalanx on digit IV is strongly deflected. The phylogenetic analysis, using 78 characters for seven ingroup and six outgroup taxa, indicates that *Nipponosaurus* belongs within Lambeosaurinae as the sister taxon to *Hypacrosaurus altispinus*.

INTRODUCTION

The skeleton of *Nipponosaurus sachalinensis* (Fig. 1) was found during the construction of the hospital at the Kawakami colliery of the Mitsui Mining Company on Japanese Sakhalin (now Russia) at the end of November, 1934 (Fig. 2). This specimen was described in 1936 by Takumi Nagao, a professor of the Hokkaido Imperial University (now Hokkaido University), thereby becoming the first dinosaur known from Japan. Nagao (1936) classified *Nipponosaurus* as a member of Hadrosauridae. At that time, those hadrosaurids described from Asia included only six species, but half of them are now regarded as nomina dubia due to their incomplete or partial nature (Weishampel and Horner, 1990). Compared to these fragmentary taxa, the Sakhalin specimen is in much better condition, consisting of more than a half of the skeleton. However, when first collected, it lacked most of the skull and the limbs except for the left hind limb and right femur. In order to collect additional remains, Nagao organized an expedition back to Sakhalin during the summer of 1937; this expedition succeeded in finding additional bones (forearms, right crus and both right and left pedes), which were described by Nagao in 1938. Thus, the additional material collected by the second excavation provided a 60% complete skeleton of *N. sachalinensis* (Fig. 1). In spite of the fact that the external surfaces of the specimens were very eroded, it was one of the best Asian hadrosaurid specimens at that time.

In the original description of *Nipponosaurus*, Nagao (1936) erected his new genus and species not based on osteological characters, but “its occurrence at a place very far from North America where above referred genera (“*Tetragonosaurus*” and “*Cheneosaurus*”) have been discovered, and moreover by the special importance from geological as well as paleontological points of view (p. 215).” He did point out that *Nipponosaurus* was similar to the two species of “*Tetragonosaurus*” and “*Cheneosaurus*” (now considered juveniles of *Lambeosaurus*, *Corythosaurus*, and *Hypacrosaurus*; Dodson, 1975) and furthermore that it had an ischial boot. However, he did not establish whether it belonged either to Saurolophinae (now included

Hadrosaurinae) or to Lambeosaurinae (both groups were then thought to have an ischial boot). Moreover, the original description provided no figures and preparation of the specimen had not yet been completed; hence, many morphological characters have remained unclear.

Since that time, *Nipponosaurus* has only occasionally been discussed systematically. For example, Rozhdestvensky (1977) mentioned that *Nipponosaurus* may have been closely related to *Mandschurosaurus amurensis* (considered a nomen dubium by Brett-Surman, 1979) from the Amur River region of Siberia. In contrast, Brett-Surman (1989) implied that *Nipponosaurus* was a basal hadrosaurid because the dorsoventrally-expanded epiphyses of its metacarpals were primitive (i.e., present in non-hadrosaurid Iguanodontia).

The maturity of the only known specimen of *Nipponosaurus* may be a confusing factor in relation to its taxonomic placement. Nagao (1936) noted “it [*Nipponosaurus*] must be an adult as indicated by its coossified sacral vertebrae, of which three are preserved (p. 215).” In contrast, Rozhdestvensky (1964) concluded that *Nipponosaurus* was a juvenile based on its size. The important characters of maturity among lambeosaurines are so far identified for their cranium (i.e., Dodson, 1975), while very little attention has been given to the postcrania of juveniles. Brett-Surman (1989) has described a few indicators of postcranial maturity, but did not mention the degree of maturity of *Nipponosaurus* beyond its small size.

This study analyzes the remains of *N. sachalinensis* in order to assess its maturity. In doing so, it also provides a clearer diagnosis of the species. Moreover, using newly-found characters of *Nipponosaurus* and other hadrosaurids, we discuss its phylogenetic position based on a numerical cladistic analysis.

Institutional Abbreviations: **AMNH**, American Museum of Natural History, New York; **MOR**, Museum of the Rockies, Bozeman, Montana; **NMC**, Canadian Museum of Nature, Ottawa, Ontario; **NSM-PV**, National Science Museum, Vertebrate Paleontology, Tokyo; **ROM**, Royal Ontario Museum, Toronto, Ontario; **RTMP**, Royal Tyrrell Museum, Drumheller, Alberta; **SMU**, Southern Methodist University Shuler Museum of Paleontology, Dallas, Texas; **YPM**, Yale Peabody Museum, New Haven, Connecticut.

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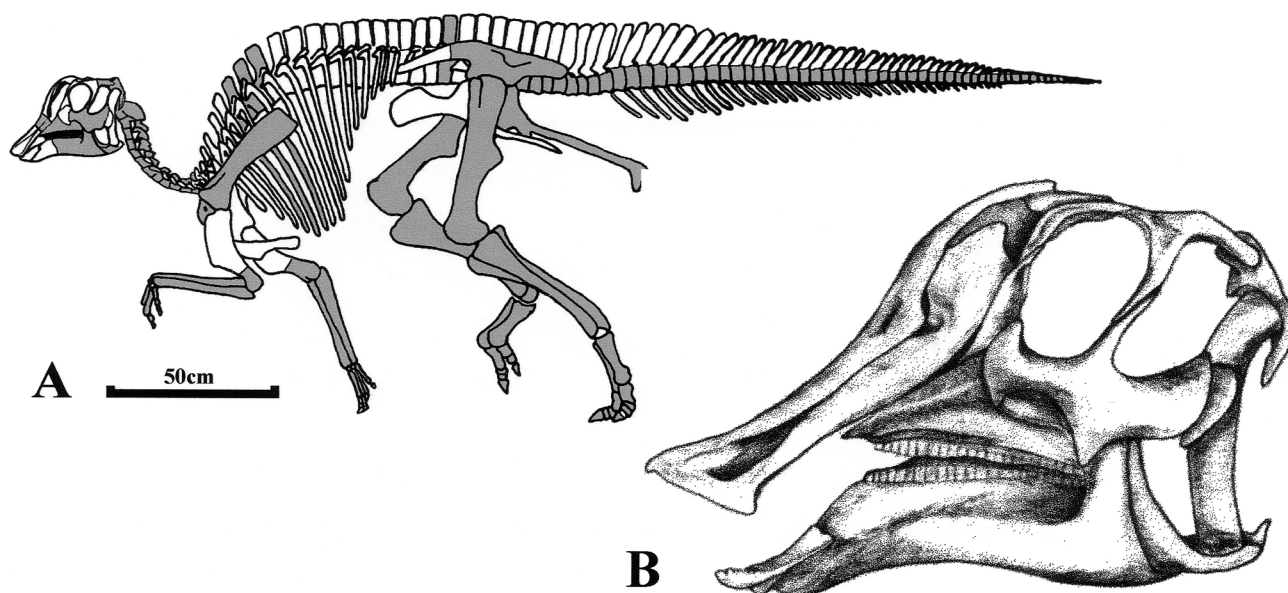


FIGURE 1. **A**, Skeletal reconstruction of *Nipponosaurus sachalinensis* UHR 6590 based on Weishampel and Horner (1990). Gray elements are those that are preserved. **B**, Skull reconstruction of *N. sachalinensis* UHR 6590 based in part on *Hypacrosaurus stebingeri* NSM-PV 20377. Note the large lacrimal, the angular ventral margin of the jugal, and the robust coronoid process of the surangular.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
 ORNITHISCHIA Seeley, 1888
 ORNITHOPODA Marsh, 1871
 HADROSAURIDAE Cope, 1869
 LAMBEOSAURINAE Parks, 1923
NIPPONOSAURUS Nagao, 1936.

Type Species—*Nipponosaurus sachalinensis* Nagao, 1936.

Holotype—UHR 6590 (University of Hokkaido Registration). Left posterior portion of the skull, included maxilla, dentary, parietal, and isolated cranial elements, cervical vertebrae, six dorsal centra, two sacral centra, nearly complete series of caudal centra, left scapula, distal part of the humeri, remaining forelimbs, left ilium, ischia, nearly complete hindlimbs (Fig. 1).

Locality and Age—Kawakami colliery of the Mitsui Mining Company, Toyohara County (Fig. 2); now Sinegorsk, South Sakhalin Russia. Upper Ammonites Bed; now Upper Yezo Group. Matsumoto and Obata (1979) advocated a late Santonian-early Campanian age, based on correlated molluscs and previous works of Matsumoto (1942).

Revised Diagnosis—Robust coronoid process of the surangular, only slight development of the neural spine of the axis, and strong deflection of the lateral margin of the first phalanx on digit IV.

Comments—Since South Sakhalin no longer belongs to Japan, it is presently impossible for additional geological research to be conducted at the Kawakami colliery by Japanese researchers. Thus, the details of this specific locality are no longer clear. Moreover, field notes made at the time of the excavation are missing. Nagao (1936), however, did note that the locality of the type specimen of *Nipponosaurus* also produced fossils of *Puzosia japonica* (now *Parapuzosia japonica*) and *Inoceramus schmidtii* (now *Sphenoceras schmidtii*), both of which belong to the middle of the Upper Ammonites beds (now Upper Yezo Group; Matsumoto, 1951b). Recent biostratigraphic studies indicate that the range of *P. japonica* and *S. schmidtii* are limited to the lower Campanian (Takayanagi and Matsumoto, 1981; Tashiro et al., 1995). Although *S. schmidtii* is known only from

the lower Campanian, dubious referrals of *S. schmidtii* to *S. sachalinensis* are often made (Hayakawa, pers. comm.); the latter is also known from the upper Santonian. Consequently, the age of *Nipponosaurus* probably ranges from the late Santonian to the early Campanian.

DESCRIPTION

Skull and Mandible

Only the posterior portion of the left side of the skull, including the maxilla, dentary, and parietal, was described and figured by Nagao (1936). An isolated frontal, postorbital (post-frontal in the original description), squamosal, and quadrate were also described, but these isolated cranial elements now unfortunately appear to be lost. We doubt Nagao's determination of both the postorbital and squamosal, because a part of the left postorbital and the squamosal were found by us during re-preparation of the type specimen and the following description will follow our reinterpretation.

Premaxilla—The preserved portion of the premaxilla of *Nipponosaurus* includes only the lower region of the anterolateral process (pmx I; Weishampel, 1981) where it articulates with the maxilla (Fig. 3). Because the dorsal process (pmx II) is missing, we cannot be certain that the external naris of *Nipponosaurus* was totally enclosed by both premaxillary processes. However, it is certain that the vestibule invades the anterolateral process of the premaxilla, identical to the condition in lambeosaurines. Here, the forward portion of the long vestibule of the nasal cavity is revealed as a deep trough and the dorsal part of this part of the vestibule bends sharply to continue anteriorly, much like the s-loop in *Lambeosaurus lambei* (ROM 869, 874; Parks, 1935; Weishampel, 1981). Laterally and medially, the surface of the premaxilla is smooth and there is no obvious vertical groove that externally marks the beginning of the s-loop, as seen in *Corythosaurus casuarius* (AMNH 5240) and *Lambeosaurus lambei* (NMC 2869), but apparently not in *L. magnicristatus* (NMC 8705).

?Lacrimal—What may be the anterior portion of the lacrimal is preserved in contact with the forward section of the

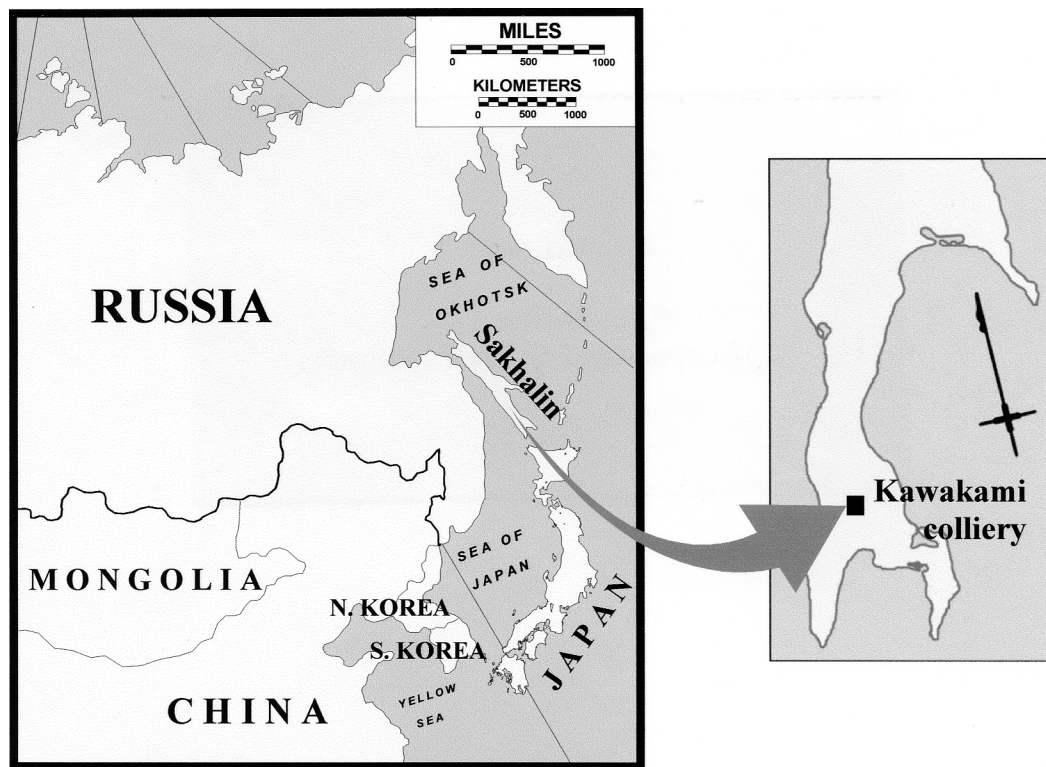


FIGURE 2. Location of Sakhalin and the locality of *Nipponosaurus sachalinensis*.

maxilla and the anterolateral process of the premaxilla (Fig. 3). Here it is thin, plate-like, and wedge-shaped in lateral view. Dorsally, it partially overlaps this latter process, as in all hadrosaurids, and is clearly visible in medial view, where it makes up the lateral wall of the nasal cavity. Unfortunately, the orbital margin and hence the opening of the nasolacrimal duct are not preserved in this specimen. However, the medial surface may include the exit of the duct. If *Nipponosaurus* is a lambeosaurine (as we believe; see systematics section), our interpretation of this element as a lacrimal is at variance with the morphology of this bone in other lambeosaurines. For example, it appears to be relatively larger and reaches farther forward than in other lambeosaurines, and in this way superficially resembles the asymmetric anterior process of the jugal in hadrosaurines. That this is not the case is suggested by the medial exposure of the element, which does not conform to the sutural surface of the jugal that contacts the maxilla. Thus, we feel that it is more likely a lacrimal, albeit a relatively large one.

Jugal—Only the posterior half portion of the right jugal is well preserved (Fig. 3A–D). The postorbital process and the posterior process are missing, but this element preserves its dorsal and ventral margins, including the ventral margin of the infratemporal fenestra. The body of the jugal is shallowly convex externally, while the dorsal margin gently slopes upwardly and the posterior margin is rounded. The ventral margin of the jugal is appeared to make an acute angle where it partially covers the coronoid process of the mandible. The anterior margin of this angle curves dorsally (Fig. 3E; see Nagao, 1936: pl. III; this region is now slightly broken). The sharp angle of the ventral margin of the jugal is similar to the condition of both adult and juvenile *H. altispinus* (NMC 8501, 2246; Gilmore, 1924), but unlike that of other hadrosaurids.

Maxilla—The remains of the maxilla occur in two sections (Fig. 3). One consists of the anterior region, which articulates by way of a transversely concave maxillary shelf with the ven-

tro-lateral process of the premaxilla (pmx I), as seen in all lambeosaurines for which this region is known (Heaton, 1971; Weishampel and Horner, 1990). Anterior part of the maxilla is too incomplete to indicate whether it supported the maxillary process. Posterior part of this section contacts anterior region of the partial lacrimal. The medial wall of this portion of the maxilla contains five special foramina (Edmund, 1957). The four tooth positions each have two functional teeth and two replacement teeth.

The other section consists of the posterior two-thirds of the maxilla, which houses eleven tooth positions. Laterally, the anterior half of this section is abraded such that the dental battery is partly exposed. Much of the dorsal region of the maxilla is missing and the position, height, and details of the dorsal process of the maxilla as well as the lacrimal and the palatine facet cannot be determined. However, a part of the articulation with the jugal and the ectopterygoid is preserved. The lateral surface of the jugal facet is adjacent to the prominent, horizontal ectopterygoid shelf (Fig. 3D, arrows). This posterior part of the superior surface is overlapped by the thin and narrow ectopterygoid, which has been interpreted as the site of origin of part of *M. pterygoideus dorsalis* (Ostrom, 1961). The ectopterygoid appears to have no articulate facet with the jugal, but we were not able to examine these portions more closely because the matrix in this region was impossible to remove. On the medial side of the maxilla, the remains of the pterygoid (only the posterior part that includes the buttressing flange, the bifurcating flange, and a part of the central plate; Heaton, 1972) is preserved. It is posteriorly displaced and there is also no articular facet for the palatine and maxilla. In addition, a part of a bone that may be the palatine can be seen anterior to the pterygoid.

Although the maxillary complex of *Nipponosaurus* is poorly preserved, it does provide important phylogenetic and ontogenetic information. For example, the presence of a maxillary shelf suggests that *Nipponosaurus* belongs to Lambeosaurinae

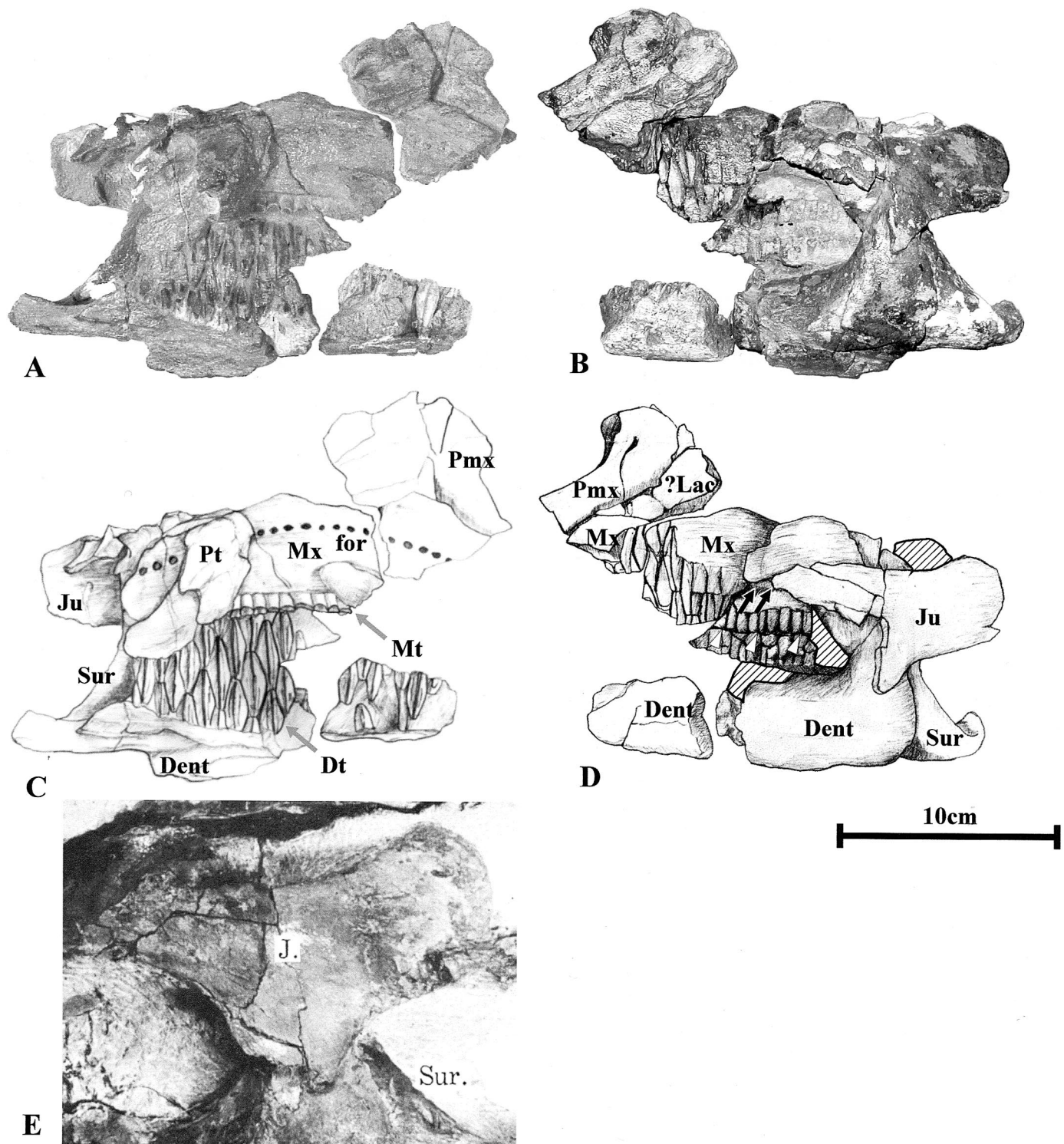


FIGURE 3. *Nipponosaurus sachalinensis*. **A**, remains of the skull elements, left medial view. Each tooth position has only two dentary teeth; **B**, left lateral view; **C**, schematic of **A**; note the secondary ridge on the dentary tooth; **D**, schematic of **B**; note the position of the lacrimal. Arrow, the ventral part of the ectopterygoid shelf; arrowhead, occlusal surface. **E**, ventral flange of jugal in *Nipponosaurus* (Nagao, 1936: plate III; the ventral flange of jugal whose region is now broken). **Abbreviations:** **Dent**, dentary; **Dt**, Dentary teeth; **Ju**, jugal; **Lc**, lacrimal; **Mt**, maxillary teeth; **Mx**, maxilla; **Pmx**, premaxilla; **Pt**, pterygoid; **for**, special foramina; **Sur**, surangular.

(Heaton, 1972; Weishampel et al., 1993). The estimated small number of the tooth positions than is seen in adult hadrosaurids implies that the specimen is a subadult.

Parietal—The parietals of *Nipponosaurus* were discovered by additional preparation of the holotype and most of this ele-

ment, although dorsoventrally compressed, is preserved (Fig. 4). Dorsally, the spool-shaped pair of parietals, completely fused to each other as in other hadrosaurids, has a sagittal crest that bilaterally divides the left and right attachment surfaces of adductor mandible muscles group. The posterior region of the

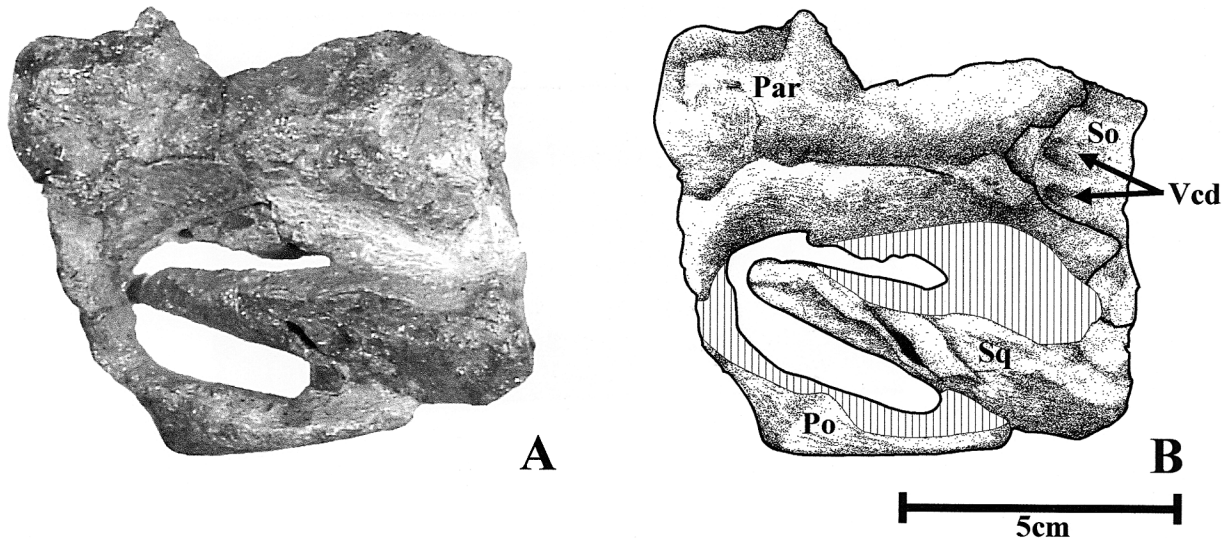


FIGURE 4. *Nipponosaurus sachalinensis*. **A**, Parietal complex, dorsal view. **B**, Schematic of **A**. **Abbreviations:** **Par**, parietal; **Po**, postorbital; **So**, supraoccipital; **Sq**, squamosal; **Vcd**, foramen for vena capitis dorsalis.

crest is high and ends in a deep notch into which the triangular supraoccipital fits. Anteriorly, the parietals articulate with the frontals by a scarf joint. The anterolateral margins of the parietals extend laterally to articulate with the posterior part of the postorbitals. Ventrally, the parietal edges are broken, but the endocranial cavity makes a deep fossa in the middle of the ventral surface of the parietal roof.

Supraoccipital—The supraoccipital, preserved beneath the parietals (Fig. 4), has two bilateral grooves on its posterodorsal surface. These lead to the post-temporal foramina, which accommodated the vena capitis dorsalis (Norman, 1980). Although the acute outline of the supraoccipital is obscured by abrasion and persistent matrix, its posterolaterally-expanded margins appear to articulate with the medial expansion of the squamosals. Posteroventrally, the supraoccipital is broken, but likely is excluded from the foramen magnum and does not appear to be fused with the exoccipitals. The lack of fusion with the exoccipitals suggests that the type specimen of *N. sachalinensis* was a subadult (Ostrom, 1961).

Postorbital and Squamosal—Two partial elements to the left side of the parietal are thought to be the postorbital process of the squamosal and the squamosal process of the postorbital (Fig. 4). These elements originally would have articulated with each other, but the margins are now broken and too fragmentary to contain information about their relationships.

Dentary—The dentary (Fig. 3) is preserved in two sections. One probably corresponds to the middle region and includes seven tooth positions, each containing fragmentary teeth. The other represents a more posterior area, which preserves the coronoid process and 14 tooth positions with teeth. Although the anterior and posterior sections are abraded and somewhat incomplete, the dorsal and ventral borders of the dentary appear to be parallel. The posterior dentition extends behind the coronoid process. Posteriorly, the dentary forms most of the coronoid process, which served as the attachment site for pseudotemporalis and adductor mandibularis externus muscle (Ostrom, 1961). The coronoid process, whose anterior margin is represented by an expansion as in other hadrosaurids, is oriented nearly 80° to the long axis of the body of the dentary. Only the part of the medial surface of the dentary beneath the special foramina is preserved and some of teeth have been damaged as the result of the loss of the alveolar parapet. Posteriorly,

the upper angular process articulates with the splenial, while the lower process, which articulated with the angular, is missing. The mandibular groove runs anteriorly from the adductor fossa and is also found on the anterior section.

Surangular—The surangular, except for its posterior part, is almost completely preserved (Fig. 3). Laterally, the anterior portion of the surangular forms the posterior margin of the coronoid process. This region is much more robust than that of other hadrosaurids in which the tip is thin and pointed (Lambe, 1920; Gilmore, 1924). Although the dorsal margin of the coronoid process of *Nipponosaurus* is covered by a fragment of bone, the surangular does not appear to taper here.

The mandibular glenoid is positioned at the posterior base of the coronoid process. The lateral buttress of the glenoid, supporting the quadrate articulation, is missing. The posterior margin of the surangular contribution to the coronoid process is moderately curved internally, implying that the glenoid is not particularly large or deep. Medially, the surangular forms the well-developed lateral wall of the mandibular fossa into which adductor externus muscles inserted (Ostrom, 1961).

Dentition—The maxillary dentition is organized into a dental battery in which the dorsoventrally-elongated hexagonal teeth interdigitate with each other to form a compacted honeycomb-shaped unit. The maxillary dental battery consists of two functional teeth and at least two replacement teeth per tooth family. The maxillary teeth are symmetrical and have a prominent carina in the middle of the enameled buccal surface, but there is no evidence of secondary ridges or denticles along the mesial and distal margins of the teeth. Otherwise, the buccal surface of the maxillary teeth is abraded and thus cannot be described in more detail. Lingually, the teeth are cylindrical and lack enamel. The occlusal surface forms a single plane that faces ventrally and lingually.

The dentary teeth also form a dental battery (Fig. 3A, B). Each tooth position consists of only two functional teeth, while other hadrosaurids have at least three teeth per tooth position (Weishampel et al., 1993). The hexagonal dentary teeth are slightly posteriorly inclined. However, the lateral angles of the crown are less clear than that of non-lambeosaurine hadrosaurids. Moreover, the anterior angle of the crown is lower than the posterior angle. Except for this point, the dentary teeth are nearly symmetrical and possess a prominent carina in the middle of

the enameled lingual side. Compared to the maxillary teeth, those of the dentary are wider, and often have faint secondary ridges. Most of the secondary ridges are present on the anterior side of the prominent median carina, but some are on both sides of the carina. The occlusal surface is directed dorsally and laterally. Marginal denticles are missing, but this condition may be due to abrasion.

The smaller number of teeth per tooth position suggests that this specimen either is a subadult or has a primitive phylogenetic position. Because these teeth are nearly symmetrical and narrower than those of immature non-hadrosaurid iguanodontians, it is best to attribute this smaller number of teeth to immaturity.

Axial Skeleton

Atlas—The atlas of hadrosaurids consists of three separate elements: an intercentrum, an odontoid process, and a pair of neural arches. Only a well-preserved odontoid process is known in *Nipponosaurus* (Fig. 5A–C). In dorsal view, it is semicircular and has a shallow, wide groove on the dorsal midline. Both lateral margins preserve shallow depressions. Ventrally, the anterior spherical region is rugose and the posterior cylindrical portion is slightly constricted transversely. In addition, the posterior surface is flat and rugose, indicating the attachment of cartilage for articulation with the anterior surface of the axial centrum.

Axis—The nearly complete axis is strongly opisthocoelous (Fig. 5D). In anterior view, the centrum is transversely broad, while its upper lateral margins are deflected and directed dorsolaterally to form the parapophyses. A rugose fossa on the upper middle surface of the centrum indicates the facet for the odontoid process. The interface between the centrum and neural arch is constricted and the neurocentral suture is visible (contra Nagao, 1936). The neural canal is much smaller relative to the size of the centrum (48%) than more posterior cervicals (57–70%). Laterally, the triangular parapophysis, which articulates with the head of cervical rib, is positioned on the upper anterior part of the centrum. The middle of the centrum is strongly constricted. Above, at the height of the neural canal, the diapophysis articulates with the tuberculum of the cervical rib, protruding obliquely onto the ridge that continues to the postzygapophyses. The tips of the neural spine and the prezygapophyses are broken; hence, their shape is not known. The axial neural spine of other hadrosaurids is large and served as muscle attachment sites (probably rectus capitis posterior and obliquus capitis magnus muscle). In *Nipponosaurus*, the neural spine does not appear to be greatly expanded posteriorly, even though it is broken here. The posterior surface of the centrum is strongly concave and smaller than the anterior surface. The postzygapophyses are incompletely preserved, but lie close together.

The neurocentral suture is present not only on the atlas, but also on the all of the other cervical (Fig. 5E), dorsal, and caudal vertebrae, further indicating that the type specimen of *N. sachalinensis* is a subadult. Moreover, the posterior reduction of the neural spine of the axis—which does not appear to be due to breakage—is not seen other hadrosaurids, even in subadult individuals (*H. stebingeri*, NSM-PV 20377; *H. altispinus*, NMC 2246). Hence, this character is thought to be diagnostic of *N. sachalinensis*.

Post-Axial Cervical Vertebrae—The type specimen of *N. sachalinensis* preserves twelve additional cervical vertebrae, including six that were found during re-preparation. These latter, although their exact position within the cervical series is not known, articulate in a dorsally-curving series and bear partial cervical ribs (Fig. 5F). One of these vertebrae is fragmentary, while the others are well preserved except for their neural arches. However, two cervical vertebrae, which were described as

the sixth and seventh (Nagao, 1936:pl. IV-4), have been lost since the time of their original description. Of the existing cervicals, the third and fourth have well-preserved centra, while the newly-prepared cervicals provide the only well-preserved neural arches known for *Nipponosaurus*. Therefore, the description of the cervical vertebrae is based on each well-preserved portion, not from a complete preserved cervical vertebra.

All of the cervical vertebrae are strongly opisthocoelous. Transversely, they are smaller than the axis. Laterally, the horizontal parapophysis is ellipsoid and becomes longer more posteriorly in the cervical series. Ventrally, the centra are transversely compressed with a robust keel. The neural canal is much larger than that of the axis, due to its excavation into the dorsal part of the centrum. As a result of this keel and excavation, the centrum is transversely heart-shaped. The two postzygapophyses extend from the top of neural canal, and lateral to each is the anterolaterally-curving transverse process. Although the tip of the transverse process laterally bears the diapophysis; this part is severely damaged by abrasion. The neural spine is incipiently found at the base of the postzygapophyses.

Dorsal Vertebrae—The number of dorsal vertebrae in lambeosaurine hadrosaurids varies from 16 (*L. lambei*; AMNH 5340) to 19 (*C. casuarius*; AMNH 5240). The type of *Nipponosaurus* appears to preserve only half of the dorsal series: eight dorsal vertebrae of the type specimen of *Nipponosaurus* were mentioned in Nagao (1936). However, he described only the five dorsal vertebrae that were collected during the first expedition to Sakhalin. As the result of re-preparation, a vertebra formerly assigned to the caudal series is now regarded as a dorsal vertebra, based on the position and the size of the neural canal. In addition, the posteriormost cervical or first dorsal vertebra has been revealed with the new preparation. In the original description, almost all parts of the anterior and middle dorsal vertebrae were preserved, but some elements are now broken (see Nagao, 1936:pls. XV, XVI, XVII, and XIX).

The newly-prepared vertebra (Fig. 5G) is thought to the posterior most cervical or first dorsal vertebra, because it has a longer and opisthocoelous centrum, but we could not decide whether cervical or dorsal vertebra because of the severe abrasion of the parapophysis. The centrum is approximately 50% longer anteroposteriorly than dorsoventrally high. Anteriorly, the articular facet is circular with a smoothly convex surface. The neural canal is large and equivalent in size to those of the cervical vertebrae. The right prezygapophysis is smaller and higher than that of preceding cervicals, while the postzygapophyses is missing.

The next smaller dorsal vertebra (Fig. 6A) is thought immediately to follow the above vertebrae. The centrum, also approximately 50% longer than high, is shallowly amphicoelous (or platycoelous; Romer, 1956) and heart-shaped in anterior view. Ventrally, a blunt longitudinal ridge, formed by the sides of the centrum, is constricted in the middle. Laterally, part of the ovoid and shallowly-concave diapophysis is preserved on the neural arch on which the base of the neural spine and the transverse process are also preserved. The neural canal is large, only slight smaller than the height of the centrum.

The three middle dorsal vertebrae known for *Nipponosaurus* consist of the centra and distal parts of the neural spines. The centra are shallowly platycoelous and slightly laterally constricted in the middle with a keel on the ventral surface. Thus, they are heart-shaped in anterior view and spool-shaped in ventral view. The length of these centra is shorter than previous dorsals; hence, the length/height ratio of the centrum is approximately 100%. The diameter of the neural canal is 50% of the height of the centrum and very different from that of the anterior dorsals. The neural spine projects nearly vertically, and is thickest and broadest distally. Although the base of the neural spine is not presently preserved, the entire height of the neural

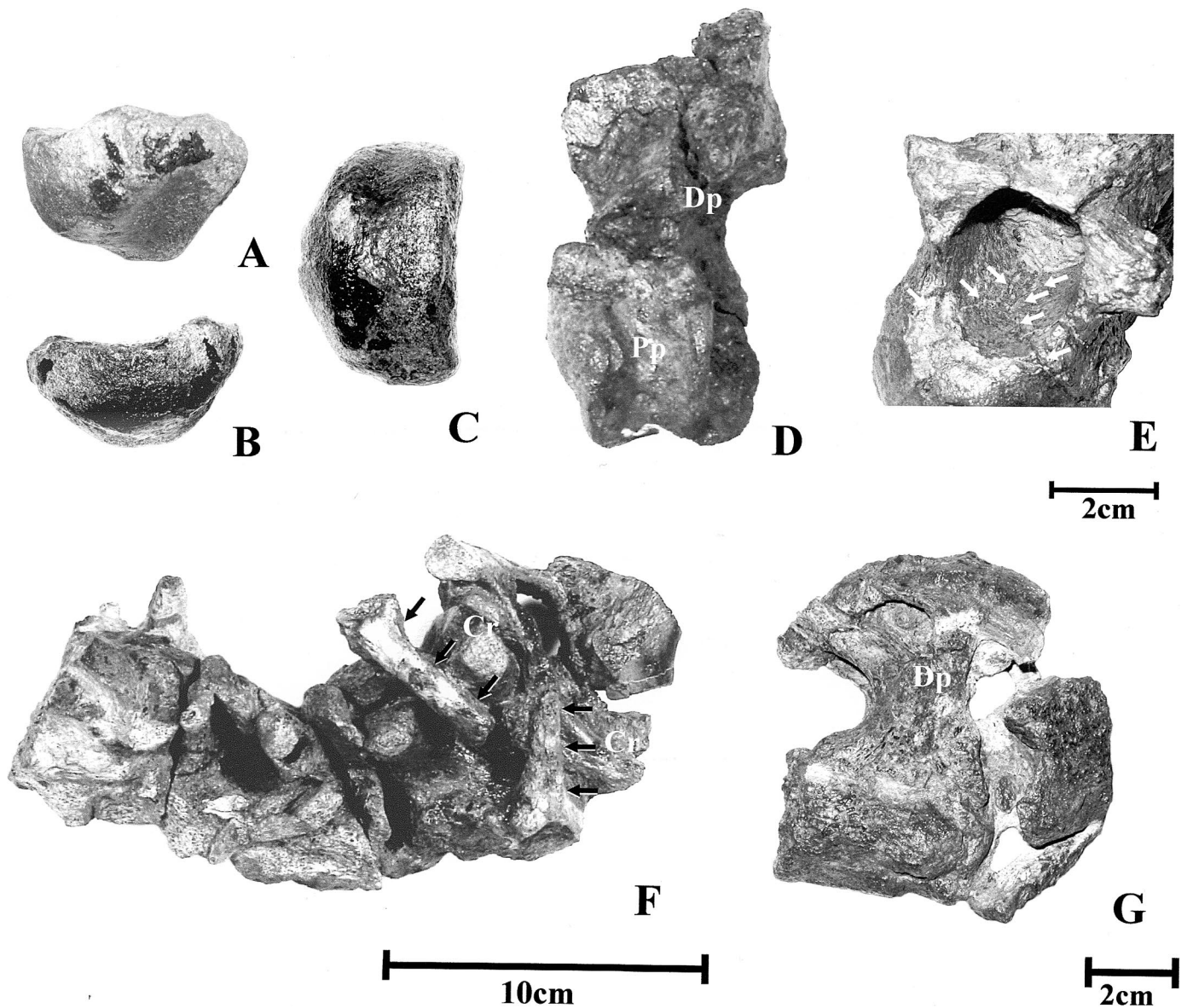


FIGURE 5. *Nipponosaurus sachalinensis*, cervical vertebrae. **A**, odontoid process of the atlas, left anterolateral view. **B**, anterior view. **C**, ventral view. **D**, axis, left lateral view. **E**, fourth cervical vertebra, anterolateral view. **A–D** are same scale as **E**. White arrows denote neurocentral sutures. **F**, six newly prepared articulated cervical vertebrae, left lateral view, probably positioned as the eighth to the thirteenth. **G**, newly prepared posteromost cervical or first dorsal vertebrae; it has a moderately opisthocelous and longer centrum than earlier cervicals. **Abbreviations:** **Cr**, cervical rib; **Dp**, diapophysis; **Pp**, parapophysis.

spine is approximately three times the height of the centrum according to the plates of Nagao (1936:pls. XV, XVII).

Most of the neural spine and the transverse process of the posterior dorsal vertebra (Fig. 6B) are present, but poorly preserved. The centrum, platycoelous and heart-shaped in anterior view, is wider than the middle dorsal centra, while the neural canal is slightly smaller. Except for these features, the centrum and the neural spine are almost the same size as the middle dorsals and their morphology is also similar, even as regards their spool shape and ventral keel.

Sacrum—The three articulated sacral vertebrae originally described by Nagao (1936) are preserved only as centra (Fig. 6C). The first of these is flat to slightly procoelous and heart-shaped in anterior view. Posteriorly, the lateral margins are deflected and widened to support the first true sacral rib. In addition, it is shortened dorsoventrally to give it a wide rectan-

gular shape. The next two vertebrae are fused and appear to follow immediately after the aforementioned vertebra. The external surface of these two centra, as well as the base of a left sacral rib, is highly eroded. Anteriorly, the first of these centra is ovoid (higher than wide) and wider than the next centrum. Ventrally, there is no keel or groove. The lack of fusion between the first and second sacral vertebrae suggests that the type of *N. sachalinensis* is a subadult.

Caudal Vertebrae—Although consisting nearly entirely of centra, 35 caudal vertebrae are known for the type specimen of *N. sachalinensis* (Fig. 7). Nagao (1936) noted that these caudals were found two groups. The first group includes 11 vertebrae preserved in situ near the pelvic girdle. The second group of 22 vertebrae was found articulated in a series near, but not in articulation with, the first group. Two additional vertebrae were found between these two groups. Judging from the number of

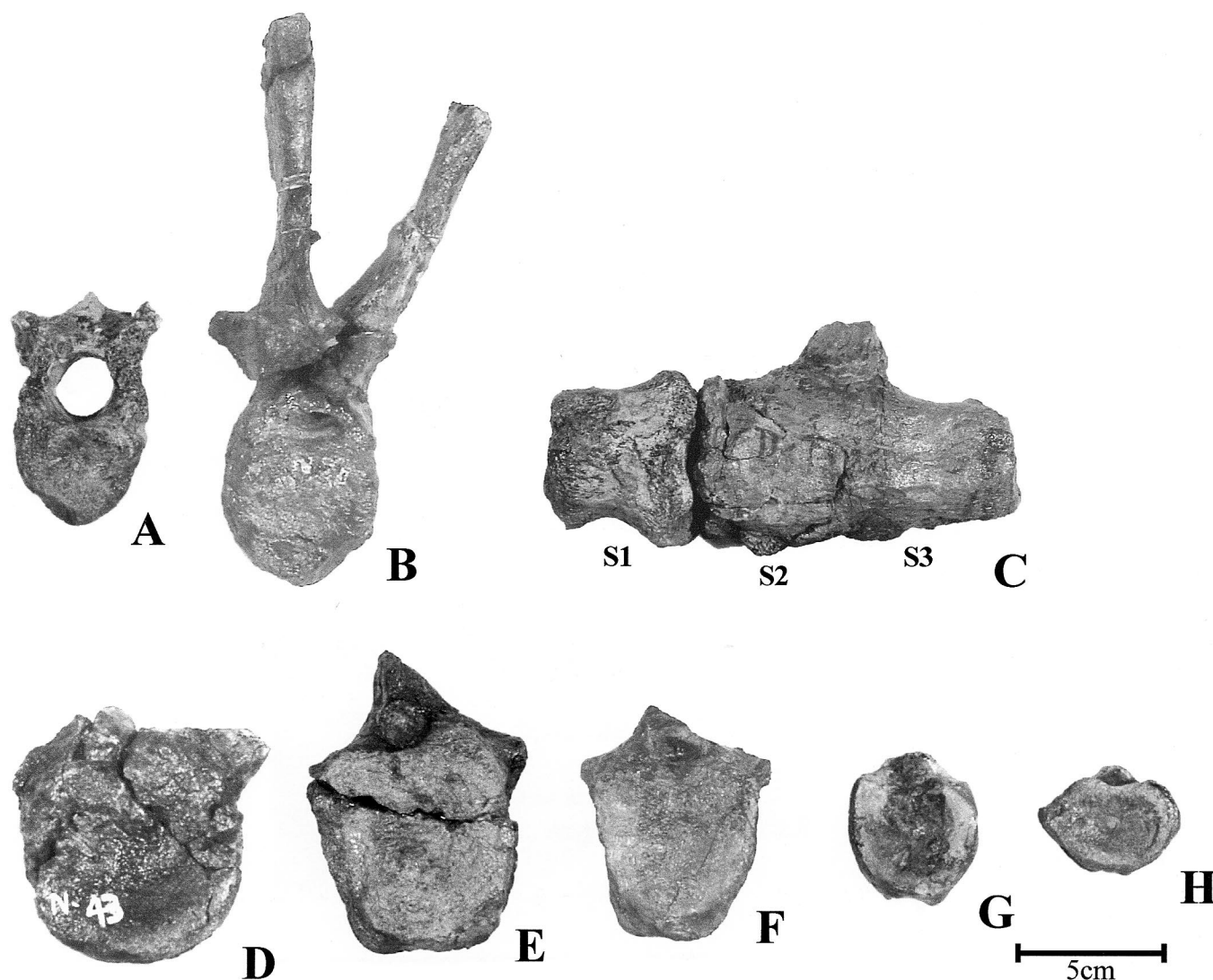


FIGURE 6. *Nipponosaurus sachalinensis*. Vertebrae, anterior views except for C. A, first or second dorsal vertebra. B, Posterior dorsal vertebra. C, three articulated sacral vertebrae, ventral view. D, first caudal vertebra. E, fourth caudal vertebra. F, ninth caudal vertebra. G, 14th caudal vertebra. H, 24th caudal vertebra.

vertebrae and the apparent size continuity between these groups, the complete series of caudal vertebrae is thought to have been recovered. All of the caudal centra except for the most distalmost are platycoelous. Those distal to the fourth centrum have chevron facets on their anteroventral margin. These chevron facets gradually become prominent and form ventral keels. In anterior view, the centra gradually change from being circular in the first three vertebrae to iso-trapezoidal (with the dorsal dimension longer) up to the 11th caudal, then becoming circular again up to the 17th caudal. Although varying in degree, the centra are platycoelous or amphiplatyan beyond the 18th caudal. The centra also gradually become heart-shaped and dorsoventrally compressed. For vertebrae distal to the 29th caudal, the chevron facets are smaller and the keels more obscure. By the 32nd caudal, chevron facets have disappeared.

Ribs—The ribs, although known, consist only of midsections from which it is impossible to discern their position or general morphology.

Appendicular Skeleton

Scapula—Even though the scapula is separated into two fragments, much of its morphology remains (Fig. 7A, B). Both

dorsal and the ventral borders of the scapular blade appear to be straight and parallel to each other for its distal two-thirds. Laterally, the blade is shallowly convex and smooth, and becomes thicker and narrower proximally. The pseudoacromial ridge does not continue onto the blade. Medially, the surface is flat with proximodistal striations, indicating the distal scar of subscapularis muscle (Norman, 1986). The other section of the scapula consists of the proximal expansion. Here the dorsal border is swollen to form a modest pseudoacromial ridge. The mediolaterally-narrow and angular ventral margin is also strongly expanded, but lacks the coracoid articulation and the glenoid due to the incomplete nature of this material.

Although the scapula of *Nipponosaurus* is broken at the middle of its curvature, the specimens show that it was almost as straight and slender, as in such lambeosaurine hadrosaurids as *L. lambei* (ROM 1218, AMNH 5340) and *C. casuarius* (AMNH 5240). However, it is different from those of subadult *H. stebingeri* (NSM-VP 20377, 20378) and also from adult *P. walkeri* (ROM 768), which are strongly curved and more robust.

Coracoid—Both left and right coracoids have been newly prepared. The right is better preserved (Fig. 7C), but the mar-

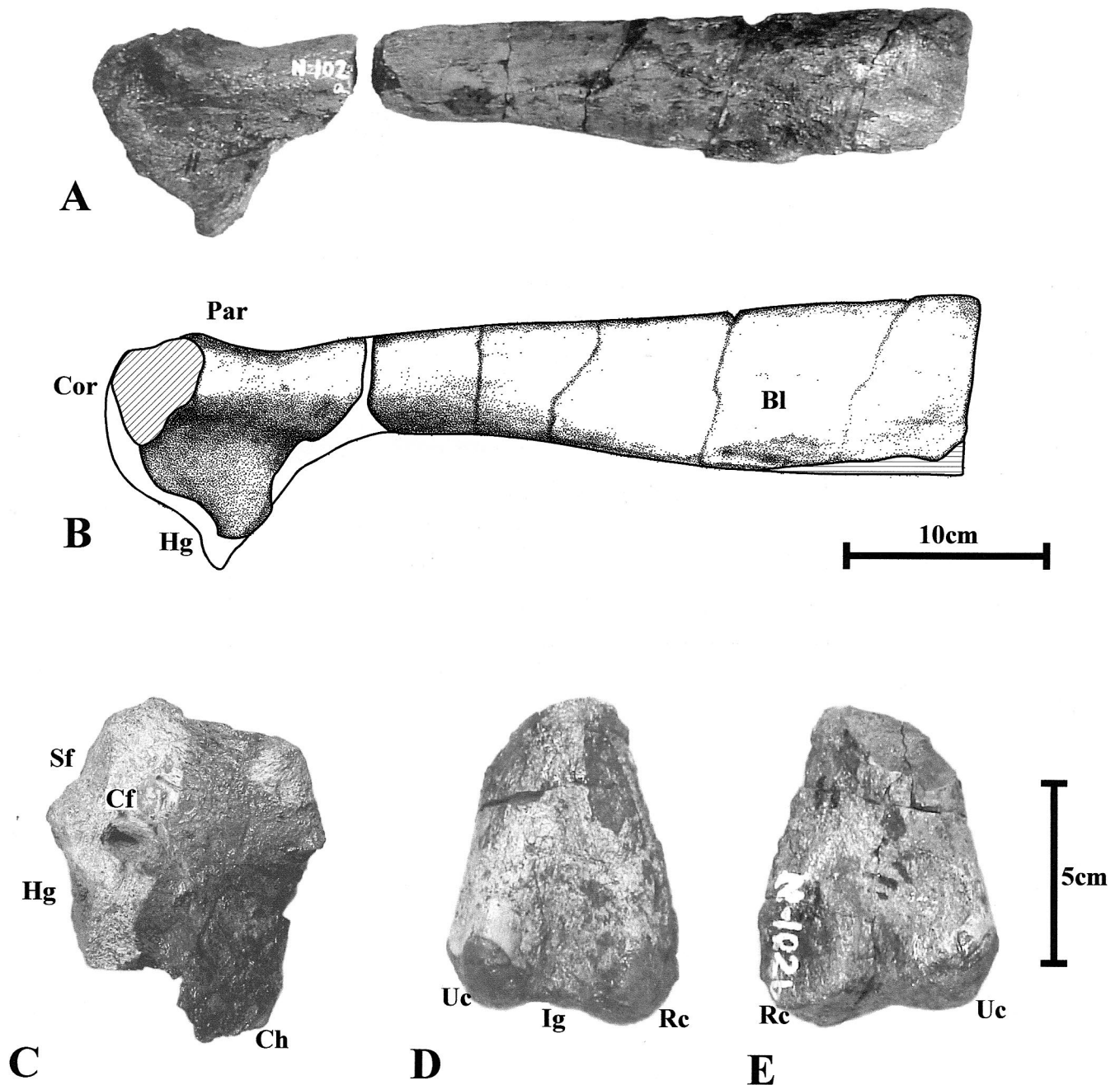


FIGURE 7. *Nipponosaurus sachalinensis*. A, left scapula, lateral view. B, reconstruction of the scapula. C, right coracoid, cranial view. D, proximal part of left humerus, posterior view; E, anterior view. C and D are same scale as E. **Abbreviations:** Bl, scapular blade; Cf, coracoid foramen; Ch, coracoid process; Cor, coracoid suture; Gl, humeral glenoid; Hg, humeral glenoid; Ig, intercondylar groove for olecranon; Par, Pseudoacromial ridge; Rc, radial condyle; Sf, scapular facet; Uc, ulnar condyle.

gin, including the tip of the coracoid process, is broken. Laterally, the coracoid is shallow convex and medially concave. The rugose, convex articular facet for the scapula is thickened and ventrally its surface makes a 150° angle with the glenoid surface, the latter almost as thick as the scapular articulation. The coracoid foramen, completely surrounded laterally by bone while immediately adjacent to the scapular articulation medially, is positioned at the height of the external protrusion, near the distal margin. The outline of the coracoid is incomplete in *Nipponosaurus*, but the distance between the ventral and dorsal margin is greater than that of hadrosaurines.

Humerus—Only the distal ends of both humeri are present

and that of the left humerus is better preserved (Fig. 7D, E). Distally, the triangular radial and ulnar condyles are separated by a intercondylar groove that is moderately deep posteriorly and shallow anteriorly. The lateral side of the radial condyle bears a shallow groove from which the extensor muscles originate and the medial side is occupied by the origins of the flexor and pronator musculature. In distal view, the ulnar condyle is two thirds as large as the radial condyle.

Ulna—Both ulnae are almost completely preserved and are approximately 9% longer than the only preserved radius (Fig. 8B, C). The shaft is nearly straight and relatively slender comparing to that of *Iguanodon*. Proximally, the hemispheric olec-

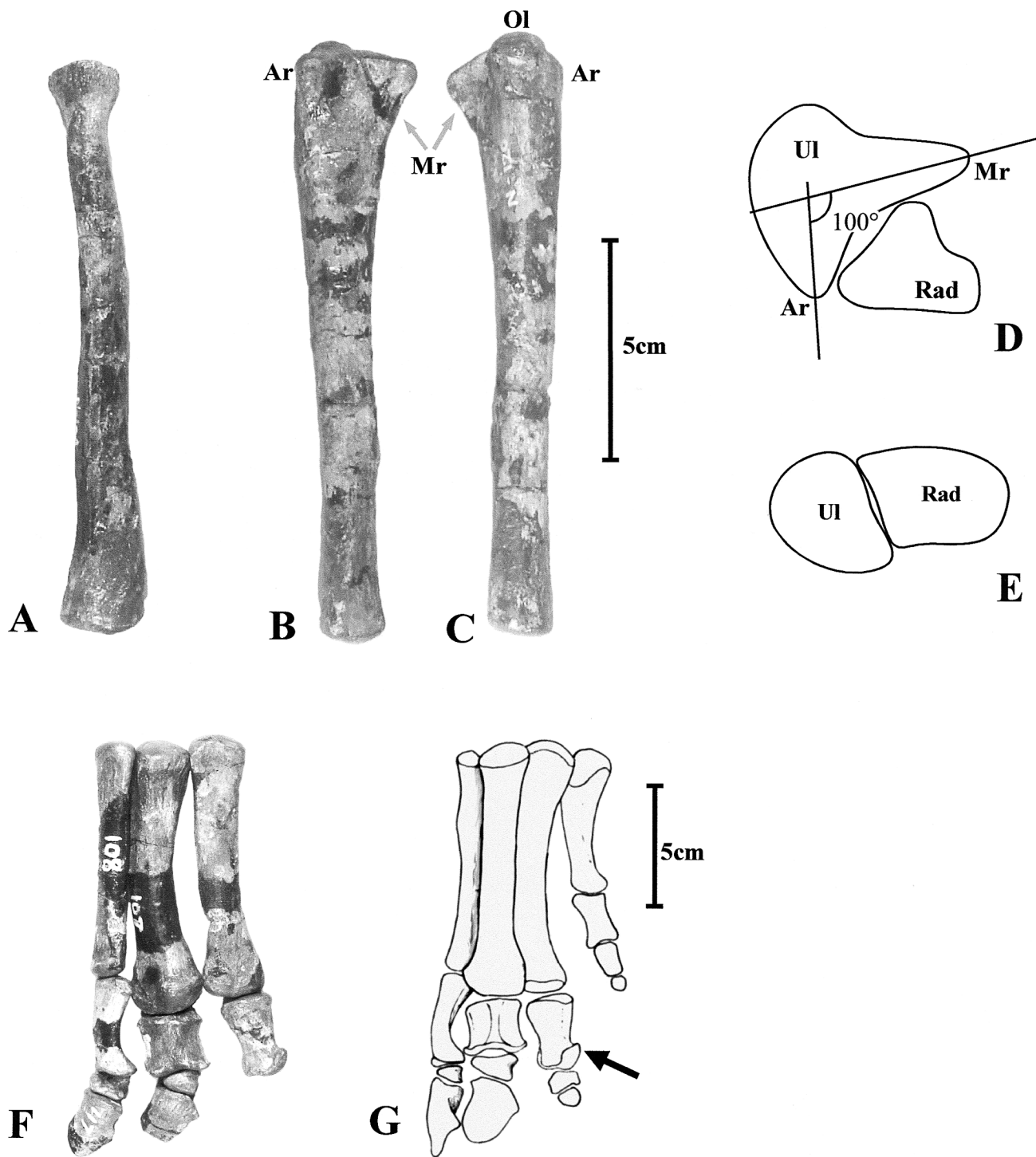


FIGURE 8. *Nipponosaurus sachalinensis*. A, right radius, anterior view. B, right ulna, anterior view; C, posterior view. D, proximal view of ulnar-radius complex. The prominent medial ridge and the smaller but the more robust anterior ridge are oriented 100° to each other, surrounding the head of the radius. E, Distal view of ulnar-radius complex. F, left manus, dorsal view. G, Reconstruction of the manus. Note the large inflection on the laterodistal articular facet in digit IV (arrow). **Abbreviations:** Ar, anterior ridge (extensor ridge); Mr, medial ridge (flexor ridge); Ol, olecranon; Rad, radius; Ul, ulna.

ranon process is poorly developed. The prominent medial ridge and the smaller but more robust anterior ridge, both of which surround the head of the radius, are oriented 100° to each other (Fig. 8D, also see Parks, 1920). The medial ridge, where the pronator teres arose, has a shallow depression in lateral side that probably accommodated the flexor digitorum longus mus-

cle. Like other hadrosaurids, this medial ridge is elongated one-third shaft down. Although the ridge is more prominent than iguanodontians, slightly smaller than adult specimens (*Gryposaurus incurvimanus*, ROM 764; Parks, 1920). The proximal and distal radial facets are triangular, with facing each apex, and more obscure than those of non-hadrosaurid iguanodon-

tians. The distal radial facet is posteriorly oriented at 45° from proximal radial facet. The ulnar shaft is slightly deflected posteriorly with a slight dorsoventral expansion. The carpal facet is obliquely D-shaped, which together with the carpal facet of the radius produces an ovoid carpal facet of the forearm (Fig. 8E).

The lesser development of the olecranon and medial ridges of the proximal region suggest that this specimen is a subadult (Brett-Surman, 1989). However, the olecranon appears to be even less well developed than in other juvenile specimens (e.g., *Hypacrosaurus stebingeri* NSM-PV 20377); therefore, there is a possibility that these are diagnostic only of *Nipponosaurus*.

Radius—The radius, also virtually complete (Fig. 8A), is slightly shorter than the ulna. Proximally, the radial head is nearly triangular in dorsal view. Immediately under the radial head, the radial shaft is strongly constricted anteriorly and posteriorly, hence the medial surface at this point has a ridge. From here, the shaft extends moderately along its length and the distal part is as robust as the ulna. Only the posterior margin of the distal facet of the radius is demarcated by a ridge that runs three quarters down the length of the shaft, while the anterior region of the facet is curved and impossible to identify clearly. The convex carpal facet is dorsoventrally expanded and offset.

Manus—All hadrosaurids have four metacarpals and the phalangeal formula is usually 0-3-3-3-3 or 0-3-3-3-4 or 5 (Fig. 8F, G). Most of the manus of *Nipponosaurus* is preserved, but regrettably, phalanx IV-3 of the left manus is now lost. The carpals are not preserved. There is longitudinal twisting of the metacarpals, as shown in Nagao (1938:fig. 2), but this morphology is due to inaccurate reconstruction in plaster (the right and left metacarpals are asymmetrical with respect to each other).

Metacarpal II is the second shortest in the metacarpus, straight, and strongly compressed lateromedially. Both the proximal and distal ends are strongly expanded dorsopalmarly, while the lateromedial thickness of the shaft is nearly constant. The medial proximal region has prominent dorsal and palmar scars for digital abductor muscles. Laterally, the shaft articulates with metacarpal III along its length. Proximally, the dorsoventrally-wide articular facet is convex with a smooth surface; all of the other metacarpals of *Nipponosaurus* exhibit the same articular morphology. Distally, the articular facet is crescentic.

Metacarpal III is the most robust and longest of the four metacarpals. In addition, this element expands more distally than proximally. Both medial and lateral surfaces are flat, except for a small fossa at the each side of the distal epiphyseal region. Proximally, the articular facet is rectangle with a dorsolaterally-expanded angulation, while the distal convex articular facet is shaped like a dorsally-elongate iso-trapezoid.

Metacarpal IV is as long as metacarpal III and is the widest of all of the metacarpals proximally. Moreover, this element is different from the others in that the width is greater than the dorsopalmar thickness. The shaft narrows distally, but the articular end is strongly expanded. Medially it articulates with the entire length of metacarpal III via a flat, slightly rugose surface. Laterally, the surface is rounded and the proximal convex part articulates with metacarpal V. The proximal articular facet is formed an enlarged D-shape, while distal facet is a mediolaterally-elongate ellipsoid.

Metacarpal V is the shortest of the metacarpals. The type of *Nipponosaurus* preserves only the proximal and distal ends of this element of the right manus. Proximally, it nearly as robust as metacarpal III and IV, but the shaft narrows strongly toward the distal end. Medially, there is a shallow and incipient groove for the articulation of metacarpal IV, which becomes wider and deeper in many hadrosaurids (e.g., *Hypacrosaurus altispinus*,

AMNH 5370) and twists to the palmar side of the distal articular facet. Distally, the articular facet has a raindrop shape.

Both proximal and distal ends of the metacarpals of *Nipponosaurus* are much more expanded than those of other hadrosaurids. Although Brett-Surman (1989) thought this feature was plesiomorphic for hadrosaurids, it is also present in juvenile and subadult hadrosaurids (i.e., *H. stebingeri*; NSM-PV 20377, 20378). We, therefore, regard this expansion of the metatarsus as a juvenile and subadult character.

The proximal phalanx in digit II (II-1) is the longest of all of the phalanges. It is hourglass-shaped and palmarly concave. Both articular facets are crescentic and slightly concave. The wedge-shaped II-2 is small, medially pointed, and laterally concave. As a result, the hoof-like, and longer than wide II-3 is directed inwardly. Because of the elongation of II-1, digit II is as long as digit III.

The first phalanx of digit III (III-1) is robust and shorter than wide. The proximal articular facet is triangular and concave. Ventrally, the articular surface is flat rather than slightly concave. Dorsally, III-1 has a dorsal longitudinal ridge on the midline. The distal articular facet is slightly inflected and has a dorsal notch, slightly lateral to the ridge. III-2 is similar to II-2 but not concave laterally. III-3 forms a broader hoof than that of II-3.

The first phalanx of digit IV (IV-1) is long, but less so than II-1. In dorsal view, the proximal articular facet is semicircular and slightly concave, with a shallowly concave ventral margin. There is a large inflection on the laterodistal articular facet. IV-2 is small, as compressed proximodistally as II-2 and III-2; however, instead of being triangular, it is discoidal. IV-3 is lost, but based on Nagao (1938) it is known to be a small circular bone, not a hoof.

The dorsal ridge on III-1 appears to be present in almost lambeosaurines; in addition, the larger individuals have two ridges on its dorsal (e.g., *H. altispinus*; AMNH 5370). However, this character is highly variable in individuals and difficult to divide between presence and absence for unstable in its prominence. We, therefore, excluded this character from the phylogenetic analysis. In lambeosaurines, digit III is same length or shorter than digit II, for shortening phalanx III-1, which *Nipponosaurus* also seen. The large inflection of IV-1 in *Nipponosaurus* is not seen in other hadrosaurids; thus, this character is diagnostic of *Nipponosaurus*.

Ilium—Only the left ilium is preserved, though incompletely, and it occurs in two sections (Fig. 9). The first consists of a fragment of the preacetabular process and the second of a large part of the iliac body. The smaller preacetabular part has a large, medially-protruded dorsal ridge (medial ridge; Fig. 9B) that may have extended from the center of the iliac body to the base of the preacetabular process. Transverse process of the first seven sacra attached to the ilium along this medial ridge (Dilkes, 1993). Ventral and anterior part of the preacetabular process is broken.

The fragment of the iliac body part includes the supracetabular process without its tip and most of the postacetabular process, while lower margin, including the pubic and ischial peduncle, is poorly preserved due to abrasion. Dorsally, the ilium is a gentle sigmoid curve, forming lateral protrude at the antitrochanter or suprailiac crest (Brett-Surman, 1989) and being concave laterally at the postacetabular process. The suprailiac crest has a dorsal smooth surface, while the dorsolaterally-facing postacetabular process is a coarsely textured surface. Laterally, the dorsal margin appears to be slightly undulatory, forming a gentle, convex curve anterior to the supracetabular process and the postacetabular process directs slightly upwardly. The quadrangular postacetabular process is very abraded, but may not taper. Ventrally, the upper margin of the acetabulum and the ischial peduncle are thickened. Medially, the iliac

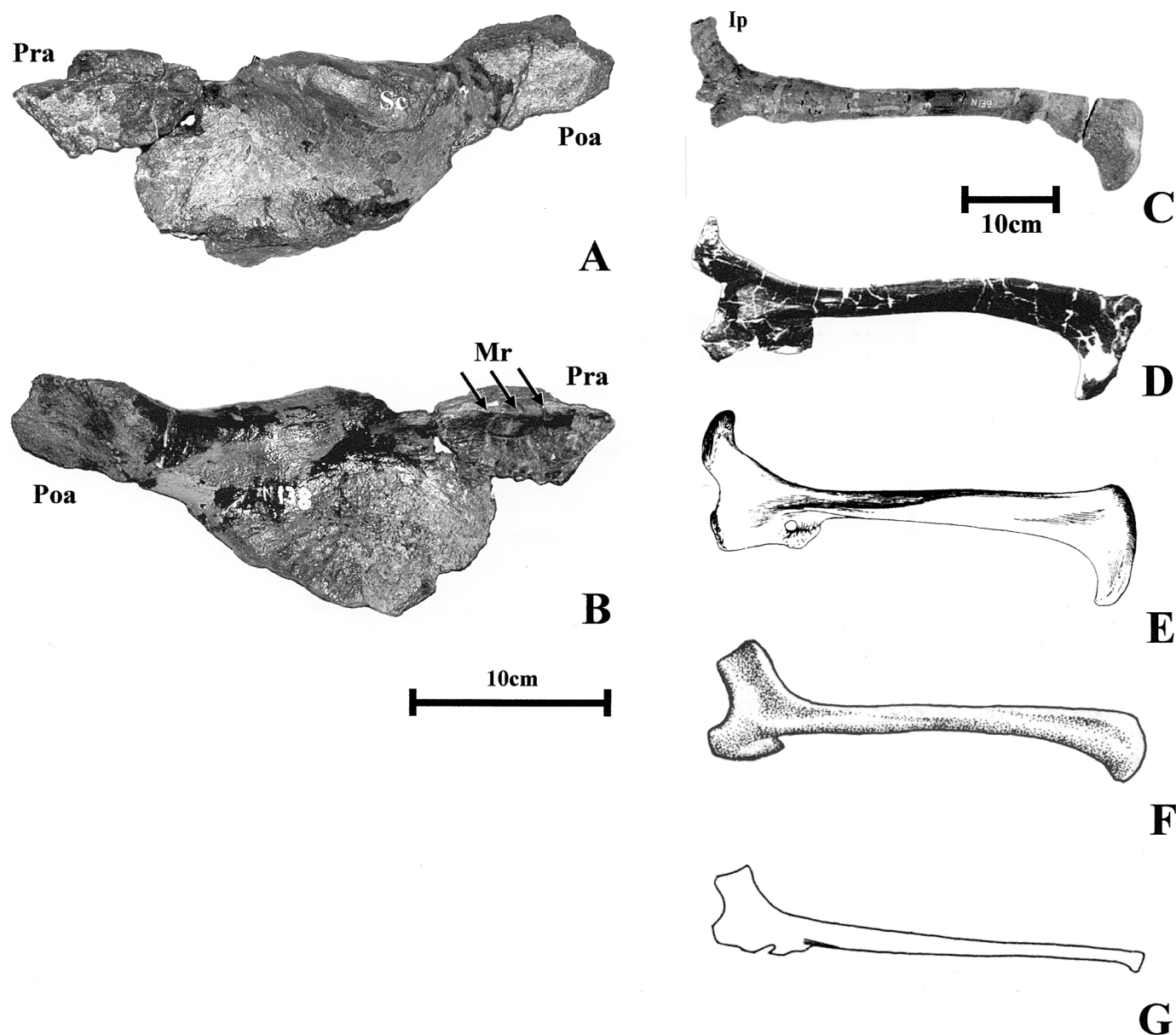


FIGURE 9. **A**, left ilium of *Nipponosaurus sachalinensis*, lateral view; **B**, medial view. **C-G**, comparison of hadrosaurid ischia. **C**, Left ischium of *N. sachalinensis* UHR 6590; **D**, *Parasaurolophus cyrtocristatus* FMNH P27393 (Ostrom, 1963; reversed); **E**, *Hypacrosaurus altispinus* NMC 8501 (Gilmore, 1924); **F**, *Corythosaurus casuarius* (Weishampel and Horner, 1990; reversed); **G**, *Anatotitan copei* AMNH 5730 (Lull and Wright, 1942). The sizes of **D**, **E**, **F** and **G** are adjusted to that of **D**. Note the distal boot-shaped expansion of **D**, **E** and **F**. **Abbreviations**: **Ip**, iliac peduncle; **Poa**, postacetabular process; **Pra**, preacetabular process; **Sc**, suprailiac crest.

surface is smooth and bears a shallow depression probably for articulation with the sacral ribs, but the medial ridge, which is developed in the smaller section, become smaller and absent at the position of suprailiac crest.

The ilium of most lambeosaurines is characterized by a pendent suprailiac crest and an untapered quadrangular postacetabular process. However, both characters are also seen in at least *Saurolophus* (Brown, 1913a; Maryańska and Osmólska, 1984) and *Prosaurolophus* (Parks, 1924), two taxa that do not belong to Lambeosaurinae. Recent studies (e.g., Weishampel et al., 1993) suggest that the presence of these characters in lambeosaurines and the latter material forms are likely due to convergence. Moreover, many variations are seen even the left and right of the same individual (Morris, 1978). Despite the lack of the tip of the supracetabular process, *Nipponosaurus* has an

ilium typical of hadrosaurids, but it is not very informative about the systematic position of this taxon for the reason given above.

Ischium—Although both ischia are partially restored, nearly all of the existing parts are well preserved (Fig. 9). These remains include the proximal region (only on the left ischium), a part of the long shaft, and the ischial boot. The iliac peduncle is abraded, so it appears more slender than it really is, while the pubic peduncle is missing. The ischial shaft does not taper proximally (in contrast of that of *P. cyrtocristatus* and *H. altispinus*), but appears to have parallel sides nearly to the end of the distal expansion (this character may not be accurate in that it is partially restored in plaster). The distally portion forms a boot-shaped expansion that is similar to that seen in *P. cyrtocristatus* and *H. altispinus*. The distal surface and margin are

rugose, indicating that a cartilage cap was present in life. In addition, the internal surface of the expansion bears rugose striations, indicating its symphysis with the adjacent ischium.

The ratio of ischial length (from the acetabular margin to the distal end of the element) to the width of the boot is nearly as great as in adult specimens of *H. altispinus* (AMNH 5204, NMC 8501) and *P. cyrtocristatus* (FMNH P27393). Although the type of *Nipponosaurus* is subadult, the proportion of ischial expansion is much larger than that of adult *Lambeosaurus* and *Corythosaurus*. Therefore, this larger-than-normal boot provides an important diagnostic feature of *Nipponosaurus*. Additionally, it may be that the shape of the boot may have an ontogenetic component. Large adult lambeosaurines (e.g., *P. cyrtocristatus* FMNH P27393, *H. altispinus* AMNH 5204) have a more angular toe and heel of the boot. In contrast, smaller, more juvenile individuals (e.g., *H. altispinus* NMC 8501) have a more rounded boot. If this pattern is more broadly true, then the rounded condition in *Nipponosaurus* also may indicate that it is a subadult.

Femur—The femur is much abraded and the position and the configurations of the anterior trochanter and the fourth trochanter are unknown (Fig. 10). In dorsal view, the femur is dumbbell-shaped, and made up of the greater trochanter and the head. The femoral head is mediolaterally longer than that of the greater trochanter, while the greater trochanter is anteroposteriorly wider than the femoral head. There is no constriction at the base of the head, which is angled approximately 135° to longitudinal axis of the shaft (a feature that may be unnaturally elevated due to postmortem deformation). A groove between the head and the greater trochanter forms the site onto which the rotator muscles (i.e., puboischiofemoralis internus muscle) attached. Distally, both femoral condyles are swollen, expanded anteriorly, and approach each other to form a cylindrical canal (intercondylar groove) for the common tendon of iliotibialis and femorotibialis muscle. The prominent notch on the lateral margin of the posterior distal condyle (forming the lateral condylid; Forster, 1990) accommodated iliofibularis muscle as it passed by this region of the femur. In distal view, the lateral and medial condyles together form an H-shaped profile in which the and the medial condyle is wider than the lateral condyle.

Both the anterior portions of the distal condyles are swollen and close each other, a condition rare in hadrosaurids (details are in the diagnosis section). In some fully adult individuals of other hadrosaurid taxa, these anterior projections of the distal condyles are hypertrophied to bridge the extensor groove and fuse with each other along the midline to form an extensor tunnel (Brett-Surman, 1989). However, this character is seen only in adult individuals. In addition, the strong incision that accommodated iliofibularis muscle on the lateral condyle is prominent in non-hadrosaurid iguanodontians, such as *Iguanodon atherfieldensis* (Norman, 1986), while in hadrosaurids it is more obscure.

Tibia—The tibia is badly abraded and its shaft, like that of the femur, is thinned by weathering (Fig. 10); otherwise, the bone is nearly complete. The proximal and distal ends are strongly expanded and angled about 90 degrees to each other, so that the fibular facets are positioned laterally at the proximal end and anteriorly at the distal end. The cnemial crest, which partially surrounds the head of the fibula, makes up the anterior one-thirds of the head. The dorsal margin of this region likely served as the attachment of the terminal tendon of iliotibialis and femorotibialis muscle. The tibial condyles are angled about 120 degrees to the long axis of the cnemial crest. The medial condyle is almost twice as large as the lateral condyle and is strong curves laterally to surround the latter. Distally, the tibia has two expansions, the medial and, with the distal fibula, the lateral malleoli. The medial malleolus is protrudes only slightly,

while the lateral part of the distal tibia expands both laterally and distally, forming a flat articular surface for the fibula anteriorly. The complex of the tibia and fibula forms the lateral malleolus, which is not as strongly projecting as the medial malleolus, but more extends distally. The distal part of lateral malleolus forms the facet for the calcaneum, which is not preserved in the type of *Nipponosaurus*. The astragalar facet on the ventral margin of the medial malleolus is coarsely striated for attachment of articular cartilage. Posteriorly, the ridge is developed from three-quarters down the shaft and it continues onto the posterior ascending process of the astragalus.

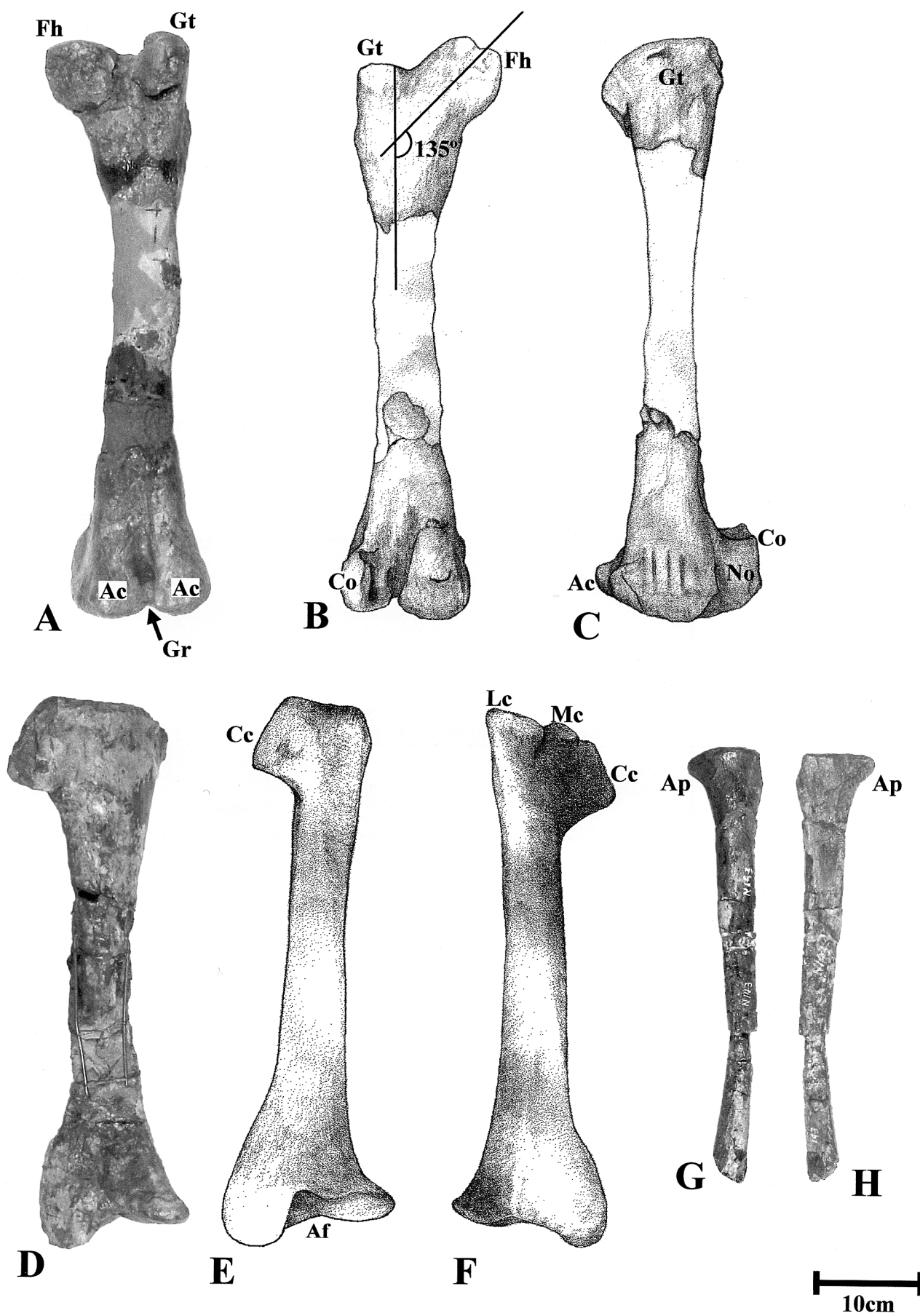
Fibula—The fibula is well preserved without abraded surfaces. The left fibula lacks the posterior portion of both proximal and distal ends, and the right fibula lacks the distal half of the shaft (Fig. 10). In dorsal view, the head of the fibula is semilunar, medially concave, and laterally convex, with a rugose surface indicating that this region was capped by cartilage in life. Laterally, the fibular head has a sharp, anteromedially-curving process. The medial concavity of the fibula fits into the lateral side of the lateral cotylus of the tibia and the anterior protrusion also fits into the concavity between the lateral cotylus and the cnemial crest. The shaft is twisted nearly 90° at midshaft, such that the lateral side faces anteriorly to articulate distally with the tibia. The medial surface is slightly concave, with longitudinal striations that extend from the fibular head. This concavity continues one-third down the shaft. Distally, the anterior surface of the fibula, which continues from the proximal lateral margin, is cylindrical. The posterior side, which articulates laterally with the distal fibular facet of the tibia, is smooth and slightly convex.

The anterior protrusion of the fibula is also seen as other lambeosaurines, but in juveniles of *H. stebingeri* (MOR 548) it is not as prominent as in *N. sachalinensis*. In contrast, it is more obscure and lobe-like in remaining hadrosaurids with the exception *Prosaurolophus maximus* (ROM 787).

Astragalus—The right astragalus, which is nearly completely except for the anterior ascending process and lateral margin, is the only tarsal element preserved in *N. sachalinensis* (Fig. 11). Dorsally, the tibial facet has two surfaces separated by a median ridge. Both surfaces are concave and rugose. The obliquely D-shaped medial surface (medial tibial facet) is more than twice the size of the lateral surface, and articulates with the ventral surface of the medial malleolus. The shallow lateral surface (lateral tibial facet) is nearly triangular and articulates with the ventromedial surface of the lateral malleolus. The calcaneal facet is broken; if one existed, it appears to be positioned lateral to the lateral tibial facet. Posteriorly, there is an elevation in the posterior margin of the medial tibial facet that has been termed the posterior ascending process by Godefroit et al. (1998). In ventral view, the surface is convex and smooth, and there is a constriction in the middle of this element.

Pes—All known hadrosaurids have three metatarsals, (that is, II, III and IV) and a phalangeal formula of 0-3-4-5-0. Virtually the entire pes of *Nipponosaurus* is well preserved, including all of the metatarsals of both pedes (Fig. 11). The third phalanx of digit IV (IV₃) of the left pes was described by Nagao (1938), but this element is now missing. Some of the metatarsals and phalanges were restored in plaster, probably based on the description of *Gryposaurus incurvimanus* (Parks, 1920).

Metatarsal II is the narrowest mediolaterally of the three metatarsals and almost semilunar shape in transverse section, including both the proximal and medial view. Proximally, the dorsal half is slightly concave to receive the convex articulation of the astragalus, while the plantar half is slightly convex. There are scars along the dorsoproximal margin, probably for attachment of tibialis anterior muscle. The shaft contacts metatarsal III along its length, curving medially to correspond to the transverse expansion of metatarsal III distally. The distal surface of



this and all other metatarsals is convex dorsoplantarly, making a hinge joint for the first phalanx.

Metatarsal III is the longest and most robust of the pedal elements. Proximally, the raindrop-shaped surface is also dorsally concave and plantarly convex as metatarsal II. The medial surface fits tightly against the lateral surface of the metatarsal II. Laterally, the surface is convex except for the distal ligamentous fossa, which may be for collateral ligaments at the metatarsophalangeal joint.

The laterally-curved metatarsal IV is dorsoplantarly compressed except for the proximal and distal end. The proximal surface is concave and D-shaped. Medially, the proximal part of the shaft is deeply concave where it fits against the lateral convexity of metatarsal III. Adjacent to this concavity, the shaft gradually becomes convex. One-third down the shaft, metatarsal IV curves laterally, separated from metatarsal III. At the distal expansion, the ligaments fossae are also developed bilaterally.

The proximal phalanx of pedal digit II (II-1) is dorsoplantarly the deepest of the three proximal phalanges, while the length of each of the other proximal phalanges is nearly same. The proximal articular facet is slightly concave. Distally, there are shallow both lateral and medial fossae, as in metatarsal III and IV, and a thin, semilunar projection is developed along the lower margin of the medial fossa. The distal trapezoidal articular facet expands downward and the interphalangeal joint is concave longitudinally. The second phalanx of digit II (II-2) is a short element, 40% the length of II-1. Proximally, the articular facet is trapezoidal. The shaft is concave at the middle length and slightly tapered distally. The distal articular facet makes also a hinge joint that faces downward. The third phalanx of digit II (II-3) is a hoof-shaped ungual, approximately like that of the manual hooves. Proximally, the articular facet is dorsoventrally concave and circular. Dorsally, the ungual is arrowhead-shaped and smooth all the way to its terminus. In lateral view, the dorsal margin is convex and concave ventrally.

The first phalanx of digit III (III-1) is the most robust of all of the pedal phalanges and its curved plantar margin is unlike that of the others. In proximal view, the ovoid articular facet is slightly concave. The shaft is symmetrical and spool-shaped in dorsal view. Distally, ligamentous fossae are also seen bilaterally on the shaft; the lateral fossa is deeper than the medial one. The distal articular surface is dorsoventrally convex and ovoid. The second phalanx of digit III (III-2) is as wide as III-1, but the former is 25% the length of the previous phalanx. The proximal facet is dorsoplantarly concave. Because the shaft does not taper, the distal articular facet is the same size as the proximal facet, and its surface is convex. The third phalanx of digit III (III-3) is the smallest in the element of the third digit. The morphology is similar to that of III-2 except for the shaft tapers. The fourth phalanx of digit III (III-4) is also a hoof-shaped ungual and therefore similar to II-3. However, it is more strongly curved downwardly and 50% wider than the latter phalanx. In addition, the lateral protrusions are proximally pendent.

The first phalanx of digit IV (IV-1) is almost a mirror image of II-1, but slightly wider and the ligamentous fossae more incipient than that of II-1. The second phalanx of digit IV (IV-2) is very similar to III-3, except that it is narrower and the concavity of the proximal articular facet is deeper. The third phalanx of digit IV (IV-3), a newly prepared element, is identical

with IV-2, although in size it is smaller. The ungual of digit IV (IV-5) is identical to II-3 except that IV-5 is slightly smaller and dorsoventrally shorter than II-3.

All of these metatarsals and pedal phalanges are very typical of the hadrosaurid pes. Although very well preserved, little is diagnostic in the pes of *Nipponosaurus*. However, it should be mentioned that IV-1 of non-lambeosaurine hadrosaurids and *Bactrosaurus johnsoni* appear to be much shorter than II-1, differing from the condition of *Nipponosaurus* and other lambeosaurines. This character is also not seen in either species of *Iguanodon* and *Ouranosaurus nigeriensis* among non-hadrosaurid iguanodontians. In addition, the outer projection of II-1 and IV-1 is not seen in *Edmontosaurus edmontoni* (ROM 867) and non-hadrosaurid iguanodontians.

PHYLOGENETIC ANALYSIS

Ingroup Selection

Nipponosaurus sachalinensis is clearly a member of Lambeosaurinae, based on characters cited in the description provided above (i.e., the form of the premaxilla). At present, 15 lambeosaurine species are known, although not necessarily from all of their skeletal elements. As a result, we have chosen seven lambeosaurines that are known at least as well as *Nipponosaurus*. These include *Lambeosaurus lambei*, *L. magnicristatus*, *Corythosaurus casuarius*, *Nipponosaurus sachalinensis*, *Hypacrosaurus altispinus*, *H. stebingeri*, and *Parasaurolophus* (a combination of *P. walkeri* and *P. cyrtocristatus*). Character information on *Charonosaurus jiyinensis* is limited (Godefroit et al., 2000), so this species has also been excluded.

Outgroup Selection

The systematic position of a number of newly-described ornithomimids appear to fall within a so far poorly resolved nexus of basal hadrosaurids and non-hadrosaurid iguanodontians. We selected and forced the following iguanodontian taxa, all of which are reasonably well preserved and whose phylogenetic positions have been described by other authors (Seren, 1986; Weishampel et al., 1993; Head, 1998, 2001) to be outgroups for our analysis. These are, in their hierarchical arrangement, (*Camptosaurus dispar* ((*Iguanodon bernissartensis*, *I. atherfieldensis*), (*Ouranosaurus*, (*Altirhinus*, (*Bactrosaurus*, Ingroup)))). For our examination of the systematic position of *Nipponosaurus*, the species or generic topology of the hadrosaurine clade is excluded and the latter is considered as a whole.

Characters

Our phylogenetic analysis is based on 79 osteological and dental characters distributed in ingroup and outgroup taxa (see Appendix II), compiled from a variety of sources, among them original observations on specimens, literature sources (Gilmore, 1909, 1924; Brown, 1913a, 1913b, 1914; Lambe, 1920; Parks, 1922, 1923; Lull and Wright, 1942; Ostrom, 1961, 1963, Taquet, 1976; Dodson, 1980; Norman, 1980, 1984, 1986, 1998; Sereno, 1984, 1986; Brett-Surman, 1989; Weishampel, 1984; Weishampel and Horner, 1986; Weishampel et al., 1993; Horner and Currie, 1994; Sullivan and Williamson, 1998; Godefroit et al., 1998; Head, 1999, 2001), and personal communications

←

FIGURE 10. *Nipponosaurus sachalinensis*. **A**, left femur, anterior view. **B**, posterior view, femoral head is angled approximately 135° to longitudinal axis of the femoral shaft. **C**, lateral view. **D**, right tibia, anterior view. **E**, schematic of **D**; **F**, posterior view. **G**, left fibula, lateral view; **H**, medial view. **Abbreviations:** **Ac**, anterior distal condyles of femur; **Af**, facet for the astragalus; **Ap**, anterior process of fibula (articulating with lateral surface of cnemial crest); **Cc**, cnemial crest; **Co**, condylid; **Fh**, femur head; **Gr**, intercondylar groove for the crural extensor musculature; **Gt**, greater trochanter; **Fh**, femoral head; **Lc**, lateral condyle of tibia; **Mc**, medial condyle of tibia; **No**, the notch for M. iliofibularis.

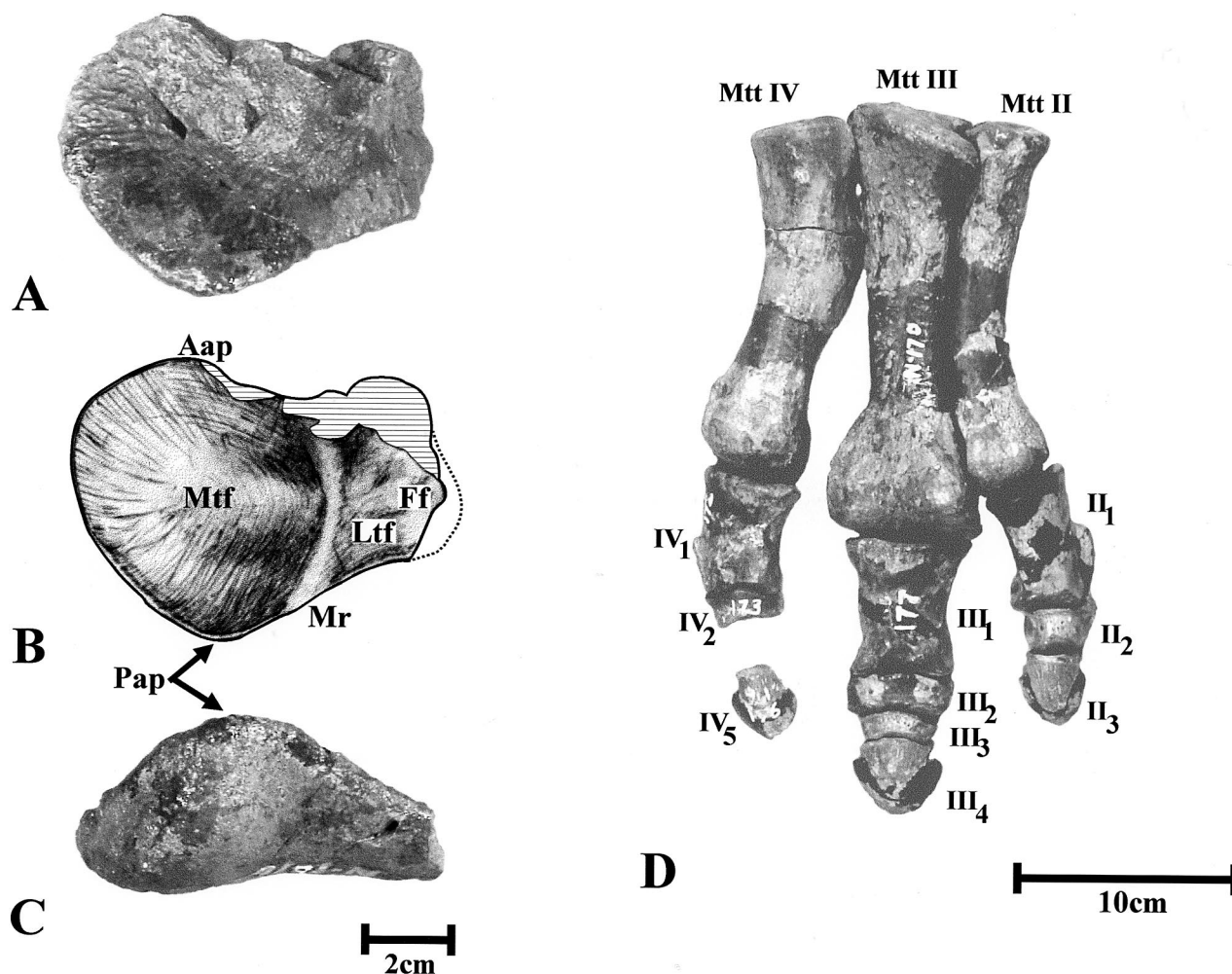


FIGURE 11. *Nipponosaurus sachalinensis*. **A**, right astragalus, dorsal view. **B**, schematic of **A**; **C**, same, posterior view. **D**, right pes; Roman numerals indicate each digit and Arabic numerals indicate each phalanx. **Abbreviations**: Aap, anterior ascending process; Aaf, astragalar facet; Ff, fibular facet; Ltf, lateral tibial facet; Mr, medial ridge of astragalus; Mtt, medial tibial facet; Mtt, metatarsal; Pap, posterior ascending process.

with colleagues. A number of characters, particularly from the literature, whose definitions were not clear have been revised in order to better discriminate the features under consideration and the polarity assigned to each.

Analysis

Tree topologies were generated using the branch-and-bound option of Phylogenetic Analysis Using Parsimony (PAUP ver. 4b10; Swofford, 2002), resulting in two most parsimonious trees (105 steps with CI = 0.82, RI = 0.9345, and RC = 0.76; Fig. 12). In both cases, *Nipponosaurus* was identified as a member of Lambeosaurinae as the sister taxon to *Hypacrosaurus altispinus*.

DISCUSSION

Systematic Position of *Nipponosaurus*

Although the type specimen of *N. sachalinensis* includes poorly preserved cranial remains, several characters of this taxon were identified as synapomorphies of Lambeosaurinae: Nasal excluded from external naris (character 6; see Appendix I), a maxillary shelf (character 13), and elongated dentary tooth (character 49).

Within Lambeosaurinae, a large boot at the distal ischium

(character 73) also appears to have phylogenetic significance. Young (1958) had previously noted that the ischial expansion of *Nipponosaurus* was not well developed, but as far as can be observed in other lambeosaurines, the ischial expansion of *Nipponosaurus* is quite the opposite: it is one of the largest among lambeosaurines. In addition, the ischial expansion of *Nipponosaurus* is distinctly boot-shaped, similar to *Hypacrosaurus altispinus* and *Parasaurolophus cyrtocristatus* (Brett-Surman, 1989). In addition, *Nipponosaurus* has a jugal with an angular ventral flange (character 21), which is seen only in *Hypacrosaurus altispinus*. Consequently, *Nipponosaurus* appears to form a clade with *H. altispinus*, which together are positioned as the sister-group to *Corythosaurus*, and *Lambeosaurus*. Because *H. stebingeri* does not have a sibling relationship with *H. altispinus* in our analysis, *Hypacrosaurus* itself may not be monophyletic. Of the features analyzed here, neural spines that are four times longer than the height of the centrum (character 51) is the only synapomorphy shared by both species *Hypacrosaurus*. *Nipponosaurus* has shorter neural spines, but this character thought to only adapt to fully grown species (Neural spines of subadult *H. stebingeri* is as long as those of *Nipponosaurus*). While two synapomorphies (characters 21, 73) are shared by *H. altispinus* and *Nipponosaurus* to the exclusion of *H. stebingeri*. Consequently, the two species of *Hypacrosau-*

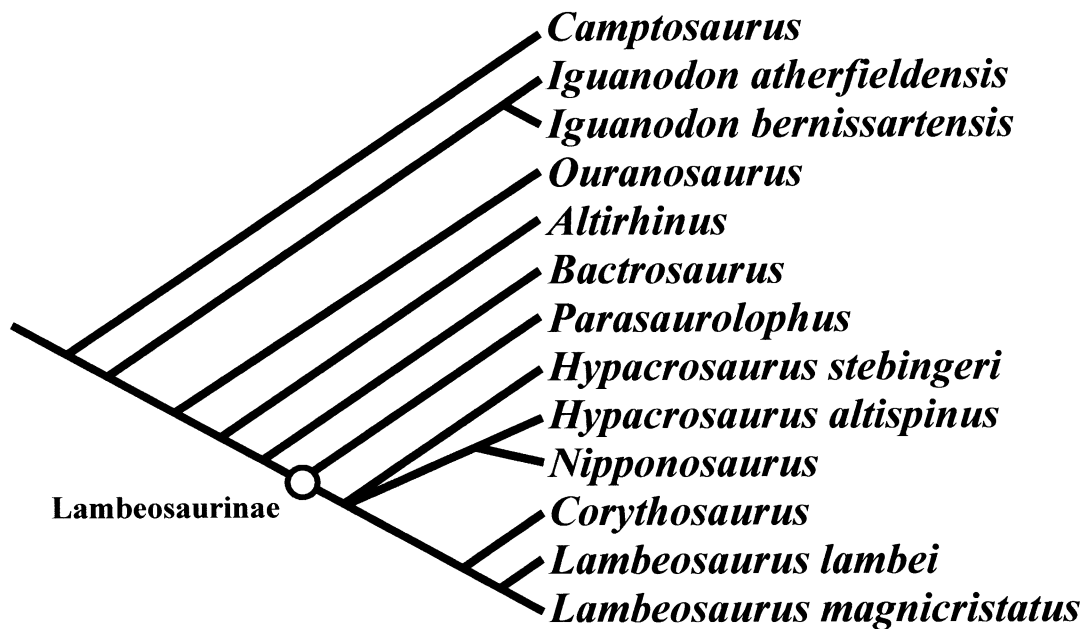


FIGURE 12. Phylogenetic hypothesis of lambeosaurines. A strict consensus of the two most parsimonious trees (TL = 97, CI = 0.8144, RI = 0.9350, RC = 0.7615) obtained from a matrix containing 78 characters for six outgroup and seven ingroup taxa. In this analysis, *Hypacrosaurus stebingeri* could be the sister taxon of a *H. altispinus* and *Nipponosaurus* clade or a *Corythosaurus* and *Lambeosaurus* clade.

rus share fewer synapomorphies than do *H. altispinus* and *Nipponosaurus*. Instead, the opposite is true—*Nipponosaurus* appears to be more closely related to *H. altispinus* than either is to *H. stebingeri*. Even though *N. sachalinensis* shares several apomorphies with *H. altispinus*, it lacks several critical cranial features that are relevant to this relationship, especially because nothing of the crest, should it have existed, is preserved. At present, therefore, we could not reject nor support the possibility that *Nipponosaurus* is congeneric with *Hypacrosaurus*. In addition, the systematic position of *H. stebingeri* is undecided (Fig. 12); the genus *Hypacrosaurus* did not justify monophyly. For this reason, it seems best to retain the genus *Nipponosaurus* for the material from Sakhalin Island.

Ontogenetic Stage of *Nipponosaurus*

The sacral vertebrae in all hadrosaurid specimens thought to be subadult (e.g., *L. lambei*, AMNH 5340) are completely co-ossified and the same is true of *Nipponosaurus*, which is roughly equivalent in size. Therefore, this feature, which Nagao (1936) used to suggest that the type specimen of *Nipponosaurus* is adult, is not appropriate. Indeed, following Rozhdestvensky (1964), almost all authors have regarded the type specimen of *Nipponosaurus* as a juvenile. However, all of these discussions have been based solely on only its size and Nagao's (1936) original suggestion that "*Nipponosaurus* is similar to *Cheneosaurus* and *Tetragonosaurus*." In this study, the presence of open neurocentral sutures, a feature often used to indicate skeletal maturity (Horner and Currie, 1994), strongly suggests that the type specimen of *Nipponosaurus* is a subadult. Our analysis indicate that the presence of only two teeth per tooth position in the type specimen of *Nipponosaurus* is not a primitive retention. Instead, this feature points to its subadult state and is in keeping with other juvenile or subadult hadrosaur specimens, which also have two teeth per position (e.g., Hall, 1993).

Consequently, six characters indicate that the type specimen of *Nipponosaurus* is subadult: (1) open neurocentral sutures in all vertebrae, (2) only two teeth per tooth position in the dentary (character 45), (3) small number of tooth positions, (4) incipient

olecranon, (5) ischial boot with a rounded tip, and (6) prominent epiphyseal expansions of metatarsals.

Diagnosis of *Nipponosaurus*

Because of its poor state of preservation, Nagao (1936) did not properly diagnose *Nipponosaurus*. However, this taxon can now be diagnosed on the following characters. Compared to other hadrosaurids, *Nipponosaurus* uniquely has a robust coronoid process of the surangular and a dorsal reflection of the first phalanx of manual digit IV. A similar robust coronoid process of the surangular is also seen in outgroup taxa such as *Iguanodon*. In the present analysis, this character cannot be the retention of a plesiomorphic at the level of *Nipponosaurus*, but instead constitutes as autapomorphic reversal at its terminal node. The swelling of the anterior portion of the distal condyles of the femur may also be diagnostic for the same reason (seen in *Tsintaosaurus* [Young, 1958] and *Gilmoresaurus* [Gilmore, 1933], but never in North American hadrosaurids). In addition, although poorly preserved, the large lacrimal wedged into the premaxilla-maxilla articulation, may be another autapomorphy of *Nipponosaurus*.

Rozhdestvensky (1977) thought that *Nipponosaurus* had a congeneric relationship with *Mandschurosaurus amurensis*, a species that most researchers have regarded as a nomen dubium. Rozhdestvensky's referral is doubtful because the type of *M. amurensis* (Riabinin, 1930) is probably a fully-grown individual, there is no swelling of the anterior region of the distal femoral condyles, and the pathway for the extensor tendons through this region is open. In contrast, anteriorly swollen distal condyles contact each other and thus make a tubular passage for the extensor tendons of the knee in *Nipponosaurus*.

Although *Nipponosaurus* is still one of the most poorly known lambeosaurine dinosaurs, it was still possible to identify autapomorphies for it and to identify synapomorphies that indicate it formed a clade with *Hypacrosaurus altispinus*. We, therefore, thought it was a hasty decision that Norman and Sues (2000) regarded *Nipponosaurus* as nomen dubium. Consequent-

ly, *Nipponosaurus* can no longer be considered an “enigmatic dinosaur.”

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APPENDIX I

Characters Used in the Phylogenetic Analyses.

Skull

1. Lateral expansion of the rostrum (Weishampel et al., 1993). The expansion is nearly as wide as that of the skull at the orbit. Absent (0), present (1).
2. Configuration of oral margin in the premaxilla (Weishampel et al., 1993). Coarsely crenulated (0), undulatory (1), denticulate (2).
3. Premaxillary foramina (Horner, 1983; Weishampel et al., 1993) in the ventral surface of the premaxilla. Present (0), absent (1).
4. Elongation of pmx I over prefrontal. Pmx I ends anterior to the prefrontal (0), over the prefrontal (1).

APPENDIX 2

| Taxon | Character number | | | | | | | | | | | | | |
|------------------------------------|------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|------------|-------|-------|
| | 5 | 10 | 15 | 20 | 25 | 30 | 35 | 40 | 45 | 50 | 55 | 60 | 65 | 70 |
| <i>Camptosaurus</i> | 00000 | 00000 | 00000 | 00000 | 00000 | 00100 | 10010 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 |
| <i>Iguanodon atherfieldensis</i> | 00000 | 00000 | 00000 | 10000 | 000?0 | 00000 | 10000 | 00010 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 |
| <i>Iguanodon bernissartensis</i> | 00000 | 00000 | 00000 | 10000 | 00000 | 00000 | 10010 | 00010 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 |
| <i>Ouranosaurus</i> | 10000 | 00000 | 00000 | 00000 | 01000 | 00010 | 10011 | 10000 | 00000 | 00000 | 10001 | 00000 | 00000 | 00011 |
| <i>Altirhinus</i> | 11000 | 0?000 | 00000 | 00000 | 01000 | 000?0 | 100?0 | 11110 | 00000 | 00000 | ?1101 | 10000 | 01100 | 111?0 |
| <i>Bacrosaurus</i> | 10100 | 00000 | 00001 | 10000 | 01110 | 00111 | 10011 | 00111 | 0?111 | 01100 | 00110 | 00100 | 1?000 | 00111 |
| <i>Parasaurolophus</i> | 11100 | 11100 | 00111 | 10111 | 11111 | 11111 | 01100 | 11121 | 11111 | 01111 | 11111 | 1111(0/1)* | 11111 | 11111 |
| <i>Corythosaurus</i> | 10111 | 11101 | 10111 | 10111 | 01111 | 11111 | 01100 | 11121 | 11111 | 11111 | 01111 | 11111 | 11111 | 11011 |
| <i>Nipponosaurus</i> | ????? | 11??? | ????? | 1???? | 111?? | ??011 | ??000 | ?0121 | 11110 | ?1111 | ?1111 | 11??? | 11111 | ?1111 |
| <i>Hypacrosaurus altispinus</i> | 10110 | 11101 | 10111 | 10111 | 01111 | 11111 | 01100 | 11121 | 11111 | 11111 | 11111 | 11111 | 11111 | 11111 |
| <i>Hypacrosaurus stebingeri</i> | 10110 | 11101 | 10111 | 10111 | 01111 | 11111 | 01100 | 11121 | 11111 | 11111 | 11111 | 11111 | 11111 | 11011 |
| <i>Lambeosaurus lambei</i> | 10111 | 11111 | 01111 | 11111 | 01111 | 11111 | 01100 | 11121 | 11111 | 11111 | 01111 | 11111 | 11111 | 11011 |
| <i>Lambeosaurus magnicristatus</i> | 10111 | 11111 | 11111 | 11111 | 01111 | ?111? | 01100 | 11121 | 11111 | 11111 | 01111 | 11111 | 1111? | 101?1 |

*Indicates missing data.

*Indicates polymorphism: *Parasaurolophus cyrtocristatus* (FMNH P27393) shows different state in character 60 from *P. walkeri*.

5. Presence of fontanelles between pmx I and nasal. Absent (0), present (1).
6. Nasal excluded from external naris (Weishampel et al., 1993). Absent (0), present (1).
7. Circumnarial depression extending onto the nasal (Hopson, 1975). Absent (0), covered by premaxilla (1).
8. Modified nasal cavity, the *cavum nasi proprium* is positioned above the orbit and skull roof (Weishampel et al., 1993). Absent (0), present (1).
9. Diminished nasal in hollow crest (Weishampel et al., 1993). More than one third of hollow crest (0), diminished and enclosed by pmx I (1).
10. Enlargement of the common median chamber in hollow crest (Weishampel et al., 1993). Absent (0), present (1).
11. Fan-shaped hollow crest (Forster, pers. comm.). Absent (0), present (1).
12. Hollow crest inclined anteriorly (Dodson, 1975). Absent (0), present (1).
13. Having maxillary shelf (Heaton, 1972). Absent and having maxillary process (0), present (1).
14. Large foramen on the dorsal margin of maxilla along the premaxillary articular surface (Weishampel et al., 1993, Godefroit et al., 1998). Absent (0), present (1).
15. Enlargement of dorsal process of maxilla (Weishampel et al., 1993). No enlargement (0), enlargement (1) and enlargement and elevation (2).
16. Lacrimal-nasal contact. Present (0), absent (1).
17. Prefrontal-nasal contact. Present (0), absent (1).
18. Laterally raised prefrontal. Absent (0), present (1).
19. Free palpebral (Coombs, 1972). Present (0), absent (1).
20. Dorsoventral expansion of the anterior end of the jugal (Weishampel et al., 1993). Absent (0), present (1).
21. Ventral flange of jugal. Rounded (0), angular (1).
22. Elongation of caudal process of jugal. The width from the lowest point of the ventral flange to the most caudal point is more than 30% for jugal width. Less than 30% (0), more than 30% (1).
23. Articulation of jugal and ectopterygoid (Head, 1999). Present (0), absent (1).
24. Elongation of the postorbital process of the jugal (Weishampel, 1984). The proportion of postorbital process for jugal length, which extracts the length of caudal process, is less than 60% (0). More than 60% (1).
25. Shape of frontals in the adult (Ostrom, 1961). Flat (0), domed-shape (1).
26. Shortened and incurved anterior frontal margin by nasal scarf joint. Absent (0), present (1).
27. Excluded frontal at the orbital rim (Weishampel and Horner, 1990). Absent (0), present (1).
28. Paraquadratic foramen (Weishampel et al., 1993). Present (0), absent (1).
29. Parietal length (Weishampel et al., 1993). The length at middle is more than 60% of infraorbital length (0), less than 50% (1).
30. Pyramidal with ventrally broad and horizontal supraoccipital (Forster, pers. comm.). Absent, subround to rectangular (0), present (1).
31. Large buttress on the posterior aspect of the upper shaft of the quadrate (Weishampel, 1984). Present (0), absent (1).
32. Narrow mandibular condyle of quadrate (Weishampel et al., 1993). Absent (0), present (1).
33. Medial rami of the paired squamosals in contact (Sereno, 1986). Absent (0), present (1).
34. Posterior border of the skull in dorsal view. Straight (0), rounded indentation (1), angular indentation (2).
35. Slight transverse narrowing of the cranium from the postorbital region posteriorly in dorsal view (Sereno, 1986). Absent (0), present (1).

Mandible

36. Diastema in mandible (Weishampel et al., 1993). Absent (0), present (1).
37. Downward curving at the middle of dentition in dentary (Weishampel and Horner, 1986). Absent (0), present (1).
38. Shrouding of the distal dentition by the coronoid process. The dentary dentition ends immediately prior to the elevation of the coronoid process (0). The distal extent of the dentary dentition is laterally shrouded by the anterior region of the coronoid process (1).

39. Anterior edge of coronoid process. Inclined posteriorly (0), approximately perpendicular (1), inclined anteriorly (2).
40. Absence of surangular foramen (Weishampel et al., 1993). Absent (0), present (1).
41. Backward elongation retroarticular process. Absent (0), present (1).
42. Position of the angular on the mandible (Weishampel et al., 1993). Exposed laterally (0), not exposed laterally (1).

Teeth

43. Maxillary teeth (Weishampel et al., 1993). Large (0), diminished in size (1).
44. Dentary teeth (Weishampel et al., 1993). Large (0), diminished in size (1).
45. Number of teeth per dentary tooth family in adult (Weishampel and Horner, 1990). Two (0), more than two teeth (1).
46. The number of tooth positions (Weishampel et al., 1993). Less than 30 maxillary and 29 dentary tooth positions (0), more than 30 maxillary and 29 dentary tooth positions (1).
47. Lanceolate-shaped dentary teeth. Diamond-shaped (0), lanceolate-shaped (1).
48. Primary carina on dentary teeth. Two or more (0), one (1).
49. Elongation of dental teeth (Forster, pers. comm.). The height/width ratio is less than 2.5 (0), more than 2.8 (1).
50. Tooth position. Perpendicular (0), distally inclined (1).

Axial Skeleton

51. Height of neural spines (Weishampel et al., 1993). Less four times than the height of vertebrate column (0), over four times (1).
52. Number of sacrum vertebrae (Weishampel and Horner, 1990). Seven or fewer (0), eight or more sacra (1).

Appendicular Skeleton

53. Constriction at the base of scapula blade. Absent (0), present (1).
54. Direction of pseudoacromial ridge of scapular. Dorsal margin (0), laterally (1).
55. Strong protuberance (i.e., insertion of *M. biceps brachii*) of dorsal margin of coracoid. Absent (0), present (1).
56. The ratio of length/width of coracoid. Approximately 1.0 (0), more than 1.5 (1).
57. Loss or reduction of carpus (Weishampel and Horner, 1990). Co-ossified (0), two small bones or completely lost (1).
58. Position of deltopectoral crest on humerus (Weishampel et al., 1993). Less than a third down the shaft (0), extend to near midshaft (1).
59. Form of deltopectoral crest (Weishampel et al., 1993). Curved (0), angular (1).
60. Ratio of radius to humeral length (Brown, 1913b). Less than 1.0 (0), greater than 1.0 (1).
61. Large, lobe-like medial ridge on ulna. Absent (0), present (1).
62. Position of metacarpals II to IV (Sereno, 1986). Diverge (0), closely appressed (1).
63. Ratio of metacarpal length to manus length. Equal or less than half the length of manus (0), greater than half the length of manus (1).
64. Manual digit I (Sereno, 1986). Present (0), absent (1).
65. Triangular shape of phalanx 2 of digit III in manus. Absent (0), present (1).
66. Shorten the phalanx 1 of manual digit III (the length of digit is digit II is same or longer than that of digit III). Absent (0), present (1).
67. Conical digit I in manus (Sereno, 1986). Absent (0), present (1).
68. Shape of unguals on manual digits II and III (Sereno, 1986). Claw-like (0), hoof-shaped, laterally projected (1).
69. Long and down curved preacetabular process. Absent (0), present (more than 30°) (1).
70. Sigmoid dorsal margin of ilium; curved dorsally (0), undulated at the "antitrochanter" (1).
71. "Antitrochanter" of the ilium (Brett-Surman, 1989). Absent or incipient (0), present (1).
72. Elongated and parallelized postacetabular process at ilium. Absent (0), present (1).
73. Boot-shaped of ischial expansion. Absent (0), present (1).
74. Straighten femur in lateral view. Absent (0), present (1).
75. Expansion of anterior condyles of femur in lateral view. Absent (0), present (1).
76. Absent expansion of posterior margin of fibular head. Expanded (0), almost straight (1).
77. Pedal digit I. Present (0), absent (1).
78. Shape of unguals in pedal digits II-IV. Claw-shaped (0), hoof-shaped (1).