

HADROSAURS OF KAZAKHSTAN *

The duck-billed dinosaurs, or hadrosaurs, are one of the most plentiful of the fossilized dinosaurs, although their dissemination was restricted to only the Late Cretaceous epoch. Hadrosaur remains are particularly well known in North America, and numerous deposits have recently been discovered in Asia, including Kazakhstan.

All of the North American hadrosaurs are, however, species with long-running specializations that attest to the rather late evolutionary stages of this group. The most ancient, and at the same time most plentiful, North American hadrosaur remains were found in the Belly River Formation which has been dated to the Campanian and Upper Santonian. From this time, an apparent “rift” in the evolution of hadrosaurs began. Their remains are numerous in subsequent deposits (the Maastrichtian Edmonton Formation), remaining until only the end of the Cretaceous (the Lance Formation), and the history of hadrosaurs can be traced rather well right up to the time of their extinction.

Most of the Asiatic discoveries are also Senonian, and it has only recently been revealed (Rozhdestvenskiy, 1966) that *Bactrosaurus johnstoni* from Inner Mongolia (Gilmore, 1933) is a primitive form that can be dated to the Cenomanian. Along with this, *Jaxartosaurus aralensis*¹ from southern Kazakhstan (Rjabinin, 1939) is also Cenomanian–Turonian, but is in fact a younger species. Thus, there is a significant gap in the initial stages of hadrosaur history.

Recent discoveries in Kazakhstan (Rozhdestvenskiy, 1964a) belonging to new species of hadrosaur make it possible to fill this gap by establishing phylogenetic links between the American and Asian hadrosaurs. The first of these discoveries, described here under the name *Aralosaurus tuberiferus*, was observed in central Kazakhstan in 1957 (the Shakh-Shakh deposit) and the second—*Procheneosaurus convincens*—in southern Kazakhstan in 1961 (the Shakh-Shakh deposit). These new discoveries were dated to the Turonian–Santonian period.

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Thus, at present the Kazakhstan hadrosaurs represent three species that are assigned to three different genera. This work is devoted to the results obtained from studying these hadrosaurs.

Although Rjabinin (1939) described the skull and other bones of *Jaxartosaurus aralensis*, his description was too brief to allow this species and its phylogenetic relationships with other lambeosaurs to be judged with sufficient clarity. Moreover, there are some inaccuracies in the descriptions of the bones. Rjabinin drew conclusions on the characteristics (diagnosis) of the genus and species concerning the shape of the lower mandible, the number of teeth, and the shape of the proximal ends of the ischium and humerus, but did not include skull data, which are the most essential for dinosaur diagnoses. It must also be noted that the skull of *J. aralensis* (specimen 1/5009) is uniquely preserved, with distinct sutures between the bones, openings for the passages of nerves and blood vessels, and other distinct details as to which there are many uncertainties even today. The results of a new study made it possible to introduce a number of refinements to the hadrosaur skull in general, including the unique articulation of the braincase with the skull roof that was observed in *Jaxartosaurus* (and in *Aralosaurus* and other hadrosaurs). This articulation is probably an amortized structure that protected the braincase. The primitive features of *J. aralensis* are extremely interesting for understanding hadrosaur evolution and for comparing this lambeosaur with the forms similar to it. They also compel us to reexamine the question of its geological age. All of these circumstances stimulate a thorough description of the *J. aralensis* skull and a diagnosis that is based mainly on this skull, because the bones of the postcranial skeleton in the collection are fragmentary and do not introduce any significant information.

Large collections of hadrosaur material contained at the Palaeontological Institute of the Academy of Sciences of the USSR have for two decades helped in no small measure the study of *J. aralensis* (and other hadrosaur material). Monographs concerning the morphology of hadrosaurs in general and their skull in particular (Lull, Wright, 1942; Romer, 1956; Langston, 1960; Ostrom, 1961) have also advanced this study.

The Shakh-Shakh discovery (a skull in base bedding along with material supplemental to it and the postcranial skeleton in talus) proved to belong to a new genus and species related to the hadrosaurs of Central Asia and North America. The skull of *Aralosaurus tuberiferus* is exceptionally well preserved with a rare occurrence of an open brain cavity, which promoted a

¹ This species is a unique hadrosaur from Kazakhstan (Rjabinin, 1939). *Bactrosaurus prynadai* which was described with it is merely a synonym (Rozhdestvenskiy, 1964b).

detailed study of the braincase, usually not having a dissectable preparation (due to its complexity) in the skulls of hadrosaurs. A fontanelle similar to that recently described (Langston, 1960) as a unique phenomenon among hadrosaurs was observed between the nasals and frontals in the skull of *A. tuberiferus*. The functional significance of this fontanelle is probably rather important, although debatable, but the accumulation of data may in time allow the essence of the fontanelle that remained unknown for a decade to be explained.

Besides its paleontological interest, *A. tuberiferus* allows the geological age of the Kazakhstan bone-bearing deposits to be refined. This is even more important in that all of the earlier dinosaur discoveries in Kazakhstan were re-deposited material that was discovered in a secondary deposit (Efrimov, 1944).

The hadrosaur skeleton that was exhumed at Tashkent (Belen'kiy, Rozhdestvenskiy, 1963; Rozhdestvenskiy, 1964a) is for the moment the most complete discovery of this dinosaur not only in Kazakhstan, but in our country as a whole. The skeleton belongs to a new species of helmeted hadrosaur of the genus *Procheneosaurus* from the Senonian of North America. Of the North American species there is only one—*P. praeceps*—that is known from a complete skeleton. Thus, in addition to being scientifically significant and an explanation of hadrosaur family history, this discovery is a rare museum specimen.

This discovery holds significant stratigraphic value because it was observed in a base deposit immediately above the so-called “dinosaur horizon”. This makes it possible to first revise the previously held opinion (Efrimov, 1944) regarding the re-deposition of the “dinosaur horizon” in the Paleogene, and second to reexamine the question of the geological age of the Upper Cretaceous bone-bearing layers in the Tashkent region from a comparison with the related American species.

Similar to *Jaxartosaurus*, a new diagnosis was given for *Procheneosaurus*. This diagnosis had a number of refinements and additions to the previous diagnosis that was made primarily from the skull material, because the more or less complete skeleton of *P. praeceps* does not allow sufficiently reliable differentiation of the generic and specific features. There is only a brief characteristic of this skeleton in the literature (Lull, Wright, 1942) and no detailed description or drawings. An incomplete postcranial skeleton from the Two Medicine Formation of Montana, ascribed to *P. erectofrons*, belongs to a small specimen, apparently a young animal (as the skull that was found with it). This material has not been processed, and Lull and Wright (1942)

generally doubted the correctness of assigning it to *P. erectofrons* because two other species—*P. praeceps* and *P. cranibrevis*—came from the same Belly River Formation (corresponding to the Two Medicine Formation).

Genus *Jaxartosaurus* Rjabinin, 1939

Type (unique) species: *J. aralensis* Rjabinin, 1939; Upper Cretaceous (Coniacian–Santonian) of southern Kazakhstan.

Diagnosis. Medium-sized hadrosaur. The skull is wide and low with a helmet-like crest in which the frontals and prefrontals do not participate. The frontals are large and inflated and they are isolated from the edge of the orbit. The supratemporal fenestrae are small, and the supratemporal arches are straight and parallel to the sagittal line of the skull.

Comparison. Besides *Jaxartosaurus*, the subfamily Lambeosaurinae numbers eight genera¹ at present (Rozhdestvenskiy, 1964b). Of these *Jaxartosaurus* is apparently the farthest removed from the cheneosaurs (*Procheneosaurus*, *Cheneosaurus*, and *Nipponosaurus*), having a narrow but higher skull in the occipital region and an underdeveloped crest that looks like a small rise in the prefrontal area of the skull. On the other hand, *Jaxartosaurus* is no less removed from *Parasaurolophus*, which has a huge long crest that extends far beyond the occipital edge of the skull and is formed from below by the nasals that are displaced from the roof of the skull, and the frontals that make up the upper edge of the orbit and rise upward from it.

Jaxartosaurus is more similar to the other four genera—*Lambeosaurus*, *Corythosaurus*, *Hypacrosaurus*, and *Tanius*—but is notably different. Thus, the frontals and prefrontals of *Lambeosaurus* participate with the nasals and premaxillae to form the crest, whereas in *Jaxartosaurus* the crest may be formed by only the premaxillae and nasals. *Corythosaurus* and *Hypacrosaurus* are the most similar to *Jaxartosaurus*. *Corythosaurus* is characterized by a skull crest that is more circular and laterally compressed. In some species this crest overhangs the occiput, making contact with the squamosal. *Hypacrosaurus* (with one species) has a dome-shaped crest that is less laterally compressed, does not overhang the occiput, and does not make contact with the squamosal. Judging by the support areas on the parietal and squamosal, the crest in

Jaxartosaurus is probably most similar in shape to that of *Corythosaurus*, differing only by the slight lateral compression as in *Hypacrosaurus* and thereby possibly occupying an intermediate position between the crests of these two lambeosaurs. *Jaxartosaurus* differs from both of these by its rather large frontals, the exterior surface of which reaches the anterior third of the orbit. According to the shape of the bones in the roof of the skull (especially the frontals), *Jaxartosaurus* is very similar to the genus *Tanius*, also known as *Tsintaosaurus* Young, 1958 (Rozhdestvenskiy, 1964b), but differs from it in the subquadrate supratemporal fenestrae² and more massive skull crest (judging by its support area). The latter was destroyed for the most part in the specimens examined by Young (1958), who reckoned this crest to be similar to that of the *Saurolophus* and assigned *Tsintaosaurus* to the subfamily Saurolophinae. Finally, *Jaxartosaurus* differs from all four of the genera similar to it by its straight supratemporal arches that are parallel to the sagittal line of the skull.

Jaxartosaurus aralensis Rjabinin, 1939
= (*Bactrosaurus prynadai* Rjabinin, 1939) (Figs. 1–6)

Lectotype³. The Museum of the Central Science and Research Institute for Geological Exploration (Leningrad), No. 1/5009: incomplete skull with no maxillofacial region; Upper Cretaceous (Coniacian–Santonian) of southern Kazakhstan (Kyrk-Kuduk region near the Aym-Tau range).

Diagnosis. The skull narrows drastically behind the orbits and has a short, underdeveloped sagittal crest that is formed by the temporals. The frontals are wedged between the nasals and removed from the edge of the orbit, being isolated from it by the broad band of the prefrontals and the postorbitals. The parietals enter between the frontals with the process that expands anteriorly. The skull is 20% wider in the postorbital region than in the occipital region. The width of the

¹ Gilmore (1933) had earlier assigned *Bactrosaurus* to this subfamily, however it must be examined as a member of the subfamily Hadrosaurinae. The differences between this genus and *Jaxartosaurus* are significant and were noted by Rjabinin (1939).

² The helmet-like shape of the supratemporal fenestrae in the image of *Tsintaosaurus spinorhinus* (Young, 1958) is most likely the result of a pathological deformation that occurred during the animal's lifetime, whereas in *Tanius sinensis* (Wiman, 1929), which is similar in all other features with the first species, the supratemporal fenestrae are ellipsoidal, which is typical for hadrosaurs.

³ Rjabinin indicated material (including portions of two skulls) belonging to several individuals as a "type"; specimen 1/6009—the most valuable—was the first to be described and imaged and must therefore be considered the lectotype.

occiput (at the level of the paroccipital process) is greater than its height from the lower point of the occipital foramen by 250%. The orbits are wide in the upper region, the infratemporal fenestrae are narrow and slit-like, and they are almost 25% as wide as the orbits. The supratemporal fenestrae are rhomboidal and more than 150% as long as they are wide. The lower jaw has 34–35 dental rows.

Material. Collection No. 5009—an incomplete skull, a fragment of another skull, and fragments of the postcranial skeleton, bones of several specimens that came from the same deposit and horizon as the holotype.

Skull Roof (Figs. 1, 2)

Rjabinin (1939) noted the character of the exterior sutures of the bones in the skull roof, stressing the surface profile of the frontals and temporals. Overall, his description of the bones was very brief and it can be augmented.

The premaxillae, maxillae, and nasals of skull No. 1/5009 were not preserved. However, judging by the anterior ends of the prefrontals and frontals that underlie them, we might think that the lower rami of the premaxillae are narrow, tapering bands that extended very far posteriorly, lying on the interior surface of the prefrontals and reaching their middle—at the joint with the frontals. The nasals occupy a medial position relative to the lower rami of the premaxillae and a lateral position relative to their upper rami (arranged along the medial line of the skull in hadrosaurs), and must have looked from behind like wide rounded ribbons, bending slightly to the outside, where they occupied a significant area of the frontals. Between the posterior ends of the premaxillae and nasals, and at the contact point of the prefrontals and frontals that underlie them, are apparently the nasal fenestrae. We can make judgments about this from the natural depression at the boundary of the frontals and prefrontals and by the structure of the interior surface of the latter, which has the explicit nature of a cavity wall. The prefrontals form half of the upper edge of the orbits and their anterior wall. They extend in an anteroposterior direction. Medially the prefrontals have a slightly striated sutural surface for contact with the premaxillae. The posterior end of the prefrontal is wedged between the postorbital and frontal, with which the prefrontal is joined by coarsely serrated sutures.

The frontals are joined together by a coarsely serrated suture and form the roof of the braincase near the forebrain, where they are noticeably swollen. The frontal is separated from the upper edge of the orbit by a wide band from the prefrontal and postorbital, but forms the upper region of the orbits. Distinct, coarsely serrated sutures separate the frontals from the adjacent bones and their external contours are reminiscent of maple leaves. Making contact with the nasals is a broad sutural surface, the medial extent of the frontals make contact with the premaxillae. Medially the frontals penetrate rather far between the nasals and laterally are slightly wedged between the prefrontals and postorbitals. From behind they form a complex suture with the parietals, which in the middle penetrate far between the frontals.

The parietals form the roof of the braincase above the mid- and hindbrain area and are at the same time the upper region of the medial walls of the supratemporal. By fusing together without an apparent suture, the parietals are wedged deeply between the frontals that expand ahead of a cuneus that has a depression on the surface. From behind the parietals form a short, but very typical sagittal crest. It is unclear as to how the parietals emerge onto the occipital surface of the skull—by separating the squamosals and lying on the supraoccipital bone: the medial ends of the squamosals that overlap the parietals were not fully preserved. Even less clear is the lower boundary of the parietals. The sutures are barely visible and we can only think it more or less probable that this boundary was horizontal and that the parietals made contact with the laterosphenoid and preotic bones from anterior to posterior, and possibly with the anterior ends of the supraoccipital bone, if we can agree that the latter emerges in the posterior node of the interior wall of the supratemporal fenestrae.

The postorbitals¹ form the posterior half of the upper edge of the orbit and the posterior part of its upper wall, coming together anteriorly with the prefrontals and excluding from the orbital ring the frontals, with which the postorbitals contact the interior lateral side. At the front of the postorbital, directly behind the orbit forming its posterior edge, a process emerged downward—in the direction of the ascending process of the jugals. The second descending, but small, process emerges from the posterior part of the bone and, by lying on a similar process of the squamosal, separates the infratemporal fenestra from the articulation socket for the upper end of the quadrate bone. From behind the postorbital, by merging with the squamosal by means of two large teeth,

¹ Rjabinin described these bones as postfrontals.

forms with this bone the upper temporal arch. Beneath, the postorbitals on the entire extent of the lower temporal arch, which the squamosals underlie.

The squamosals are a complex configuration and participate in forming the posterolateral corners of the skull roof. Their anterior growths, like two large teeth, dorsally penetrate the postorbitals and ventrally form the lower surface of the temporal arch, reaching the anterior corner of the supratemporal fenestrae. Two rather long process that bound the socket for entering the quadrate bone emerge downward from the ventrolateral surface of the squamosal. The hindmost of these processes, by lying on the postotic and exoccipital bones, participate slightly with the paroccipital process to form them. The posterior boundaries of the squamosal that exit onto the occipital surface of the skull have the nature of an undulating line that is defined by contact with the supraoccipital and exoccipital bones.

The bones of the zygomatic region and palatal surface are unknown.

Braincase (Figs. 3–5).

This area of the skull was completely preserved, and most of the sutures between the bones are well differentiated. The occipital area of the braincase includes unpaired supra- and basioccipital bones as well as paired exoccipital bones that fuse together. The otic region includes two bone pairs—the prootic and opisthotic—and is characterized by the least explicit ends of the bones. The base of the skull has been formed by the well-ossified basisphenoid and parasphenoid, the boundaries of which are usually poorly distinguished in most hadrosaurs because of bone fusion. The anterior region of the braincase was formed by a complex of sphenoid elements—an unpaired presphenoid and unpaired latero- and orbitosphenoids, well ossified and distinctly delimited.

The location of the supraoccipital is unclear in most hadrosaurs. Rjabinin (1939) makes reference to its being located above the occipital foramen, which indicates relatively low height and the presence of a lengthwise crest on the bone, but does not present precise data about its limits and shape. Rjabinin's data can be augmented. The supraoccipital contacts the exoccipital from below and from the sides, and contacts the squamosals and parietals from above. The lateral sutures with the exoccipitals are finely serrated. The supraoccipital is isolated from the foramen magnum by a rather wide band of exoccipitals that fuse together. Its boundary with these is distinct and almost

horizontal, slightly depressed above the center of the occipital foramen. On the occipital surface of the skull, the supraoccipital has a long and narrow, but massive posteriorly sloped plate. The lateral flanges are pulled into the sides far beyond the limits of the occipital condyle. A low, smooth medial crest runs along the central region of the supraoccipital. Posteriorly this crest transforms into a round enlargement that hangs slightly above the exoccipitals and the center of the foramen magnum. There are two enlargements that look like low columns in the upper part of the supraoccipital along the sides from the medial crest. These enlargements enter the corresponding depressions in the squamosal. There are openings in the sides of these columns that are not revealed by dissection. They probably opened into the supratemporal fenestrae and may have served as passageways for blood vessels, especially the dorsal head vein. It is unclear whether these openings are homologous with the post-temporal fenestrae that are typical of many reptiles. The anterior boundaries of the supraoccipital are less certain because the parietals and squamosals overlap them for a considerable extent. We may only assume that the sloping serrated sutures running along the interior surface of the supratemporal fenestrae from the posterior lower node on a diagonal to the center.

The exoccipitals fuse together with no explicit suture between them and embrace the foramen magnum for almost their extent. Rjabinin (1939) characterizes the exoccipitals as bones having “unspecified boundaries”; considering the lateral flanges that take part in forming the occipital surface of the paroccipital processes to be postotic bones. There are, however, no sutures on the occipital surface that might be seen as the boundary between the postotic and exoccipitals. As usual, this boundary is hard to see from the outside because of bone fusion. For this reason the question of the extent to which these bones participate in forming the paroccipital processes is debatable.

The visible boundaries of this boundary on the occipital surface of the skull run: in the center from the supraoccipital, and dorsolaterally from the squamosal. The lower contact—from the basioccipital—was not preserved because this part of the skull was destroyed. The base area of the exoccipitals in the posterior surface of the uncinat paroccipital processes are fairly high proximally but then quickly narrow and drop somewhat below the foramen magnum. A massive rod-shaped crest, beneath which the surface of the exoccipitals is concave, had developed on the center of the exoccipitals in parallel with the boundary with the supraoccipital. A short, small swelling at the point where the exoccipitals probably fused emerges from the center of the crest

downward to the foramen magnum. Each exoccipital forms at least a third of the occipital condyle, the lower part of which had been destroyed.

With regard to how the exoccipitals participate in forming the lateral surface of the braincase, Ostrom (1961) apparently relates to this negatively, bounding them in his drawings to the occipital surface, whereas most other authors (Romer, 1956; Goodrich, 1958; Langston, 1960) show the exits of the exoccipitals on the lateral wall of the skull where they include openings for nerves IX–XII as in contemporary reptiles. The boundaries for the exoccipitals were not seen on the lateral surface of the *Jaxartosaurus aralensis* skull. Bearing in mind the usual location of nerves IX–XII within the occipital, presumably beyond the anterior boundary with the opisthotic, we can raise the crest-overhang that passes obliquely posteriorly from the base of the skull to the paroccipital process, between the fenestra ovalis and the opening for nerves IX–XI. This opening opens outward immediately below this crest. The opening behind is the exit for nerve XII. Langston (1960) shows several (at least three) exits for nerve XII in *Lophorhothon atopus*, but there are only two openings behind the fenestra ovalis on the lateral wall of the *J. aralensis* braincase. Therefore, the anterior of these may have been interpreted merely as a common opening for nerves IX–XI, which agrees with the observations of Ostrom (1961), who was studying casts made of the endocranial cavity of various hadrosaurs. The opening for IX–XI splits in two¹—the anterior is fairly large and the posterior is small. From their sizes we may think that nerve X must have passed through the anterior, and nerve XI through the posterior. Nerve IX apparently exited with nerve X, as casts of the brain cavity from various hadrosaurs indicate (Ostrom, 1961), although Langston (1960) linked the IX nerve exit with the otic capsule in *Lophorhothon atopus*. The opening in *J. aralensis*, being interpreted here as common for nerves IX and X, actually has a canal into the otic capsule, but it is more likely that this connecting canal was designated not for nerve IX, but for the jugular vein as Ostrom (1961) assumes because this passage is very small for a major vein in the head and was more likely for the perilymphatic duct.

As to jugular vein, it is likely that it exited the skull area through the cranioquadrate rather than the base of the skull as Ostrom (1961, pg. 138, fig. 5) shows, because in general venous blood was exported through the foramen magnum as in archosaurs (crocodiles) and birds.

The basioccipital that forms the base of the occipital condyle was almost completely destroyed, a fact that Rjabinin did not note. It is difficult to make judgments about the boundaries

¹ All of these details were revealed after the skull openings were treated with a solution of hydrochloric acid.

of this bone. Starting from the area occupied by the exoccipitals, we might think of the basioccipital as a narrow band that formed the ventral region of the occipital condyle, and that the occipital foramen was between the tubera of the exoccipital.

The opisthotics form the lateral walls of the posterior region of the braincase near the medulla oblongata. In most hadrosaurs the opisthotics merge with the neighboring bones without any visible sutures. In *J. aralensis* the boundaries of the opisthotic are seen as a distinct suture for the lower anterior crest of the bone that is bounded with the basisphenoid. Because of the merging of the bones this contact is usually unknown in hadrosaurs, and a position that clearly belongs to the basisphenoid sometimes rises beyond the surface of the anterior otic bone (Ostrom, 1961). The boundary suture in *J. aralensis* in the form of a fine, slightly serrated line descends from the region of the fenestra ovalis located in the anterior node of the opisthotic to the base of the braincase. The boundary between the opisthotic and prootic is seen as a faint crest-like suture directed from the fenestra ovalis dorsally and posteriorly to the joint with the horizontal overhang. The upper boundary of the opisthotic is unclear, but the horizontal overhang above the fenestra ovalis may possibly be the front of it.

Even less clear is the boundary between the postotic and exoccipitals; in this capacity we may conditionally adopt the crest that passes above the opening for nerves IX–XI. The fenestra ovalis, or vestibular region of the otic capsule, is located at the junction of three bones—the preotic, postotic, and basisphenoid—and looks like a subrhomboid-shaped depression split into two halves by a septum. The upper half probably corresponds to the fenestra ovalis, and the lower half includes the fenestra rotunda. Three openings are visible at the base of the lower half; the anterior opening was possibly the exit for hyomandibular ramus of nerve VII, as it is treated in some hadrosaur species (Langston, 1960; Ostrom, 1961). According to Goodrich (1958), the middle cerebral vein might have passed through this opening, discharging in the otic capsule area into the lateral head vein. As has been mentioned, the posterior opening originates a canal that communicates with the canal for nerves IX and X and probably merges with the perilymphatic duct.

The prootics form the anterior region of the otic capsules, separating drastically into upper and lower parts by a transverse horizontally hanging crest. Rjabinin (1939) and then Ostrom (1961) note only the boundary between the prootics and postotics. However, in *J. aralensis* even the upper boundary of the prootic with the temporal may have followed a long horizontal suture

that separates the upper part of the temporal fenestra from the lower. The anterior boundary is a highly visible vertical suture with the laterosphenoid. The posterior boundary passes through (or at) the origin of the fenestra ovalis, dorsal from which the prootic contacts the postotic and ventrally contacts the basisphenoid into which the prootic is wedged by a shallow “pocket” below the exit opening for nerve V (trigeminal foramen), which lies almost entirely within the prootic. The prootic is slightly concave at its center, forming the anterolateral wall of the otic capsule. The horizontal overhang mentioned above makes a slight bend in this region. Above the horizontal overhang, the upper portion of the prootic occupies the posteroventral position on the inner surface of the supratemporal fenestra, and is subtriangular in shape. Here the most acute apex of the bone is rotated posteriorly. The lower portion of the prootic, lower than the horizontal overhang, has an irregular shape. The location of the opening for the nerve V exit in this region looks like a deep (due to the thick-walled prootic) and circular funnel. The boundary of the prootic with the laterosphenoid passes through its anterior wall. Within the prootic is a semicircular canal that is open from above, the anterior wall of which is the anterior boundary of the prootic and is denoted by a distinct suture. The canal is directed ventrally from the trigeminal foramen and apparently closed on the trigeminal nerve (n. trigeminus II), separating further on into maxillary and mandibular branches. It is possible that the inferior orbital artery, being a branch of the stapedia artery, also passed through this canal, as is seen in contemporary reptiles (Romer, 1956; Goodrich, 1958). Posterior and ventral to this canal is a depression that originates immediately behind the trigeminal foramen and crosses ventrally over onto the lateral surface of the basisphenoid. The pronounced profile provides a basis to presume that this depression has a special purpose, e.g., for the mandibular artery, being the lower branch of the otic artery. True, this structure is seen in lizards, whereas in crocodiles the mandibular artery departs from the ventral aorta (Goodrich, 1958) rather than from the otic artery. Therefore, the interpretation proposed for *J. aralensis* may be debatable. Below the trigeminal foramen, at the boundary of the prootic and basisphenoid, is another small opening that is probably the exit for nerve VII—more accurately, for the palatine branch.

The basisphenoid is very massive and tall, and is the axial region of the skull between the exits for nerves VIII and VI. Rjabinin did not describe these bones. The posterior and upper boundaries of the basisphenoid diverge at an acute angle: the first ventrally, making contact with the opisthotic, and the second more or less horizontally, descending below the trigeminal foramen

where the basisphenoid contacts with the prootic and further on bending the protruding area of the laterosphenoid in order to reach the exit opening for nerve VI. From here the boundary of the basisphenoid, which contacts the parasphenoid as a faint suture, descends ventrally. The boundary of the basisphenoid with the basioccipital, almost totally lost, remains unknown. The general shape of the basisphenoid, looking from the side, resembles an irregular quadrangle, the centro-posterior angle of which has descended significantly below the anterior. The lateral surfaces of the basisphenoid in the center ahead of the cuneiform, or pterygoid processes¹, carry from each side at least two pairs of small mammiform processes that had been directed ventrally. The entry into the carotid canal (which could not be opened) for the internal carotid artery, initially directed into the hypophyseal cavity and from there into the brain cavity, is at the same level as the posterior of these processes. It is possible that the palatine branch of nerve VII entered the carotid canal together with the internal carotid artery in order to exit through the noted opening at the boundary of the basisphenoid and parasphenoid along with the palatine artery departing from the internal carotid artery, as in modern reptiles (Romer, 1956).

The parasphenoid continues ahead of the basisphenoid, with which it merges with no visible suture in most hadrosaurs. This boundary is unclear in *J. aralensis*. It most likely ran from the opening for nerve VI ventrally, somewhat ahead of the mammiform processes of the basisphenoid. In this case the parasphenoid looks like a small, thin, flat, subquadrangle bone. The ventral process is directed anteriorly and was not completely preserved. Rjabinin mentions the parasphenoid as merely a fragment. It is possible that he had a somewhat different picture of the contours of these bones. More distinct are the contacts between the parasphenoid and the orbitosphenoids that bound it from above, and between the presphenoid that abuts it anteriorly and dorsally and immediately above the anterior process. Along with the bones that have been mentioned, the parasphenoid participates in forming the interorbital septum. The suture between parasphenoid and orbitosphenoid originates from two openings, the large (lower)² of these which was probably the exit for nerve VI and possibly for the hypophyseal vein; the smaller (upper) for the exit of nerve III. Ostrom (1961) shows an exit opening for nerves III and VI in *Corythosaurus casuarius*, which can be explained by the conditions under which it was preserved and prepared. The boundary runs farther horizontally, immediately above two rather large openings in the base of the orbitosphenoid.

¹ These processes were not preserved, but we can approximate their location by the drastic widening of the ventral surface of the basisphenoid.

The presphenoideum,³ only the posterior region of which was preserved, is bounded posteriorly and ventrally by the parasphenoid and the orbitosphenoids, from which it is separated by a distinct suture, and of which it is the anterior extension. Dorsally the presphenoid abuts the frontal bone and splits into two rami that together with the orbitosphenoids form the anteriormost region of the braincase—near the highly developed (we can judge this from the exit opening from the braincase) olfactory lobes of the forebrain.

The laterosphenoids that merge with adjacent elements without sutures in most hadrosaurs are very distinctly delimited in *J. aralensis*. The laterosphenoids form the lateral walls of the braincase near the midbrain and the posterior expansion of the large hemispheres. From behind the laterosphenoid borders with the prootic: dorsally it borders with the parietal posteriorly and with the postorbital anteriorly. The anterior boundary of the laterosphenoid does not pass along the crest that separates the orbit from the supratemporal fenestra as Ostrom (1961) showed in *Corythosaurus casuarius*. By participating in forming the orbit, the small flange of the laterosphenoid wedges between the frontal bone and the V and VI nerve openings and extends to make contact with the basisphenoid. Because of the horizontal canal, the aforementioned area seems to be separated from the base area of the bone. In general the laterosphenoid looks like an extended rectangle that bends outward in the anterior region (near the forebrain) with a process that emerges ventrally. Ostrom (1961) proposes that the laterosphenoid area served as the attachment for the supplementary orbital muscle—the levator bulbi muscle (Fig. 6). The canal itself undoubtedly served as the orbital branch (deep ophthalmic branch) of the trigeminal nerve, along with which the superior orbital artery and lateral head vein or its orbital branch (ophthalmic vein) possibly passed, as in modern reptiles (Romer, 1956; Goodrich, 1958).

The laterosphenoid contact with the postorbital does not look like the usual suture, but like the articular fossa on the postorbital into which the laterosphenoid enters with a rounded end. Such a connection between the laterosphenoid and postorbital has not been noted in the literature on hadrosaurs. Rjabinin had nothing to say about it. However, a similar connection between the laterosphenoid and postorbital was rather widespread mainly among the hadrosaurs. It can be traced in the skulls of *Saurolophus angustirostris* and other species of Hadrosaurinae. Predatory dinosaurs and crocodiles (including modern species) have such a connection and it is more

² The size of this opening is probably somewhat enlarged owing to the way it was preserved or treated.

pronounced in the long-snouted animals than in the short-snouted. Because the other sutures of the laterosphenoid and postorbital with the adjacent are serrated, making these bones immobile, it is impossible to assume mobility in the laterosphenoids. There is a gap between the articular processes of the laterosphenoid and the depression in the postorbital that must have been filled with cartilage during the animal's lifetime. According to L. I. Khozatskiy (in a verbal communication), who studied reptilian biomechanics, a similar structure might have been an amortizer, although it was not unique. The quadrates enter the deep articulation fossa of the squamosals by their head. The quadrates are in turn supported on the column-like areas of the supraoccipitals. As with the laterosphenoid there are gaps between the contacting bones which in modern crocodiles are filled with cartilage. The likely purpose of these amortizers is to protect the braincase from the concussion that occurs when the mandibles are suddenly closed. The presence of three amortizers probably reduced the force of the concussion, distributing it in several directions. The analogy in the connection of the skull roof and the braincase of crocodiles and hadrosaurs gives occasion to presume that the latter may feed on not only vegetation, but on small water animals by rapidly (consequently, suddenly) closing the mouth.

The orbitosphenoids, or orbitocuneiform bones are bounded dorsally by the frontals, posteriorly by the laterosphenoids, ventrally by the parasphenoid, and anteriorly by the presphenoid. Rjabinin (1939) mentioned in text that upwardly the parasphenoid borders with the orbitosphenoid, but the alisphenoid¹ apparently corresponds to the orbitosphenoid in his drawings (Figs. 3,5). Contrary to what is seen in most hadrosaurs, all of the orbitosphenoid sutures in *J. aralensis* are quite visible. The orbitosphenoid is oval shaped, the lower part of which is vertical and has openings for the exits of the cranial nerves. The upper, larger part turns sharply outward, forming the ventrolateral surface of the braincase and the area in which the forebrain hemisphere begins.

Several openings for the anterior cranial nerves are found on the orbitosphenoid. The interpretation of these openings is complicated by the fact that in modern reptiles the orbitosphenoids do not ossify. For this reason the literature contains many contradictory interpretations. There are three large openings on the lower part of the orbitosphenoid along the flexure line. Above the middle opening is another small opening that extends slightly horizontally.

³ Rjabinin (1939) mentioned this bone in the text (p. 10), but did not show it in the figures (3, 5). Apparently the bone identified as the orbitosphenoid in Fig. 5 is the presphenoid.

The posterior opening, isolated from the opening for nerve VI beneath it by a septum, is the exit for nerve III. A larger opening that is somewhat expanded upward lies anterior and dorsal to the exit. This opening leads into the brain cavity and may be the exit for only the optic nerve and the small opening above it (at the most dorsal location of all the cranial nerves) is undoubtedly the exit of nerve IV. The anteriormost opening is located ahead of the exit for nerve II and does not lead to the cranial cavity, but by a narrow canal joins with an analogous opening in the oppositely located orbitosphenoid, significantly below the bottom of the cranial cavity. This connection is a possible route for the venous anastomosis that connects the left and right orbital sinuses, as is seen in modern reptiles. It is possible that the ophthalmic artery exited along with nerve III. This artery is separated from the internal carotid artery immediately ahead of it by the entry into the cranial cavity from the hypophyseal artery. The joint exit of nerve III and the ophthalmic artery was seen in the skulls (Romer, 1956), whereas in lizards it exits along with nerve II. However, the position of the exit of nerve II significantly anterior to the exit of nerve III in *Jaxartosaurus aralensis* apparently excludes the possibility that the ophthalmic artery exited with nerve II.

Cranial fenestrae. The largest are the orbits, which are significantly larger than the infra- and supratemporal fenestrae. The upper area of the orbits is unusually wide, almost four times that of the infratemporal fenestrae and roughly two and a half times as wide as the supratemporal fenestrae. The lower boundaries of the infratemporal fenestrae are unknown and we can only talk about their width. They are very narrow, almost rimose. In their upper region they are somewhat narrower than the articular fossa in the squamosal (for entry of the quadrate) and much narrower than the supratemporal fenestrae. Looking at the skull from the front, the latter are subrhombic along the upper contours and subtriangular along the lower contours.

Cranial crest. Rjabinin (1939) suggested that *Jaxartosaurus* had a helmet-like crest like *Hypacrosaurus*, because of the connection by the anterior region of the parietals on which, in Rjabinin's opinion, the crest was supported. The judgment is sufficiently valid because the expanded suture surfaces of the frontals and prefrontals at their boundary with the premaxillae and nasals testify to the substantial weight and large area of the latter. The wide support areas are not intrinsic to the usual sutures in hadrosaur skulls and developed to support the heavy crest. In any event, similar suture surfaces in the prefrontal area were quite undeveloped in the flat-headed dinosaurs (Hadrosaurinae) which lacked the crest.

¹ In reptile skulls this bone is more properly called the laterosphenoid.

It is extremely difficult to evaluate the shape of the crest because the crest itself was not preserved. However, we take exception to Rjabinin, who thought this crest was the same type as is seen in *Hypacrosaurus*. In the latter, by raising the frontals to the front, the crest is not supported on the parietals. At the same time a possibly natural cleavage between the squamosals may indicate the contact of this region with the crest that overhangs the occiput. In this case the crest in *J. aralensis* was possibly more similar to that of *Corythosaurus*, but different in its greater thickness, judging from the support areas.

Measurements of <i>Jaxartosaurus aralensis</i> skull, Rjab., No. 1/5009 (centimeters)			
Width in the orbital region	25.0	Width, orbits	11.0
Width in the occipital region	20.0	Width, infratemporal fenestra	3.0
Occiput height from the lower point of foramen magnum	10.0	Width, supratemporal fenestra	4.5
		Length, supratemporal fenestra	6.5

Genus *Aralosaurus* Rozhdestvenskiy, gen. nov.

Type (unique) species: *A. tuberiferus* sp. nov. Upper Cretaceous (Beleutinsk Formation) Central Kazakhstan.

Diagnosis. The skull is moderately wide in the zygomatic region. The nasals are shaped like an arch and make an enlarged crest in the central region. The frontals participate in forming the orbits, but to a very small degree. An elliptical fontanelle runs between the nasals and frontals at their boundary. The lacrimal bone is very large. The orbits are rounded ovals, much wider than the infratemporal fenestrae. The supratemporal fenestrae are small. The posterior end of the postorbital is trident-shaped. In its upper region the quadrate is curved. The upper jaw contains approximately 30 tooth rows and rises upward in the front at almost a right angle and its apex is very wide. The teeth in the lower jaw have a supplementary crest. The humerus has a small upper epiphysis and slightly developed deltopectoral ridge. The internal and external distal condyles of the femur are well developed but do not come together from the front. Metatarsal III is very wide laterally at the proximal end of II and IV at the distal end, but much larger in the anteroposterior direction than in the lateral direction.

Comparison. The subfamily Hadrosaurinae, to which *Aralosaurus* is related, combines seven genera, not counting *Aralosaurus* (Rozhdestvenskiy, 1964b). The skulls of two of these—*Claosaurus* and *Hadrosaurus*—are unknown. The latest two—*Edmontosaurus* and *Anatosaurus*—from the Maastrichtian and Danian, respectively, are sharply distinguished from all of the hadrosaurs by the absence of any kind of growths on the nasals. Three genera—*Bactrosaurus*, *Lophorhodon*, and *Kritosaurus*—are the most similar to *Aralosaurus*.

The proportions of the orbits and infratemporal fenestrae are similar to *Bactrosaurus* (Gilmore, 1933; Rozhdestvenskiy, 1966). Both skulls are moderately wide near the jugals, and the frontals participate in forming the orbits. There is a similarly shaped fontanelle (much larger in *Aralosaurus*) which is absent in *Lophorhodon* (Langston, 1960)¹. *Aralosaurus* differs from *Bactrosaurus* by the crest on its nasals; a large number of teeth, the relatively short, tall upper jaw; and small supratemporal fenestrae.

Aralosaurus is similar to *Lophorhodon* by the presence of a fontanelle (even though it differs in size and shape), a more highly developed crest on the nasals, the participation of the frontals in forming the orbits, and a large lacrimal bone. It differs by the small supratemporal and narrow infratemporal fenestrae and the large number of teeth.

In its overall configuration of the skull and shape of the nasals, *Aralosaurus* is most similar to *Kritosaurus* (Brown, 1910; Lambe, 1914; Lull, Wright, 1942). It differs in its small temporal fenestrae; very high and well-developed lacrimal bone; broad apex of the upper jaw, bent by the quadrate, and small number of teeth².

Thus, *Aralosaurus* is quite distinct from any other genus of the subfamily Hadrosaurinae.

As Table 1 shows, two genera—*Edmontosaurus* and *Anatosaurus*—are indistinguishable in their essential features, which leads us to assume that they did in fact belong to one genus, but being distinct in more subtle features, they might belong to a different species.

*Aralosaurus tuberiferus*³ gen. et sp. nov. (Figs. 7–12)

Holotype. Paleontological Institute No. 2229/1; incomplete skull; lower half of the Upper Cretaceous (Beleutinsk Formation); Central Kazakhstan, Shakh-Shakh plateau, approx. 80 km to the north of Karmachka (from Dzhusala).

Diagnosis. A mid-sized hadrosaur. The dorsal surface of the skull has a low tubercular enlargement of the nasals and a well-developed fontanelle, the length of which is almost one-third as wide as the skull is in the orbital area, exceeding its width by less than one and a half times in

¹ Langston was the first to encounter a fontanelle in hadrosaurs and he considered them to be unique and intrinsic to young animals. The presence of the fontanelle in *Aralosaurus* and *Bactrosaurus*, in which it is found in mature animals, attests to a much wider dissemination of this formation.

² There are 42-45 tooth rows in the type species *K. notabilis*. A later species, *K. navajovius*, had 42-47 tooth rows; however, this species was described from a skull that lacked an anterior region, and it is possible that *Aralosaurus* is closer to *Anatosaurus* than to *Kritosaurus*.

the occipital region. The orbit is subtriangular in shape and wider at the top. The supratemporal fenestra is narrow, one third the maximum width of the skull. Infratemporal fenestra is narrow, barely wider than the quadrate; its length to height ratio is 7:4. The upper jaw has 30 tooth rows and it is only twice its height. The tooth crown is three times as tall as it is wide. Ahead of the medial crest on the lower jaw teeth is a supplementary tooth that rises above the center of the crown. The epiphyses of the humerus are of equal width, the apex of the ridge is barely above the center of the bone. The distal condyles of the femur are the same length, somewhat less than the distance between the anterior and posterior sides of the bone on its lower surface. The proximal end of metatarsal III is wide, comprising half its entire length. The distal ends of metatarsals II and IV are roughly twice as large from front to rear as they are laterally.

Material. Collection No. 2229—the skull and individual bones from the skeletons of several specimens taken from the same deposit and horizon as the holotype.

Description

Judging by the length of the skull, the total length of which was approximately 65 cm, the size of the animal must have been as much as 6.5 m. The skull possibly belongs to a fairly young (at least, not very large) animal. This is confirmed by the distinct sutures between the bones, most of which easily separated because the bones had not fused.

The skull is known from a single example, the anterior region of which was destroyed. Considering the greatest similarity with the genera *Bactrosaurus* and *Kritosaurus*, we may think that the snout region of *A. tuberiferus* was moderately widened because intense widening was intrinsic to only the later genera *Edmontosaurus* and *Anatosaurus*. The skull is widest in the orbital area, narrowing slightly toward the occiput. The skull roof has a massive growth, or tubercle, in the nasal region that rises sharply in front of the orbits; the posterior region of the skull roof is slightly elevated.

Skull Roof (Figs. 7–9)

³ The species designation “tuberiferus” means ‘bearing a tuber’.

The structure of the premaxillae is unknown and the nasals were not well preserved. We can make some judgments about the premaxillae by their contacts with the nasals and supratemporals: they apparently did not run far beyond the anterodorsal node of the premaxillae and beyond the nasal fenestrae that terminated above this node.

The nasals, separated by the anterior region of the premaxillae, bounded the dorsal and posterior edges of the nasal fenestrae. It is hard to say which part of the nasal fenestra's dorsal contour was formed by the nasal and which by the premaxillae. From behind, the nasal fenestra is rounded and somewhat narrower than the nasal and lower ramus of the premaxilla that bounds the nasal fenestra from above. The posterior region of the nasal fenestra has contours that are similar to those seen in *Anatosaurus annectens* (Lull, Wright, 1942). The nasals, nearer the posterior and very thick, rise like a tubercle contained within a small band that probably had a connection with the nasal fenestrae and might have been an auxiliary air reservoir. Among the Hadrosaurinae this is as yet a unique case of the nasals forming a hollow swelling. In front of this swelling (the dorsal surface of which was not preserved) the nasals have a slightly uneven surface, like a scattered shagreen, that was possibly intrinsic to the swelling. It is difficult to say what the significance of the shagreen was—possibly a base for a bony covering or a muscle attachment.

The prefrontals are comparatively short and wide. They overlay the posterior area of the nasals as a wide surface immediately behind the previously described swelling. As usual, they form the anterodorsal edge of the orbit. On the ventral side, the prefrontals have a sharp, laterally slanted crest that separates the orbit from the nasal region. At roughly the middle they are penetrated by a small opening, probably for blood vessels and possibly a nerve. Ventrally the prefrontals overlie the lacrimals, connecting with them by means of a suture surface and a coarsely serrated suture in their posterior region. The posterior suture of the prefrontals is a continuation of the posterior suture of the nasals—along this slightly serrated line running from the medial fontanelle obliquely posteriorly to the orbit, the prefrontals and nasals abut the frontals.

The frontals form the roof of the braincase in the forebrain area. They taper laterally toward the orbits, participating in forming their upper edge for only a short distance. The posterolateral contact of the frontals with the postorbitals looks like a slightly serrated suture and is almost symmetric with the anterior suture of the frontals. The suture with the parietals is obscure because this area was destroyed. Also obscure is the nature of the contact of the frontals with each other because they were destroyed here. As in other flat-headed hadrosaurs the frontals are flat, and even

in the destroyed region above the large hemispheres were insensitive to trends to swelling as seen in the lambeosaurs. The long elliptical fontanelle lies two-thirds of its length between the frontals and one-third between the nasals. A similar, but quite small, fontanelle is seen in *Bactrosaurus johnsoni*¹ recovered in 1959 at the Iren Nor Formation from the Upper Cretaceous of Mongolia (Rozhdestvenskiy, 1966). A wider, rhombic fontanelle was described for *Lophorhothon atopus* from the Selma Formation, Alabama (Langston, 1960). The purpose of this fontanelle, situated near the olfactory lobes, is as yet unclear, but is characteristic of only the flat-headed hadrosaurs; therefore, it is logical to assume that it is connected with the olfactory organs or respiratory system that varies widely among the hadrosaurs.

The parietals have the usual shape for flat-headed hadrosaurs and form the fornix of the braincase above the posterior region of the forebrain and near the midbrain and cerebellum. From behind, the parietals make contact with the squamosals and divide into two processes that overlay the supraoccipital and exit onto the occipital surface of the skull from the interior side of the column-like swellings of the supraoccipital. The boundary with the frontals was destroyed, just as the sagittal crest that forms on the parietal joint. The lower anterolateral nodes of the parietals are supported at the juncture of the frontals, postorbitals, and laterosphenoids to form with the latter the anterior region of the inner wall of the supratemporal fenestrae, being separated from them by a faint horizontal suture. The parietal boundary also runs horizontally—along the contact with the ears.

The postorbitals are straight, in contrast to most hadrosaurs in which they are slightly convex to the outside; forming the upper and posterior edges of the orbits in the anterior region, their postorbitals contact the frontals dorsally, and ventrally have an articular fossa for the anterior laterosphenoids. A rather massive process that separates the orbit from the infratemporal fenestra and joins with the ascending process of the zygomatic bone emerges ventrally from the anterior region of the postorbitals. There are two small openings for vessels on the dorsal surface of the anterior end of the postorbitals. From behind, the postorbitals, combining with the squamosals by means of the trident and with them forming the supratemporal arch, run via the lower process beyond the posterior edge of the infratemporal fenestra, whereas the two upper processes terminate at its posterior boundary.

¹ The specimen described and imaged by Gilmore (1933) did not show this fontanelle, which is probably explained by the low degree of preservation.

The squamosals originate almost from the anterior edge of the supratemporal fenestrae, underlying the postorbitals ventromedially, but on the dorsal surface of the skull—only at the posterior edge of the supratemporal fenestrae forming the posterolateral corners of the skull roof and the upper area of its occipital surface. A small process that separates the infratemporal fenestra from the articular fossa of the quadrate emerges ventrally at the dorsal junction of the squamosals and postorbitals. This fossa on the squamosal is bounded posteriorly by a second descending process on the squamosal, lying on a small extension to the anterior surface of the paroccipital process. The posterior boundary of the squamosal—on the occipital surface—where they lie on the lateral and upper occipitals, look like two sigmoid lines that meet gently near the cervical notch where the squamosals come together to form a fairly high crest, the anterior region of which is formed by the parietals. The anterior edge of the squamosals form the posterior wall of the supratemporal fenestrae. Overall, the squamosals have a very complex shape that is generally typical of most hadrosaurs. A distinguishing feature of this species is the nature of the contact with the postorbitals, into which the squamosals enter as two small, tooth-like processes, whereas in most flat-headed hadrosaurs this union is accomplished by one long, tooth-like process.

Lateral Surface of the Skull (Fig. 8)

The maxillae are comparatively short and tall. They are bounded anteriorly by the premaxillae, dorsally by the lacrimals, and laterally by the jugals which lie on the maxillae along the broad sutural surface. The maxillae of *A. tuberiferus* differ from those of most other hadrosaurs by their steep anterior region, because of which their apex is wide and rectangular to the front. A crest that separates the lateral surface of the bone, above which it projects slightly from the dorsolateral surface, runs along the maxilla from the lower contact point of the jugal to the posterior end of the maxilla. The latter looks like the platform, or “shelf”, that is characteristic of all hadrosaurs (Ostrom, 1961). This shelf runs obliquely dorsally to the medial plane of the skull and is usually interpreted as the point of attachment for the *M. pterygoideus* muscle. On the lateral surface of the maxilla the shelf is one-third the length of the bone. Anterior to the crest that bounds the shelf are four openings for vessels and nerves. Three of these are immediately below the contact with the jugal and one is significantly forward, near the anterior edge of the maxilla. These openings (at any rate, the three posterior ones) connect with the funnel in the anterior region of the

shelf and were possibly the attachment point for the dorsal part of *M. pterygoideus* (Ostrom, 1961). The lateral surface of the maxilla is convex along the line defined by the crest and the openings, above and below which it is slightly inclined medially. The upper region of the maxilla is divided into thin medial and lateral walls. Anteriorly they diverge widely, creating a large depression or funnel-shaped opening that was possibly not entirely filled by the maxilla, remaining as an interbone cavity. Posteriorly, the middle wall flexes laterally and, along with the lateral wall of the maxilla and the upper edge of the jugal, forms a deep, narrow fissure for the lacrimal. Along the middle of the elevation of the lingual surface of the maxilla is an arched series of openings that lead to the tooth row and the corresponding number of teeth (30).

The lacrimals are transom-like in shape, thin but fairly large, forming more than a third of the orbit's anterior edge. Dorsally they are covered by the prefrontals, ventrally they enter a depression in the jugal and maxillae. The anterior region of the lacrimal was destroyed, and its relationship with the nasals, premaxillae, and maxillae is unclear. The wide posterior wall of the lacrimal that forms the orbit was perforated in the center by a wide but short opening—the lacrimal channel which passed obliquely ventrally through the bone and covered anteriorly on its medial surface.

The jugals have a large contact area for joining with the maxillae, on which they lie by their generally rounded lobe, but have small triangular processes: two of them dorsal, one anterior, and one ventral. As a whole, the jugal is almost symmetrically widened anteriorly and posteriorly. It has a constriction in the middle from below and an ascending dorsal process that, by joining with the descending process of the postorbital, separates the orbit from the infratemporal fenestrae. The jugal departs radically to the side after making contact with the maxilla, forming a slight convexity in the middle behind which it turns slightly medially so that the posterior lobe of the bone is oriented almost parallel to the axial line of the skull. In its overall configuration the jugal of *Aralosaurus tuberiferus* is fairly similar to the respective bone in *Kritosaurus notabilis*, differing only by its more highly developed anterior lobe, its processes, and the wide lower rounding of the posterior lobe.

The quadrates, which form the posterior contour of the skull in lateral view, are curved markedly dorsally, sloping posteriorly. The upper area of the quadrate is fairly thin with a narrow subtriangular head that enters the articular fossa of the squamosal. The ventral end of the quadrate, which connects with the lower jaw, is more massive. Somewhat below the middle, at the anterior

edge of the quadrate, is a fairly deep, semicircular notch, usually covered by the quadratojugal, which was not preserved here. Level with this notch and somewhat above the interior surface of the quadrate is the pterygoid process for contact with the pterygoid. This process is thin and laterally convex like an extremely significant flange. Judging by the part of this flange that was preserved, we might think that its pterygoid connection, having the nature of a planar overlay, made some mutual mobility in these bones possible. The articular surfaces of the quadrate above and below especially must apparently have at least allowed the quadrate to move back and forth, although not every author (Ostrom, 1961) agrees with this view.

Braincase

This part of the skull is almost completely known, although the lower region was destroyed at the surface and the contacts with the upper half were lost, which makes it difficult to exactly locate the exit openings for the cerebral nerves. The occipitals—supraoccipital, exoccipital, and basioccipital—merge together and with the opisthotics to form a bone unit with no visible sutures.

The supraoccipital. It is difficult to talk about the boundaries of this bone because the sutures are very faint. It was apparently lost at the occipital surface and preserved here as two symmetrical, column-like enlargements alongside the medial plane of the skull. The squamosals are supported on these columns, freely separating from them. Fairly large, round openings (approximately 0.3 cm in diameter) are located on the lateral and medial sides of these columns. These openings lead to channels that open into the temporal fenestrae. The lateral channels are short (approximately 3 cm long) and separate the supra- and exoccipitals and terminate anteriorly below the anterior boundary of the squamosals and opisthotics. The medial channels are long (approximately 5 cm), run along the lateral wall of the braincase below the posterior temporal process, and lead to a large, throughgoing opening inside the braincase at the junction of the laterosphenoids, prootics, and parietals. The purpose of these channels is unclear, but they are associated with the cranial nerves. These were probably the passageways for the occipital blood vessels, and the lateral openings—judging by their location—may correspond to the post-temporal fenestrae of other reptiles. Between the medial channels is a rectangular wafer that rises slightly anteriorly and has a lengthwise ridge in the middle. This wafer, which is apparently the foundation and at the same time the anterior process of the supraoccipital, forms the posterodorsal wall of the

braincase near the cerebellum. and possibly the medulla oblongata, descending in the latter case to the upper boundary of the foramen magnum, which is an arcane feature.

The exoccipitals have extremely obscure features, with the exception of the distinct boundary with the squamosals that lie freely on them, if we consider the posterior surface of the paroccipitals to have been formed by the exoccipitals. It is possible that the exoccipitals did not connect each other, being disconnected by the supraoccipital, and in this case they did not participate in forming the upper edge of the foramen magnum. The lower parts of the exoccipitals, which form the lateral tubercles of the occipital condyle, were not present, just as the larger portion of the bones' lateral surface was destroyed near the exit for nerves IX–XII. At least three openings that may be thought of as the exits for nerves IX–XII are seen in the lateral wall of the braincase behind the auditory capsule. The most anterior of these is of rather large diameter and pierces the wall of the braincase anteriorly at an angle, opening into the endocranial cavity near the exit for nerve VIII. This opening had a large lateral connection with the auditory capsule that was probably the channel for the perilymphatic duct, whereas the same opening generally served as the passageway for nerves IX and X. The fact is that behind the opening, turning away from it posteriorly and toward the brain cavity and at the exit to the outside, being separated by only a thin septum, is a fairly large opening that can hardly be accepted as anything other than the channel for nerve XI, because the next one behind it is a fairly large opening—the last in the lateral wall of the braincase is, of course, the exit for nerve XII. The close proximity of the exit openings for nerves IX–XII to each other is typical of hadrosaurs (Ostrom, 1961).

The basioccipital, which forms the posteroventral region of the braincase, was almost totally destroyed.

The opisthotics form the lateral walls of the braincase posterior region but fuse with adjacent bones without any visible sutures. Dorsally the opisthotics fuse with the column-like areas on which they are based. These columns apparently belong to the supraoccipital and are drawn posteriorly as the paroccipital processes, forming their anterior surface in some small measure. We can only conditionally lay out the boundary between the opisthotics and exoccipitals on the lateral side of the braincase, considering the profile along the crest that passes diagonally through the openings for nerves IX–XI. Anteriorly, the opisthotics participate in forming the auditory capsule by merging with the prootics, possibly along a line of the overhang and a slightly curved line. Somewhat below the auditory capsule the opisthotics bounds with the basisphenoid, but this

boundary cannot be traced because of the extent to which this part was destroyed. The auditory capsule itself was partially destroyed, and the semicircular channels were revealed as three depressions dorsally and two ventrally. The latter converge together and possibly correspond to the ampullae channels. Behind these is an opening through the braincase, probably for nerve VIII.

The prootics, merging posteriorly with the opisthotics, are distinctly separated from the parietals dorsally and the laterosphenoids anteriorly. The ventral regions of the prootics were not preserved. The dorsal boundary with the parietals looks like a horizontal, slightly undulating fissure, whereas the anterior boundary with the laterosphenoid is a vertical, lightly serrated suture that runs from the previously described opening at the juncture of the parietal, prootic, and laterosphenoid to the exit for nerve V. The dorsal region of the prootic slopes medially, forming the lateral wall of the braincase and cerebellar region. The opening for the nerve VII¹, situated at the boundary of the prootics and basisphenoid in some hadrosaurs, is found at the trigeminal foramen and fenestra ovalis in *Aralosaurus tuberiferus*.

The laterosphenoids form the anterior half of the lateral walls of the braincase near the midbrain and the posterior region of the large hemispheres, and are distinctly separated from adjacent bones, except the lower contact with the basisphenoid that is obscure because this portion was poorly preserved. From behind, the laterosphenoids are separated from the prootics by a vertical suture. Dorsally it is separated from the parietals by an almost vertical boundary, and anteriorly is separated from the frontals by a serrated suture that passes the crest more rostrally. This crest delimits the orbital and infratemporal fenestrae. The laterosphenoid surface looks like a concave subtriangle that lowers one apex between the openings for nerves IV and V. In the upper anterior node, the laterosphenoids enter the fossa in the anterior region of the postorbitals where the latter extend below the zygomatic process by this articular process, similar to that of *Jaxartosaurus aralensis*.

The basisphenoid forms the axial region of the skull, and is massive and relatively low. It was not preserved in its entirety, and almost the entire outer surface was destroyed in the unit of bone that remained, which obscured its boundaries with other bones. It is difficult to make judgments regarding the actual features of the basisphenoid. A dual carotid artery channel penetrates the lower region of the basisphenoid. This channel served as the passageway for the internal carotid

¹ In comparison with the other cranial nerve exits, the location of this exit is less certain even among the subfamily Hadrosauridae.

artery and possibly the palatine branch of the facial nerve. The channel is almost straight and anterior from below upward. In the dorsal region of the basisphenoid, forming the bottom of the brain cavity, penetrated by two rather short anteriorly descending channels for nerve IV; they originate at the trigeminal foramen level and open into a hypophyseal cavity. Because the laterosphenoid of hadrosaurs from the inside descends below the bottom of the brain cavity and even lower than the level of nerve VI, we are compelled to assume that from the outside this bone overlaps the basisphenoid and the contacts with it must be like a rather large internal sutural surface.

The cuneiform bones, which take part in forming the interorbital septum—the orbitosphenoids, presphenoid, and parasphenoid—were not preserved.

Basic Skull Features

With the exception of the long, narrow posterior region, the shape of the nasal fenestrae is unknown because of incomplete preservation. The orbits widen dorsally where their edge is almost straight; ventrally they are equally tapered, having a rounded ventral edge. The infratemporal fenestrae are much narrower than the orbits, but more extended dorsally—like a long, narrow parallelogram with rounded corners, similar in shape to the infratemporal fenestrae, more like some dinosaurs from the subfamily Lambeosaurinae than Hadrosaurinae. The supratemporal fenestrae, located on the roof of the skull and somewhat posterior to the infratemporal fenestrae, have a subtriangular form that widens anteriorly. Their length is equal to that of the upper edge of the orbit. The supratemporal arch, as in other Kazakhstan hadrosaurs, is characteristically straight and not laterally convex—in contrast to most other hadrosaurs. The fontanelle between the nasals and frontals is almost 80% as long as the supratemporal fenestra or the upper edge of the orbit, and a width that is approximately one-third the characteristic length is a feature of *Aralosaurus tuberiferus*.

Teeth (Fig. 12)

The teeth in the left maxilla of the holotype were completely preserved, forming approximately 30 vertical tooth rows. Additionally, there are several individual upper jaw teeth

and one lower jaw tooth. The teeth in the lower jaw differ slightly from those in the upper jaw (as in other early hadrosaurs and iguanodonts, although this has not yet attracted attention) by the presence of an additional ridge on the crown anterior to the medial or basic ridge. This additional ridge is raised above the crown center and possibly reached its apex (with an available, incomplete tooth). The crown of the teeth in both the upper and lower jaws looks like an extended rhomboid with a length-to-width ratio of 3:1. The anterior angle of the rhomboid in the lower jaw teeth descended lower than the posterior, but just the opposite occurred with the upper jaw teeth. This asymmetrical structure in the teeth is apparently inherent to all hadrosaurs, although their teeth usually display as quite symmetrical. There are approximately 20 small denticles on each side of a complete tooth on the anterior and posterior edges of the crown, in the distal half.

Besides the holotype, there is the posterior half of a very small, lower right half of a mandible (the preserved length is 4.5 cm for a maximum height of 3 cm). This is a very young specimen, which we can validate not only by absolute dimensions but by the number of tooth rows, which if the mandible is reconstructed could barely have exceeded 20. The small number of teeth in young specimens is inherent to other hadrosaurs (Gilmore, 1933).

Postcranial Skeleton

The very same bone-bearing horizon that yielded the described skull also yielded vertebrae and components of the limbs. Judging by their size, they belong to several specimens that are, however, only barely associated with the holotype. The teeth that were collected with these bones are identical to those of the holotype. Therefore, there is no basis to assign these bones to any other species.

The humerus was almost complete (approximately 30 cm long), excluding the origin of the upper epiphysis. It has an almost straight shaft, with a slight rotation of the upper epiphysis relative to the lower. The epiphyses are approximately identical, being less than one-quarter the length of the bone. The apex of the faint deltopectoral crest is barely lower than the center of the bone height.

The forearm bones—ulna and radius—were only preserved as the distal or proximal ends.

The carpus is unknown, as are the bones of the pectoral and pelvic girdles.

The femur is represented by a fragment of the distal epiphysis which has features similar to the quadrate. The outer and inner condyles on the anterior side of the bone are not connected and are the same width, which is somewhat less than the interval between the lengthwise notches on the anterior and posterior surfaces of the epiphysis. This bone belonged to a small animal.

The tibia, fibula, and astragalus are known only as fragments.

Of the metatarsals, only metatarsal III, 21 cm long, was preserved. It is notably widened at the proximal end, where the lateral diameter is half the length of the bone. The proximal end is twice as narrow anteroposteriorly, making the general shape of the upper epiphysis elliptical. Metatarsals II and IV, of which only the distal ends were preserved, are, in contrast to metatarsal III, characterized by the drastic widening in the anteroposterior diameter, which is twice that of the lateral.

Of the pedal phalanges, only the first phalanges of digits II and IV, second phalanx of digit III, and the ungual phalanges of the lateral digits were preserved. The first phalanx of digit II (approximately 8 cm long) is characterized by a notable widening of the distal end, which is wider than the proximal and is half the length of the bone. The ratio of phalanx length to its minimal width is 8:3. The interior edge of the bone is acutely concave. The first phalanx of digit IV (approximately 6.5 cm long)¹ is characterized by the same indicators, but it is shorter—its length to minimal width ratio is 2.1. The second phalanx of digit III is wide and short (low) so that its width exceeds its length by two and a half times. The ungual phalanges belonging to the lateral (II or IV) digits have a subtriangular shape in plan view, terminating in a slightly blunted apex. The length to width ratio of this bone is 4:3.

Genus *Procheneosaurus* Matthew, 1920

Procheneosaurus Matthew, 1920

(= *Didanodon* Osborn, 1902; = *Tetraganosaurus* Parks, 1931)

Type species: *Tetragonosaurus praeceps* Parks, 1931; Belly River Formation, Alberta (Canada).

Diagnosis. Comparatively small (up to 5 m long) crested hadrosaur. The skull is short and tall, with a lower crest that was formed by the premaxillae and nasals. The upper branch of the premaxilla is separated from the lower branch by means of the open nasal fenestra. The nasals are fairly small and outline the nasal fenestrae posteriorly and partially dorsally. The lacrimals are triangular or trapezoidal, ranging in size from moderate to large. The infratemporal fenestrae range from being moderately wide to narrow, with an increase in its length-to-width ratio of as much as three. There are 40 tooth rows¹ in the upper jaw and 33 in the lower. There are 30 presacral vertebrae, of which 13 or 14 are cervical, 16–17 are dorsal, 10 are sacral, and as many as 57 are caudal. Along the last dorsal, sacral, and anterior caudal vertebrae are ossifying tendons. The scapula is slightly curved, with a slightly developed coracoid region; the overall length of the scapula is roughly one and a half times that of the humerus. The radius is slightly longer than the humerus. The ilium is low, with a long, narrow, anterior lobe (process); overall, the bone is roughly four times as long as it is high. The antitrochanter is asymmetrical with a longer and steeper anterior edge. The ischium has a thin trunk; its iliac and pubic processes are almost the same size and the distal end is moderately widened. The pubis has a short prepubis and a short postpubis that makes up approximately one third the length of the ischium. The knee and talocrural joints are notably extended anteroposteriorly. The femur is slender, less than twice as long as the humerus and only two and a half times larger than metatarsal III. The tibia is roughly the same length as the femur, or only slightly smaller; the medial condyle of the upper epiphysis is significantly wider than the lateral condyle.

Species composition: Four species: *P. convincens* sp. nov.; *P. praeceps* (Parks), 1931; *P. erectofrons* (Parks), 1931; *P. cranibrevis* (Sternberg), 1935.

Distribution: Central Asia (Southern Kazakhstan) and North America (Alberta, Canada and Montana, USA).

Geological Age: Santonian–Campanian (Dabrazin, Belly River, and Two Medicine Formations).

*Procheneosaurus convincens*² sp. nov. (Figs. 13–15)

¹ The bones whose dimensions were derived are in no way part of the same specimen.

¹ A complete set of teeth has been observed in only *P. cranibrevis*.

Holotype. PI No. 2230; almost complete skeleton excluding the anterior region of the skull, distal regions of the forelimbs and left hind limb, and last caudal vertebrae; Senonian (Dabrazin Formation) Southern Kazakhstan, Shakh-Shakh Formation, 45 km north of Tashkent.

Diagnosis. The skull crest is low and short, its highest point is slightly in front of the orbit. The lacrimal is trapezoidal in shape and fairly large and wide, making up more than half the width of the orbit. The frontal swelling is much closer to the occipital edge than to the highest point on the skull crest. The quadratojugal completely isolates the jugal from the quadrate. The infratemporal fenestra is narrow, almost two and a half times narrower than the orbit. The neural processes of the dorsal vertebrae are moderately high, whereas for the anterior caudal vertebrae they are long, more than three times the height of the vertebral centrum. The scapula is moderately long, roughly seven times its minimal width. The anterior lobe of the ischium is more than twice as long as the posterior lobe, and the base of the bone has a well-developed pubic process that is almost one and a half times its height. The length of the anterior process of the pubis is less than twice its maximum width. The minimum diameter of the ischial process is one seventh the height of its proximal region. The distal condyles of the femur, extended anteroposteriorly, are almost one third as long as the entire bone and much less than twice its width. Of the proximal condyles of the tibia the medial is more than twice as wide as the lateral.

The skull, just as with cheneosaurs, is tall and narrow, its height in the orbit area being almost twice its width. Toward the occiput, which is just as tall and comparatively narrow, the skull narrows even more. The anterior region of the skull was destroyed (see Fig. 13), but judging by the posterior half, we may think that the crest, formed by the premaxillae and nasals, was not tall and slightly elevated above the dorsal surface of the skull, achieving its greatest length somewhat in front of the orbit. It is difficult to judge the shape of the nasal fenestrae because they are known only by their posteriormost region, located at roughly the same level as the upper edge of the orbit. We may assume that the nasal fenestrae of *P. convincens* must have been similar to those of the low-crested species of procheneosaurs in its features. The orbits are oval, slightly narrowing ventrally; their length is roughly one and a half times their maximum width. They are oriented at somewhat of an angle, thanks to which the infratemporal fenestrae are isolated from them ventrally by means of an overlapping bar as if they run below the orbits. The infratemporal fenestrae look like long, narrow ellipses, extended slightly ventrally and oriented at an angle, like the orbits. The

² *convincens* = indisputably proven, bearing in mind the Cretaceous age of the “dinosaur horizon”.

infratemporal fenestrae are three or four times as long they are wide. The supratemporal fenestrae are small, more than twice as short as the infratemporal fenestrae, rhomboid in shape and extended slightly along the medial line of the skull.

Skull Roof (Figs. 13–14)

The premaxillae are known only by their lower branches in their posteriormost region where they bound the nasal fenestrae cavity almost vertically. At the upper end, on the same level as the upper edge of the nasal fenestrae, the lower branches of the premaxillae contact the nasals which bound the nasal fenestrae dorsally by means of a short, straight suture. Posteriorly the lower branches of the premaxillae lie on the lower end of the frontals and lacrimals to form a slightly broken line. In those areas that were preserved the premaxillae are almost the same width as the lower end of the frontals and the upper end of the lacrimals, but taper slightly at the apex. The nasal fenestrae look like deep, fairly wide cavities that almost match the width of the skull in the nasal area and are overlaid laterally by the lower branches of the premaxillae. The nasal fenestrae reached the posterior edge of the latter and connected to an outwardly closed cavity, looking like a small rounded pocket within the nasals, where the latter form a ridge.

Excluding the anterior region, the nasals were almost completely preserved to outline the nasal fenestrae dorsally. Above the posterodorsal edge of the nasal fenestrae, the nasals are a dome-shaped swelling that forms a small, low crest (tubercle) within which is a cavity that connects with the nasal fenestrae. According to the shape and location of the crest, one of the most essential features of the cheneosaurs, *P. convincens* is similar to *P. praeceps*. The nasals are widest near the crest, making contact with the lower branch of the premaxillae and anterior region of the prefrontals which lay on the nasals along a slightly undulating line. Behind the crest-like swelling they narrow radically and look like slender, slightly posteriorly sloped wafers that lie between the prefrontals, but terminate prior to the latter. In the posterior region the nasals again widen slightly and make contact along a slightly serrated suture with the frontals, wedging slightly between them.

The prefrontals are wide in the area where they overlay the nasals and form the anterodorsal edge of the orbit. The prefrontals abut the lower edge of the premaxillae anteroventrally and include the apex of the lacrimals ventrally. The posterior boundary with the postorbitals looks like a slanted, non-uniform suture that runs from the highest point of the orbit's upper edge in the

direction of the anterolateral corner of the supratemporal fenestrae. The second posterior suture between the frontals and prefrontals is directed almost symmetrically to the first as a somewhat non-uniform line from the juncture of the postorbitals and frontals to the posterolateral nodes of the nasals. The boundaries of the medial surface of the prefrontals are indistinguishable.

The frontals are bounded anteriorly by the nasals and posteriorly by the parietals which are slightly wedged between them and isolated from the orbits by the wide band of the prefrontals and postorbitals. Along their periphery the frontals are slightly concave, and medially they form a substantial, round swelling that only slightly exceeds the nasals in size and serves as the roof for the braincase near the large hemispheres.

The parietals form the medial walls of the supratemporal fenestrae and are very short. Excepting the anterior boundaries with the frontals, it is only with some difficulty that we note the posterior boundaries where the squamosals form the sagittal ridge that rises above the parietals. The ventral boundaries of the parietals were quite indistinguishable.

Anteriorly the postorbitals look like a wedge on the dorsal surface of the skull, on the lateral side of which the upper posterior edge of the orbits is formed, and whose medial side bounds the prefrontals and frontals. The posterior portion of the postorbitals wedges into the squamosals by means of two tooth-like processes—the large process is the lower and the small process is the upper. The lower process is above the middle head of the quadrate and the upper extends to the center of the lateral edge of the supratemporal fenestra. Laterally, at a slight angle to the dorsal surface, the postorbitals yield a thin, but fairly long descending process that descends below the center of the orbit, isolating it and the ascending process of the jugal from the infratemporal fenestra. The boundaries of the postorbitals on the lateral surface are not clear.

The squamosals, which bound the supratemporal fenestra from the outside and behind, have a complex shape as is seen in other hadrosaurs. The postorbitals overlie the squamosals anteriorly, and together with them form the supratemporal arches while one anterior process of the squamosal underlies the postorbital ventromedially, extending to the anterolateral node of the supratemporal fenestra—and the second descends vertically downward, isolating the postorbital and quadrate and bounding the quadrate anteriorly. This second process of the squamosal is parallel to the ventral process of the postorbital, but is roughly twice as short and is far from the jugal and quadratojugal. The posterior surface of the process bounds the articular fossa in the squamosal for the quadrate, behind which is yet another descending process of the squamosal. This process is longer and

includes the quadrate posteriorly, overlaying the paroccipital process. Opposite this process the squamosals turn medially at a right angle, merging medially as the sagittal crest and forming the occipital surface of the skull. At the point of a very short contact between the squamosals and occipitals are corresponding half-moon shaped depressions in the squamosals for the exoccipitals to enter, and the suture surfaces of the squamosals form an overhang above the supraoccipital.

Occipital Surface (Fig. 15)

The supraoccipital, which underlies almost the extent of the squamosal cross-section, has a small, but very wide, rise, more than three times the height; the lateral flanges of the bone run far laterally beyond the occipital condyle. The dorsomedial region of the bone looks like a column above which the squamosals come together. From laterally and ventrally the supraoccipital is surrounded by the exoccipitals, the lateral sutures with which are finely serrated, and the lower suture is like an almost horizontal straight line.

The exoccipitals in their general features have the typical hadrosaurian two symmetrical ginglymi along the sides of the occipital condyle. By merging at the center without a suture they isolate the foramen magnum from the supraoccipital by a fairly wide band, below which the exoccipitals are notably concave, thanks to which the supraoccipital slightly overhangs them. The boundaries of the exoccipitals with the opisthotics, with which they form the paroccipital process, are not seen even though they are common in other hadrosaurs. The ventral boundary with the basioccipital is not clear owing to the deformation and destruction of the occipital condyle (this portion was reconstructed in Fig. 15). We may only assume that this boundary ran in the same manner as in other cheneosaurs.

Lateral Surface of the Skull (Fig. 13)

Only the posterior portions of the maxillae were preserved. They were included with the skull in a monolithic block and are therefore inadequately exposed. Posteriorly they terminate at the level of the coronoid process on the lower jaws, where they join dorsally with the lower processes of the pterygoids. Because the maxillae of hadrosaurs differ insignificantly even within families, we may assume that in *P. convincens* they are similar to those of the other cheneosaurs.

The lacrimals are subtrapezoidal in shape and wide, similar to the same bones in *P. praeceps* and *P. erectofrons*. Anteriorly they are separated by a straight suture that runs dorsally at an angle from the premaxillae. The lower suture—with the jugals—is a slightly undulating line with a depression in the middle for a small growth of the jugals. The dorsal boundary of the lacrimals with the prefrontals is not very clear, but in any case it rises upward at an angle from the premaxillae and then, as if descending to the anterior edge of the orbit, enters the prefrontals, in contrast to other species of *Procheneosaurus*, in which conversely the prefrontals enter the lacrimals. Posteriorly the lacrimals form the anterior edge of the orbits in their central part.

The jugals have the typical hadrosaurian shape and are especially similar to those of *P. erectofrons*. These are fairly thin, flat bones that are slightly convex laterally. Anteriorly they widen, forming a rounded cavity that overlaps the maxillae and lacrimals. How they interrelate with the premaxillae is unclear because the anterior portion was destroyed. Above, the jugals form the ventral boundaries of the orbits and the infratemporal fenestrae, separating them by means of the ascending process which originates at the center of the bone. This process, by meeting the descending process of the postorbitals in the center of the orbits and underlying it posteriorly, reaches almost to the dorsal edge of the infratemporal fenestra. The ventral edge of the jugal forms a notch below the orbit (symmetric with the upper edge) and again widens above the coronoid process, descending to the level of the teeth in the lower jaw. Posterior to the coronoid process, the lower edge of the jugal rises somewhat, reaching the quadrate. The posterior boundary of the jugal with the quadratojugal is unclear.

The quadratojugals, located between the quadrates and jugals, are shaped like a half-moon that mimics the posterior shape of the jugals. Due to the incomplete fossilization or surface loss on the thin and fragile bone, the dorsal and anterior boundaries of the quadratojugals are unclear. If the bones have been reconstructed correctly (Fig. 13), then they completely (or almost completely) isolate the quadrates and jugals as in *P. erectofrons*, although Ostrom (1961), for example, did not attempt to carry the boundaries between the jugals and quadratojugals when illustrating specimen No. 5461 of this species.

The quadrates enter the depression in the squamosals via their dorsal end and enter a notch in the lower jaws via the ventral end. The base trunk of the bone, which outlines the posterior profile of the skull, is slightly anteriorly concave. The lateral surface of the bone, widening from the epiphyses to the center, forms a deep, round notch for the quadratojugals here, dorsally and

ventrally from which the quadrate acquires the nature of two small round, anterior-leaning lobes. The medial surface, forming an angle with the lateral surface, transforms anteriorly into a broad triangular, thin, process flatly adjoining the oncoming process of the pterygoid.

The rounded shape of the dorsal and ventral quadrate condyles confirm its mobility, although Ostrom (1961) contradicts this because there is a descending process on the squamosal ahead of the dorsal quadrate condyle and a close union with the pterygoid. However, the dentary suture between the pterygoid process and quadrate processes that Ostrom found in *Corythosaurus casuarius* was not seen in *P. convincens*. Also, the descending process of the squamosal anterior to the quadrate condyle in *P. convincens* is very small, and the articular fossa of the lower jaw is rather large, explicitly allowing mobility.

Palatal Surface (Fig. 15)

The pterygoids consist of three regions, or processes: dorsal, ventral, and anterior (Fig. 15). The dorsal occupies the greatest area—a thin quadrate process that medially underlies the anterior quadrate process and traverses ventrally into a ridge-like ski-abutment that runs along the ventral edge of the anterior process of the quadrate. The mammiform pterygoid process of the basisphenoid descends anteriorly from each side into the depression formed by the vertical portion of the pterygoid quadrate process and its transverse ski. The articulation of the basisphenoid with the pterygoids apparently allowed motion in this region, thereby elevating the streptostyly near the quadrates. Anterior to the ridge-like ski-abutment, a rather thin, subtriangular process departs ventrally. This process is supported on the dorsal surface of the posterior end of the maxillae. The anterior pterygoid process contact with the palatine is poorly traced because of inadequate stripping of the skull in this area. For the same reason it is difficult to characterize the other bones on the palatal surface.

The palatines are the most accessible bones. The impression is created that the contact between the pterygoids and palatines was sliding and that the pterygoids probably underlie the palatines laterally and somewhat ventrally. The anterior ends of the pterygoids and palatines rise acutely, extending beyond the center of the orbit elevation and meeting at the anterior end of the parasphenoid.

Braincase

We have previously described the bones of the skull roof that form the roof of the braincase, and the bones of the occipital surface that form its posterior wall. The lateral walls and base of the braincase, not distinguished because of poor preservation, are partially covered laterally by other bones. On the lateral surface that was accessible for observation, the sutures between the bones were quite invisible. This makes it extremely difficult to describe these bones, and little can be used to characterize the species. We will only note that the union of the laterosphenoids with the skull roof by means of an articular process that is characteristic of other hadrosaurs was observed here to be only slight. This fact gives reason to assume that, analogous to crocodiles, the described articulation between the laterosphenoids and postorbitals is more highly developed in the long-snouted hadrosaurs, in which the force of collision arising when the jaws closed must have been greater, and correspondingly there is a more developed amortization. It is therefore possible that the primitive lambeosaur *Jaxartosaurus aralensis*, in which the previously mentioned type of articulation is well developed, maintained a fairly long snout in contrast to its descendants which became short-snouted, which may be associated with other adaptations to feeding and breathing.

Lower Jaws (Figs. 13, 15)

Only the posterior ends of the lower jaws were preserved. They are characterized by very high coronoid processes that reach the foundation of the orbital fenestrae and exceed the height of the dentaries by a factor of almost two. The lower jaw rami are so close to each other that there is practically no interstice between the dental batteries on both sides. Such closeness of the mandibles leaves a very narrow passageway for food, and a movable joint between the quadrates and the axial skull compels us to assume the possibility of motion within the skull itself. The sliding overhang of the jugal and quadrates and the sliding contacts of the pterygoids testify to this.

Teeth

The crowns of the teeth are barely visible and, what is more, are present as vertically long rhomboids with a single medial ridge and lacking supplementary ridges on the sides only at the end of the mandibles.

Hyoid Apparatus

Parallel to the lower jaw rami, almost abutting the mandibles, are the hyoids—apparently ceratobranchials I (Romer, 1956; Ostrom, 1961). They look like narrow, slightly curved wafers that contact each other in their broad anterior regions, extending beyond the anterior edge of the coronoid processes.

Vertebral Column

The structure of the vertebral column in *P. convincens* is rather typical for hadrosaurs in general and for lambeosaurs in particular. The number of bones is apparently the same as in *P. praeceps*, although the behavior of the boundaries between the vertebrae is arguable. Thus, the following formula is adopted for *P. praeceps*: 14 cervical, 16 dorsal, 10 sacral, and as many as 57 caudal vertebrae. But Parks (1931) noted that there may have been one fewer cervical and one more dorsal vertebra. Such a correction may be appropriate for *P. convincens* because the 14th vertebra, located behind the anterior edge of the scapula, had a tubercular neural process (the neural process is barely evident in the first 13 vertebrae, excluding the axis) and a rather long rib. In general, the number of presacral vertebrae in *P. convincens* is the same as in *P. praeceps*, 30. The substantial height of the neurapophyses on the dorsal vertebrae of *P. praeceps*, more than two to three times the height of the vertebral centra (Lull, Wright, 1942), was not seen in *P. convincens*, which may in fact be explained by the incomplete preservation of the neurapophyses.

There may be as many as ten sacral vertebrae, as in *P. praeceps*, but the first two have no direct contact with the ilia, even though they are located between them: the connections to the costal vertebrae, as is visible at least on the second of these, runs along the ilia, not touching the latter. It would probably be more correct to name these vertebrae false sacral vertebrae.

Approximately 40 vertebrae from the caudal region were preserved, and the first of these have very long neurapophyses, more than three times the height of the vertebral centrum. On the very first caudal vertebra, the wide-based, triangular processes grew abundantly and tend to approach the ilia. Highly developed ossified tendons that are intrinsic to *P. praeceps* are seen along the dorsal, sacral, and caudal vertebrae of *P. convincens*.

Pectoral Girdle and Forelimb

The sternum has the typical hadrosaur shape—its proximal area looks like a wide lobe that tapers notably upward, and ventrally ends as an uncinat process; distally this lobe transitions into the body of the bone, gradually widening at the end where the cross-section is almost twice the greatest minimum diameter of the body. The length of the bone body (to the uncinat process) is roughly equal to the lobe height.

The scapula looks like a fairly thin wafer, moderately concave along the ventral edge and almost straight along the dorsal edge. Above the dorsal edge the coracoid region the scapula projects slightly ventrally, without making an abrupt transition anteriorly, as though “truncated”, and does not extend beyond the glenoid region. The distal end of the scapula widens ventrally and is somewhat wider than the proximal end; and the minimum diameter of the scapular blade is approximately one seventh its overall length. The distal ends of both scapulae were somewhat destroyed (as a consequence of their extreme thinness and brittleness, or incomplete fossilization), but there is no reason to presume that the destroyed area was significant and may have significantly altered the ratios presented here.

The coracoid, like the sternum and scapula, is a fairly flat, light bone. Its ventral process does not look uncinat as is often seen in hadrosaurs, but subtriangular with a straight proximal side. This process is highly developed, descending significantly below the glenoid cavity, thanks to which the length (height) of the coracoid is more than one and a half times its width.

The humerus has the typical hadrosaur shape but is not massive, and has a moderately developed deltopectoral ridge. The dimension of the humerus is three quarters the length of the scapula.

The forearm bones, ulna and radius, also have the typical hadrosaur structure and they are both insignificantly longer than the humerus.

The carpus is unknown, but we may assume that it too had the typical hadrosaur form because the free-hanging forelimb apparently had a less functional load than the hind limbs, and its structure is therefore extremely unique in all hadrosaurs.

Pelvic Girdle and Hind Limbs

The ilium is long, slightly curved, and low, such that it is more than four times as long as it is tall, and the fraction of the anterior process (lobe) is almost half the entire bone. The posterior lobe is subtriangular, slightly more than twice as short as the anterior process. The pubic process is broad, only slightly wider than the ischial, thanks to which the bone base is almost one and a half times its height. The antitrochanter projection is asymmetrical—its posterior boundary is perpendicular to the dorsal surface of the ilium, and the anterior boundary is steeply inclined toward it.

The pubis has a short but wide anterior lobe (prepubis), so that its length is less than twice its maximum width. The dorsal edge of the prepubis looks like a broken line—initially a smooth curve and then straight—which bounds the widest portion of the lobe. The postpubis is small, the portion that was preserved being less than one-third the length of the ischium, although it was probably somewhat larger.

The ischium is characterized by a highly developed pubic process that is almost as wide as the ilium. The dorsal boundary of the bone shaft is almost straight, and the ventral is slightly concave. The bone shaft is thin, its minimum diameter being one-seventh the height of the proximal region. The bone widens notably toward the distal end—no less than two times in comparison with the minimum width of the shaft¹.

The femur is characterized by substantial anteroposterior extension of the distal condyles, reaching almost one-third the length of the bone. The lengthwise measurement of these condyles is almost twice that of their cross-section. The medial condyle is one and a half times wider than the lateral condyle. The condyles merge together, bounding an oval foramen, which is circular in most hadrosaurs. Here the oval must extend the condyles in not only posteriorly, but the anteriorly as well. Because of this the anterior surface of the femur is noticeably curved both proximally and

¹ The distal ends of both ischia were somewhat destroyed, and judgments about proportions can be made only on the basis of the portion that was preserved.

distally. The fourth trochanter looks like a scalene triangle in which the upper of the two outer sides is smaller than the lower.

The tibia is as long as the femur or slightly shorter (the left leg is not the same measure as the right leg). The upper shaft is much wider in cross-section, so that the lengthwise diameter is greater than the cross-sectional diameter by a factor of less than two. There is a deep, narrow notch between the condyles.

The upper shaft of the fibula is extended anteroposteriorly, just like the shafts of the femur and tibia, comprising two-thirds the lengthwise diameter of the upper shaft of the tibia.

The tarsals are represented by the astragalus and calcaneum, but were badly damaged in the holotype.

The metatarsals also have shafts that have been anteroposteriorly extended. Here the measurements of the upper shafts are on average twice that of their cross-sections. The difference between the lengthwise and cross-sectional measurements of the lower shafts are even less. The upper shafts of all three metatarsals very tightly abut one another, and are pear-shaped in plan view, widening inward from metatarsal IV to metatarsal II. The shaft of metatarsal II is very wide anteriorly and convex medially as well as on side facing the shaft of metatarsal III, which has a corresponding notch where the bones make contact. The metatarsal III and IV shafts are half-moon shaped in plan view as is metatarsal II in general, but more symmetrical. The lower shafts do not tightly abut one another. The metatarsal II shaft is fairly narrow and the smallest of the three, having a bean-like shape, whereas metatarsal III shaft is the largest of the three and has a subquadrangle shape in plan view, and the metatarsal IV shaft is of intermediate size and has a trapezoidal shape. In contrast to the lower shafts, the area of the upper shafts proceed in reverse order: the largest belongs to metatarsal III, next is metatarsal II, and the last is metatarsal IV. Overall, the metatarsus is fairly long and metatarsal III is two and a half times shorter than the femur. The lateral metatarsals are notably smaller than the middle, and metatarsal IV is shorter than metatarsal II.

All but the distal (ungual) phalanges are known. The first row of phalanges on all three digits is fairly long, their lengths substantially exceeding their widths, even including the central digit. The first phalanges of the lateral digits (II and IV) are the same size. The second phalanx of the digit II is subtriangular in shape, but with a very tapered anterior facet and interior boundary. The other phalanges of the III and IV digits are wide and short as in most hadrosaurs.

Analyzing the measurements, we can see asymmetry between the left and right sides, and this affects the postcranial skeleton as well as the skull. Especially noteworthy are the differences in the hind limbs: the bones of the right leg—femur + tibia is 4.5 cm longer than the same combination of the left leg. Because the left pes was not preserved, it is not clear whether this difference was compensated to some extent by the pes or, on the contrary, was enhanced. In any event, the differences in the framework of a single specimen compel us to bear in mind the more significant magnitudes of individual and age variability commonly accepted as taxonomic features (Rozhdestvenskiy, 1965).

It is therefore possible, for example, that the small specimens from the Two Medicine Formation (Montana) were assigned to *P. erectofrons* on the basis of its greatest similarity with it in the skull. These specimens were in fact members of *P. cranibrevis* that proceeded from the higher horizon of the Belly River Formation (Alberta) than the first species. The similarity with the earlier (judging by the stratigraphic level in the Belly River Formation) species—*P. praeceps*—in the postcranial skeletal structure is fully understandable in terms of evolutionary changes that presented the more conservative region with respect to the skull. The longer snout region of the young Montana specimen in comparison with *P. praeceps* and *P. erectofrons* also does not contradict assigning it to the fairly long-snouted *P. cranibrevis*. Here a situation may occur, analogous with *Saurolophus*, in which the young specimens of a later species are closer in terms of skull structure to the adult specimens of the ancestor than to its own species.

Comparison. The fundamental in the skull of *Procheneosaurus convincens* with other species of the same species can be seen in Table 2.

It follows from the table and the description that *P. convincens* is closer to *P. praeceps* and *P. erectofrons*, with which it is similar by way of the lower skull crest and overall configuration of the skull. *P. convincens* differs from *P. praeceps* in its large, broad lacrimal, substantially more posterior location of the frontal distension, separation of the quadrate from the jugal, and narrow infratemporal fenestrae. It differs from *P. erectofrons* in the trapezoidal shape of its lacrimal, more posterior location of the frontal distension, and substantially narrower infratemporal fenestra.

P. cranibrevis is the species most remote from *P. convincens*, as well as from *P. praeceps* and *P. erectofrons*, and differs from all of them by its highly developed skull crest which extends to the level of the posterior edge of the orbit with an overhang above the frontal distension. Also, differences between *P. convincens* and *P. cranibrevis* are seen in the lacrimal (trapezoidal and

triangular) and in the infratemporal fenestra—it is very narrow in *P. convincens* and broad in *P. cranibrevis*; the quadratojugal of *P. convincens* completely isolates the quadrate and jugal, but only partially separates them in *P. cranibrevis*.

Phylogenetic Relationships of Kazakhstan Hadrosaurs with Kindred Forms from Asia and America

Rjabinin (1939) correctly assigned *J. aralensis* to the subfamily Lambeosaurinae, noting important features such as the frontal distension and separation of the frontal from the upper edge of the orbit by a wide band formed by the prefrontals and postorbitals. The proportions and features of the orbits and temporal fenestrae of *Jaxartosaurus* are also intrinsic to the Lambeosaurinae. At the same time the wide skull with a low occiput and a long, narrow supraoccipital of *Jaxartosaurus* are very characteristic of the Hadrosaurinae. It is possible that the missing snout area of the skull was longer than what was intrinsic to the Senonian short-snouted lambeosaurs. Such a coincidence in the features of the two subfamilies may indicate that the Lambeosaurinae may have descended from the Hadrosaurinae, and that *Jaxartosaurus* must probably be placed at the beginning of the Lambeosaurinae genealogy. However, the morphological differences between *Jaxartosaurus* and other Lambeosaurinae, especially those such as between the cheneosaurs and *Parasaurolophus*, indicate that we do not as yet know all of the lambeosaur genealogical branches. Along with all this, the presence of a helmet-like crest in *Jaxartosaurus* says that if it cannot be an ancestor of the cheneosaurs, which did not have such a crest and have even been segregated by some authors (Lull, Wright, ~942) into an independent subfamily (Cheneosaurinae), then it may be considered a likely ancestor or a form close to it of the lambeosaurs proper which had the helmet-like crest.

The morphological level of *Aralosaurus tuberiferus* allows some things to be said about the place of this species in the family history. In many ways the structure of *A. tuberiferus* is primitive: a large lacrimal, small number of tooth rows, and the presence of an additional ridge on the crown of the lower jaw teeth, the underdeveloped deltopectoral ridge of the humerus, narrow lower shaft of the metatarsals, etc. These features represent fairly early stages of hadrosaur evolution; although, for example, the hollow tuber on the nasals and the absence of a fontanelle on the skull roof all testify to the specialization of the species that led it away from the fundamental line of flat-

headed hadrosaurs: *Bactrosaurus*—*Anatosaurus*. According to its level on the whole, *Aralosaurus* apparently occupies a middle spot (see Table 1) between *Bactrosaurus*, which is more primitive and the very earliest genus whose age can be dated as Cenomanian (Rozhdestvenskiy, 1966), and the Early Senonian *Lophorhothon* and *Kritosaurus*, whereas the late hadrosaurs—*Edmontosaurus* and *Anatosaurus* (Late Senonian–Danian)—are undoubtedly farther removed from *Aralosaurus*.

It may have been a mistake, however, to think of *Aralosaurus* as a direct descendant of *Bactrosaurus* and the ancestor of *Lophorhothon* and *Kritosaurus*. *Aralosaurus* stands out from this series mainly by its narrow infratemporal fenestrae. If it stands between *Bactrosaurus* and *Lophorhothon* according to the shape of the skull fontanelle and the extent of its development (completely absent in *Kritosaurus*), then it has more tooth rows than *Bactrosaurus* and *Lophorhothon* and fewer than *Kritosaurus*. *Kritosaurus* differs not only from the other three, but from other flat-headed hadrosaurs in that the frontals take no part in forming the orbits, i.e. by a feature that is characteristic of the helmeted (lambeosaurs), but not the flat-headed, hadrosaurs. Therefore, the true phylogenetic links here are much more complicated than can be shown at first glance.

We can evaluate the phylogenetic relationships in *Procheneosaurus* species by the development of their skull crest as a supplementary breathing apparatus for adapting to breathing while feeding underwater, because the degree of complexity and perfection of this apparatus must unconditionally reflect the level of development of this or another species. Therefore, we may think that of the four cheneosaur species *P. cranibrevis* is the latest and most progressive, whereas *P. convincens* is the earliest and most primitive.

However, in the cheneosaurs, along with some differences between one species, similarity is seen in the same features among other species. This complicates efforts to classify the true picture of the phylogeny of the genus *Procheneosaurus* and establish precise age (geologic) interrelationships between the Asiatic and American species. Thus *P. convincens*, being well distinguished from any of the American species in at least a few features, is at the same time similar to other species in each of these features that distinguish it from a given species.

In point of fact, *P. convincens* is notably different from *P. cranibrevis* in its skull configuration, yet by these same features it is very similar to *P. praeceps* and *P. erectofrons*, and judging by the location of the highest point on the skull crest immediately in front of the orbit is

closer to *P. praeceps*. However, the frontal distension in *P. convincens* is shifted posteriorly not only farther than in *P. praeceps*, but even farther than in *P. erectofrons*.

Thus, if we consider *P. praeceps* to be more primitive and ancient than *P. erectofrons*, then *P. convincens* clearly destroys this relationship because according to the shape and location of the crest it may be set alongside *P. praeceps* or maybe even between *P. praeceps* and *P. erectofrons*, whereas by the position of the frontal distension it goes beyond *P. erectofrons*. Unfortunately, it is impossible to compare the premaxillae and nasals of *P. convincens* (because they were destroyed in the holotype) and other species that are distinctive among themselves by their structure.

According to the trapezoidal shape of the lacrimal, which is most highly developed in *P. convincens* and may be regarded a relatively primitive feature, this species is close only to *P. praeceps* in which it may be subtriangular or trapezoidal, whereas in *P. erectofrons* and *P. cranibrevis* it is triangular, in *P. erectofrons* it is fairly tall and narrow, and is wide and short in *P. cranibrevis*. It turns out that, according to the structure of the lacrimal, *P. convincens* is beyond the outer limits of *P. praeceps*—*P. cranibrevis*.

In its narrow infratemporal fenestra (wide in *P. praeceps* and *P. cranibrevis*), *P. convincens* is also closer to *P. praeceps*, not occupying an intermediate position among the American species, whereas in the well-developed quadratojugal *P. convincens* unexpectedly proves to be close only to *P. erectofrons*—in both species it completely separates the jugal and quadrate. According to this feature, the next position is occupied by *P. cranibrevis*, and then *P. praeceps* in which the quadratojugal is small and only partially separates the quadrate and jugal.

However, in all the features within the hadrosaur genera we have examined, we have seen large variations that apparently have no specific direction. It is not likely that these variations, repeated numerously during the course of hadrosaur evolution, should be thought of as the result of adaptive radiation.

Fairly close to *Procheneosaurus* is a species from another genus—*Cheneosaurus tolmanensis*, two specimens of which (the skull and posterior region of an adult and the skull of a young specimen) were found in Alberta, but at a higher elevation than the Edmonton Formation, consistent with the Maastrichtian.

The single unique difference between this species (and genus) and the species of *Procheneosaurus* is the structure of the nasal fenestrae which are closed laterally by the compact premaxillary rami, whereas in the species of *Procheneosaurus* the nasal fenestra is open. Although

this feature may be considered important because it is associated with the structure of the respiratory apparatus, it varies greatly among the genera of lambeosaurs in general.

We will examine the structural features of *C. tolmanensis* that had been indicated as generic and specific features (Lambe, 1917a; Lull, Wright, 1942). *C. tolmanensis* was a moderately sized dinosaur having a short, but high skull that tapered anteriorly and widened posteriorly. This characteristic is similar for any of species of *Cheneosaurus*. Because of the size, shape, and location of the skull crest, *C. tolmanensis* occupies an intermediate position between *P. cranibrevis* and the other species in this genus. The long lower jaw with a sharply ventrally curved anterior edge in *C. tolmanensis* is almost identical to that in *P. cranibrevis*. The shape and proportions of the orbits and infratemporal fenestrae are roughly the same as in *P. convincens*. The trapezoidal lacrimal is also similar between *C. tolmanensis* and *P. convincens*. As in the species of *Procheneosaurus* the lacrimal of *C. tolmanensis* does not reach the maxillae. The premaxillae form a digitiform suture with the nasals as in *P. erectofrons*. The quadrate is relatively short and slightly curved as in *P. convincens* and *P. praeceps*. The squamosals are not separated by the parietals as in *P. convincens*¹. The quadratojugal is partial and separates the quadrate and jugal as in *P. praeceps*. The structure of the dental system in *C. tolmanensis*, including the number of tooth rows, is typical of most lambeosaurs. As far as the indications of two functioning teeth in a row are concerned, they are not clear and are possibly determined by the degree to which the tooth rows are exposed, whereas in all hadrosaurs, including the most primitive forms, there are no fewer than three teeth in every vertical row.

Thus, according to all of the features, excluding the premaxillary structure, *C. tolmanensis* is contained within the diagnosis of the genus *Procheneosaurus*, being distinguished from any of its species by no more than they are among themselves. On one hand this testifies to the conditional nature of genetic boundaries (Rozhdestvenskiy, 1966), and on the other hand makes us think that perhaps it would have been more correct to assign all the species of *Procheneosaurus* and the single species of *Cheneosaurus* to the single genus of *Cheneosaurus* (beginning from their priority). However, the author of this work does not consider himself fit to do this because he has not had an opportunity to visually study the American material; moreover, they have not been fully described.

¹ There are no data relative to other species of *Procheneosaurus*.

The study of the Kazakhstan hadrosaurs shows that they belong to three phylogenetic branches of the family Hadrosauridae—Hadrosaurinae (*Aralosaurus*), the cheneosaurs (*Procheneosaurus*), and Lambeosaurinae (*Jaxartosaurus*)—that characterize the early stages in the history of this family. The fourth branch of the hadrosaurs—Saurolophinae—are known from Central Asia (*Saurolophus angustirostris*) and North America (*S. osborni*). Thus, the Kazakhstan hadrosaurs merely emphasize the close bond that existed between the Asian and American dinosaurs, although even recently it has been almost impossible to say anything on this topic, and the famous American paleontologist O. Marsh (1897) perceptively wrote that “the Russian dinosaurs, like the snakes of Ireland, are known only by the fact that they are absent”.

Geologic Age of the Bone-bearing Layers in the Upper Cretaceous of Kazakhstan

Comparing *Jaxartosaurus* with the close genera of American lambeosaurs, the remains of which are known from the Belly River and Edmonton Formations which correspond to the Maastrichtian and Campanian, give us reason to think that *Jaxartosaurus* need not be significantly different from them in terms of geologic age. The latter can be placed not in the Cenomanian–Turonian interval as Rjabinin (1939) thought, but as Coniacian if not Santonian. The upper age boundary is the Santonian, limited by the discovery in the Tashkent region, immediately above the “dinosaur horizon” with *Jaxartosaurus*, of the skeleton of *Procheneosaurus convincens*, kindred species of which are known from the Belly River Formation of North America. As far as the age of the Chinese *Tanius* (“*Tsintaosaurus*”), to which *Jaxartosaurus* is very similar, is concerned, then the location of the Wangshih Formation containing the remains of *Tanius* within the bounds of the Upper Cretaceous is unclear. To assign this formation to the Cenomanian below the Iren Dabasu Formation (Lull, Wright, 1942) with the remains of *Bactrosaurus* is hardly proper because this species is the most primitive of the hadrosaurs, close to the late iguanodonts (Rozhdestvenskiy, 1966), whereas *Tanius*, from the morphological point of view, is undoubtedly a later form. For this reason the most likely location of the Wangshih Formation is, as the layer with *Jaxartosaurus*, in the Coniacian–Santonian interval.

The relationship between *Aralosaurus tuberiferus* and the other hadrosaurs makes it possible to determine its geologic age as being in the Cenomanian–Early Senonian, and more likely the Turonian–Coniacian. Nikiforova (1960), using general geological observations and

paleontological material (dinosaurs, turtles, vegetation), dated the Beleutinsk Formation to the Turonian–Santonian interval. A study of *A. tuberiferus* that came from this formation confirms and refines Nikoforov's data, allowing the pre-Senonian age of the Upper Cretaceous deposits that contained remains of this dinosaur to be established fairly reliably.

As far as *Procheneosaurus* is concerned, considering the rapid evolution of this genus in North America (during the Late Santonian-Campanian are three species) and the closeness of *P. convincens* to *P. praeceps* and *P. erectofrons*, it follows that in its age relationship the Kazakhstan species cannot be separated from the North American species by a large time span, and if we allow here that it is somewhat more ancient than them, its age may be accepted as earlier than Santonian. The upper limit of the possible geologic age of *P. convincens* must be considered Campanian. The discovery of a *P. convincens* skeleton in a fundamental position above the “dinosaur layers” allows us to not only correct the previously held concept of “re-deposition” of all the “dinosaur layers” of Tien Shan in the Paleogene, with which the author of this concept, I. A. Efremov (1963) agrees, but to reexamine the age of the “dinosaur” as well as the bone-bearing layers that lie above them. The latter, in which the skeleton of *P. convincens* was found, were dated to the Upper Turonian based on a study of mollusks (Belen'kiy, Mirkamalova, 1965; Belen'kiy, Rozhdestvenskiy, 1963; Rozhdestvenskiy, 1964a; Belen'kiy, Mirkamalova, (1965). The morphological similarity of *P. convincens* to the American species compels us to reject the Upper Turonian age of the bone-bearing layers in the Tashkent Chules and consider it to be younger—Santonian.

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Table 1. Similarities and differences in genera of the family Hadrosaurinae*

Feature	<i>Bactrosaurus</i>	<i>Aralosaurus</i>	<i>Lophorhothon</i>	<i>Kritosaurus</i>	<i>Edmontosaurus</i>	<i>Anatosaurus</i>
Nasals	flat, no crest	flat crest	small, pyramidal crest	crest	flat with no crest	
Fontanelle between nasals and frontals	small, ellipsoidal	moderately developed, ellipsoidal	highly developed, rhomboidal	nonexistent		
Frontal	participates in forming orbits			does not participate in forming orbits	participates in forming orbits	
Lacrimial	very large and tall			large but not tall	moderately developed, small	
Maxillae	low	tall with a broad apex			short with a narrow apex	
Jugal	moderately developed				highly developed	
Infratemporal fenestrae	fairly broad	narrow	broad		narrow	
Number of maxillary tooth rows	27	30	25	35-47 (?)	more than 50	

*Data obtained from Cope, 1883; Marsh, 1892; Brown, 1910; Lambe, 1914, 1917b; Gilmore, 1924; Sternberg, 1926; Lull, Wright, 1942; Langston, 1960; Rozhdestvenskiy, 1964b, 1966.

Table 2. Fundamental differences in skull structure among members of *Procheneosaurus*

Morphological feature	<i>P. convincens</i> sp. nov.	<i>P. praeceps</i> (Parks, 1934)	<i>P. erectofrons</i> (Parks, 1934)	<i>P. cranibrevis</i> (Sternberg, 1935)
Skull crest	low, with highest point ahead of orbit			fairly tall, helmet-like, highest point above the orbit
Lower branch, maxillary ramus		wide in middle of nasals	may overlap nasal fenestra in middle	almost completely covered by anterior region of nasal fenestra
Nasals		small, undivided anteriorly, begin at center of nasal fenestra and reach middle of orbit	small, separated anteriorly, originate at anterior edge of nasal fenestra, extend to center of orbit	large, unseparated anteriorly, originate from anterior edge of nasal fenestra, extend to center of orbit
Lacrimal	?	may reach maxillae		quite distant from maxillae
Frontal distension	much closer to occipital edge than to skull crest	midway between skull crest and occipital	somewhat closer to occipital edge than to skull crest	below skull crest
Quadratojugal	completely separates quadrate and jugal	does not completely separate quadrate and jugal	completely separates quadrate and jugal	completely separate quadrate and jugal
Infratemporal fenestra	two and a half times as narrow as orbit	twice as narrow as orbit	almost as wide as orbit	one and a half times as narrow as orbit

Cranium¹		Pubis	
Height in orbital region	23.0	Overall length	>44.0–48.0
Width in orbital region	12.0	Prepubis, length	23.0–23.0
Width in occipital region	10.5	Prepubis, maximum width	12.5–15.0
Length of orbit	10.0–9.5 ²	Postpubis, length	20.0–24.0
Width of orbit	6.5	Ischium	
Length of infratemporal fenestra	10.0	Length	>54.0
Width of infratemporal fenestra	3.0–2.7	Proximal region, width	21.0
Dorsal vertebra (11th)		Distal region, width	7.0
Neurapophysis, length	>6.5	Shaft, minimum width	3.0
Centrum, height	6~0	Femur	
Caudal vertebra (1)		Length	56.0–50.0
Neurapophysis, length	19.5	Distance from proximal end to origin of fourth trochanter	18.0–18.0
Centrum, height	6.0	Medial distal condyle, width	6.0
Sternum		Lateral distal condyle, width	4.0
Overall length	22.5	Lengthwise diameter of distal condyles	18.0
Proximal region, height	13.3	Tibia	
Body length	13.5	Length	56.0–59.0
Distal region, width	4.8	Lengthwise diameter of proximal shaft	>14.0–18.5
Coracoid		Cross-sectional diameter of proximal shaft	10.0–10.0
Length (height)	11.0–11.5	Medial distal condyle, width	6.0
Maximum width	7.0–8.0	Lateral distal condyle, width	3.0
Scapula		Fibula	
Length	>43.0	Length	52.0–55.0
Proximal region, width	10.0	Metatarsal II	
Distal region, width	11.0	Overall length	18.5
Minimum width	6.0	Lengthwise diameter of proximal shaft	10.0
Humerus		Metatarsal III	
Length	33.0–31.5	Length	23.0
Proximal end, width	9.0–9.5	Metatarsal IV	
Distal end, width	8.0–?	Length	17.0
Proximal end to lower point on deltopectoral ridge	21.0–18.0	Phalanx II-1	
Radius (right)		Length	5.5
Length	34.0	Phalanx III-1	
Ulna (right)		Length	7.0
Length (without olecranon)	35.0	Phalanx IV-1	
Ilium (left)		Length	5.5
Overall length	51.0		
Length of base	18.0		
Height at base	13.0		
Preacetabular process, length	24.0		
Postacetabular process, length	11.0		

¹There is a slight deformation in the skull near the temporal fenestrae

²Dual measurements are shown when there is a difference between the left and right sides

Figure Captions

Figure 1. *Jaxartosaurus aralensis* Rjabinin. Skull, dorsal view. *Eo* – exoccipital; *F* – frontal; *Ls* – laterosphenoid; *P* – parietal; *Po* – postorbital; *Pf* – prefrontal; *Prot* – prootic; *Sq* – squamosal.

Figure 2. *Jaxartosaurus aralensis* Rjabinin. Skull, ventral view. *Bo* – basioccipital; *Bs* – basisphenoid; *Opot* – opisthotic; *Pas* – parasphenoid; *Prs* – presphenoid. Other designations are the same as in Figure 1.

Figure 3. *Jaxartosaurus aralensis* Rjabinin. Skull, posterior view. *So* – supraoccipital. Other designations are the same as in Figure 1.

Figure 4. *Jaxartosaurus aralensis* Rjabinin. Skull, right lateral view. *II-XII* – exits for cranial nerves; *c.v.a.* – channel for venous anastomosis. Other designations are the same as in Figures 1 and 2

Figure 5. Diagram showing blood vessels in the braincase area of *Jaxartosaurus aralensis* Rjabinin. *a.b.* – basilar artery; *a.c.a.* – anterior cerebral artery; *a.cbl.* – cerebellar artery; *a.c.i.* – internal carotid artery; *a.cr.a.* – anterior cranial artery; *a.m.* – mandibular artery; *a.o.i.* – inferior orbital artery; *a.o.s.* – superior orbital artery; *a.oph.* – ophthalmic artery; *a.p.* – palatine artery; *a.st.* – stapedial artery; *c.v.* – entry into carotid sinus; *d.p.* – channel for perilymphatic duct; *v.c.l.* – lateral capitular vein; *v.h.* – hypophyseal vein; *v.j.* – jugular vein; *VII_m* – mandibular branch of facial nerve; *VII_p* – palatine branch of facial nerve. Other designations are the same as in Figures 1 and 2.

Figure 6. Reconstruction of the musculature of the orbito-temporal region of *Jaxartosaurus aralensis* Rjabinin. *M.L.* – levator bulbi muscle; *M.o.* – oblique muscle; *M.r.* – rectus muscle; *M.p.*, *M.m*, *M.s.* – deep, middle, and superficial portions of external mandibular adductor muscle; *M.pt.* – pseudotemporalis muscle; *O* – contour of orbit; *II-XII* – exits for cranial nerves.

Figure 7. *Aralosaurus tuberiferus*, gen. et sp. nov.; skull in dorsal view, holotype No. 2229/1. *J* – jugal; *N* – nasal; *f* – fontanelle. Other designations are the same as in Figure 1.

Figure 8. *Aralosaurus tuberiferus*, gen. et sp. nov.; skull in lateral view, holotype No. 2229/1. *D* – dentary; *L* – lacrimal; *Mx* – maxilla; *Pd* – prementary; *Pmx* – premaxilla; *Q* – quadrate; *Qj* – quadratojugal; *Sa* – surangular. Other designations are the same as in Figures 1 and 7.

Figure 9. *Aralosaurus tuberiferus*, gen. et sp. nov.; skull in posterior view, holotype No. 2229/1. Designations are the same as in Figures 1 and 3.

Figure 10. *Aralosaurus tuberiferus*, gen. et sp. nov.; braincase, holotype No. 2229/1. a – lateral view; b – dorsal view. Designations are the same as in Figures 1–5.

Figure 11. *Aralosaurus tuberiferus*, gen. et sp. nov.; brain cavity in ventral view, holotype No. 2229/1. *c.a.* – zygomatic cavity; *Cbl* – cerebellum; *Cbr* – cerebral hemisphere; *f.s.* – supratemporal fenestra; *L.o.* – olfactory lobe; *ms* – mesencephalon; *mt* – metencephalon; *ml* – medulla oblongata; *ps* – prosencephalon. Designations are the same as in Figures 1–7.

Figure 12. *Aralosaurus tuberiferus*, gen. et sp. nov.; teeth. a – left lower jaw tooth crown from lingual side, No. 2229/2; b – upper left jaw tooth from labial side.

Figure 13. *Procheneosaurus convincens*, sp. nov.; skull in lateral view. Designations are the same as in Figures 1-8.

Figure 14. *Procheneosaurus convincens*, sp. nov.; skull in dorsal view, holotype No. 2230/1.

Figure 13. *Procheneosaurus convincens*, sp. nov.; skull in posterior view. *pt* – pterygoid. Designations are the same as in Figures 1-8.