R. Barsbold

CARNIVOROUS DINOSAURS FROM THE CRETACEOUS OF MONGOLIA

THE JOINT SOVIET-MONGOLIAN
PALEONTOLOGICAL EXPEDITION

(Transactions, vol. 19)

Transactions of the Joint Soviet-Mongolian Paleontological Expedition 19: 5-119, 30 figs.

translated by C. Siskron and S. P. Welles
translation edited and emended by M. Carrano: [text in brackets] has been added or altered from original translation, or represents an unclear original translation.

??? SECTION

CHAPTER I

COMPARATIVE MORPHOLOGY OF CARNIVOROUS DINOSAURS

SKULL

The skull of carnivorous dinosaurs, in spite of a series of detailed studies, has been largely known in general terms. As a rule, its structure has been illustrated in external view, and often the external appearance and proportions were given too great a significance. In many cases a combination of the completeness and preservation of the skull material limited the [ability to perform] a more detailed study to a great extent. Until recently, cranial features were based on the study of hardly more than ten kinds of carnivorous dinosaurs. In addition, only single specimens displayed a more or less high degree of preservation and, as a result, a corresponding wealth of information. It is apparent that a series of basal elements in the skull construction of carnivorous dinosaurs have not been sufficiently illustrated, particularly with the plan of revealing certain features common to entire lineages of carnivorous dinosaurs. In many ways, this concerns the construction of the neurocranium and other skull structures and complexes, without sufficient knowledge of which it has been impossible to discuss the details of morphological groups.

Recently a wealth of new information has become known regarding the construction of the skull in carnivorous dinosaurs. The facial crest of oviraptorids, a characteristic sphenoid capsule in the base of the skull, and the inner ear bones of Mongolian ornithomimids and saurornithoidids were noted among the most interesting features (Osmólska, Roniewicz, and Barsbold, 1972; Barsbold, 1974). A pocket was found in the ear region of the central Asiatic *Itemirus* that was originally described as "inner auditory" (Kurzanov, 1976a). The question of the development of the semicircular canals of the inner ear was raised, discussed controversially until recently (Rozhdestvensky, 1968; Kurzanov, 1976a; Ostrom, 1964), and now has been decided negatively. Foremost, the study of these listed features on the whole helps [to develop] a deeper knowledge of skull anatomy in the carnivorous dinosaurs. On this basis an attempt was undertaken to sort out new groups of carnivorous dinosaurs that revealed themselves more clearly upon study of their skull and that of the aforementioned *Itemirus* (Kurzanov, 1976a). Some of the features had been acknowledged as unique (as it turned out, without sufficient basis), and this was reflected in the characteristics of the taxon of the corresponding class.

The material presently accumulated of Mongolian carnivorous dinosaurs clearly reveals a series of peculiarities in the construction of the basicranium and ear region. This justifies the need for addressing a series of questions on the skull anatomy of carnivorous dinosaurs in greater detail, and subsequent interpretations of the general aspects of their morphological evolution follow from their conclusions.

Facial Region. The facial region (Fig. 1) is considerably elongate and fairly low in most small carnivorous dinosaurs, especially in a series of "narrow-skulled" forms such as dromaeosaurids (*Velociraptor*), saurornithoidids, ornithomimids, etc. At the same time, the facial region often becomes fairly tall as the skull becomes larger, which is characteristic primarily of carnosaurs and "high-skulled" dromaeosaurs. Small-sized oviraptorids are characterized mostly by their shortened facial region.

The upper jaw was dentigerous in the majority of forms, or edentulous, as in garudimimids, the first group of carnivorous dinosaurs to become well known as being equipped with a horny beak (Marsh, 1881). Later, oviraptorids were added to this group (Barsbold, 1976a, b; Osborn, 1924), and most recently caenagnathids (Osmólska, 1976), of which only the lower jaw is known (Sternberg, 1940; Cracraft, 1971). *Erlicosaurus* is a special case in which the front part of the jaw was toothless. The upper jaw in ornithomimids, which comprises the bony base of the upper beak covering, is elongated and slightly widened, and on the whole preserves the proportions known in the toothed forms. The upper jaw of oviraptorids is completely opposite – it was extremely tall, yet the main bone comprising it is the premaxilla, with a wide lateral surface that serves as the basis for the horny beak. The jaw bones are highly shortened, which is uncharacteristic for carnivorous dinosaurs. In segnosaurids, the general proportions of the upper jaw are approximately the same as in toothed forms, however the premaxilla and the anterior region of the mandibular bones were edentulous, whereas the greater part of the dentary in the lower jaw bore fine teeth of a "carnivorous" nature. The dimensions and shape of the toothless portion of the upper jaw reveal the shortening and slight widening of the horny covering.

The external nares are usually located on the anterior end of the facial region. Only in oviraptorids were they placed posteriorly and sharply dorsally, higher than the antorbital fenestra, which is an essential deviation from the norm in carnivorous dinosaurs. The nasal sinuses in segnosaurids are more unusual, extending for more than half of the facial region.

The jaw bones anterior to the antorbital fenestra are perforated by one or two small openings that are usually called accessory antorbital fenestrae (Osborn, 1912). However, the medial construction of the jaw bones turns out to be fairly complex. Isolated regions are [present internal to] the nasal process of the maxilla that are interconnected but divided by a partition, the maxillary septum (Madsen, 1976a). The thinness of the medial wall does not match their preservation in the excavated condition, and this has prevented a more detailed understanding of their construction until now. A similar structure has been observed in ceratosaurids under the name of the jaw region or maxillary sinus (Hay, 1908) and, [subseuquently], in *Allosaurus* and *Marshosaurus* (Madsen, 1976a), apparently in *Deinonychus* (Ostrom, 1969a, b), and also in the Mongolian ankylosaur *Saichania* (Maryanska, 1977). Apparently this region was connected with the nasal, and so they should be called maxillary sinuses. They begin immediately behind the external nares and open laterally to the antorbital fenestra. In oviraptorids, maxillary sinuses are located above and behind the posterodorsal displacement of the external nares. In allosaurids (Madsen, 1976a), the sinuses are perforated anteriorly and posteriorly, and consist of two chambers divided by the maxillary septum. Each of these chambers has a separate medial and dorsal opening. The sinuses stretch along the inner surface of the maxilla along the occupied space corresponding to the palatal processes contacting each other, which can be clearly observed in tyrannosaurids.

The dorsal surface of the facial region in some groups is highly sculptured. Among some ceratosaurs there is a large projection with the appearance of a widened nasal horn, and in others paired sculptured crests extend along the edges of the nasal and prefrontal to the lacrimal. The greatest expression is reached in *Dilophosaurus*, and to a lesser degree in allosaurids (Marsh, 1884; Hay, 1908; Gilmore, 1920; Madsen, 1976a, b). However, these are all Early Jurassic forms. Later lineages are known only by the later development of characteristic bone extensions. The unpaired, laterally compressed, tall, elongate crests in oviraptorids (Barsbold, 1981) extend from the upper part of the premaxilla to the anterior edge of the frontal, inclusively (Fig. 2). The premaxilla carries one more extension besides the usual nasal processes, that being the most anterior one, which rises from the anterioventral edge of the bony crest. The nasal and maxillary processes bound the large, elongated external nares. The large posterior part of the crest, apparently formed from the nasal bone, has very narrow and elongate anterior processes that form the dorsal edge of the external nares, above which passes the highest part of the crest. The frontals participate in its posterior edge via their massive extensions, which the dorsal edge of the crest passes as it falls obliquely. The lateral surface is not solid, but is composed of thin, braiding bone. The lateral walls of the crest are [appressed] almost to the point of contacting one another. The anterodorsal, more or less solid bony edge of the crest bears narrow, elongate paired opening or pockets, not clearly delineated and divided by a lateral projection. The depth of the opening could be limited by the width of the solid bony edge, [but] they freely connect with the narrow space between the walls of the crest. Its open structure testifies to the fact that the crest could have had a horny covering (as in cassowaries) that demanded a great deal of blood. In the cassowary, the bony base of the horny crest occupies the roof of the skull all the way to the parietal, and is also considerably distinguished by the porosity of its bone. It should be noted that the bony crests are particularly notable in the skulls of larger oviraptoroids, and absent in other forms – *Ingenia.* In this, the only skull of smaller size and somewhat doubtfully classified among oviraptoroids, the crest is absent, allowing us to note age or sex variations.

The Anterior Neurocranium. It is sufficient to limit the study of this part to the laterosphenoid and orbitosphenoid, rather than other elements that are more subject to modification in different types of carnivorous dinosaurs. Laterosphenoids are present in all the studied groups. Often they form a large part of the lateral wall of the neurocranium (Fig. 3), form the orbital wings in the ventral part of the anterior section of the skull, and also enter into the region surrounding the optic nerves. The lateral wall of the laterosphenoid is connected with the parietal for a considerable extent. This edge is mobile in character and belongs among the elements considered critical for the appearance of metakinesis among carnivorous dinosaurs. The connection of the orbital wing of the laterosphenoid with the postorbital and frontal is usually solid. In several groups, the laterosphenoid lies on the prootic part of the posterior hypophyseal cavity. The laterosphenoid often participates independently in the formation of the opening for the passage of the optic nerve. It sometimes considerably surrounds this passage, a feature that is also present in saurornithoidids and dromaeosaurids. The laterosphenoids in tyrannosaurids come close to the optic foramen, but do not directly participate in its formation because they are separated by the orbitosphenoids. An analogous condition is observed in allosauroids (Madsen 1976a). The laterosphenoids can extend considerably forward from the level of the deviation of the orbital wing, and participate in the formation of the ventral surfaces of the anterior neurocranium. In this case they border the orbital part of the frontals, as observed in oviraptorids.

The position of the orbitosphenoids is quite variable. They may be reduced, occasionally to complete absence. This is apparently the case in saurornithoidids and dromaeosaurids, whereas the reduced orbitosphenoids in ornithomimids only occupy a region limited to the lower edge of the optic foramen. In tyrannosaurids, as noted, the orbitosphenoids completely surround this foramen and extend forwards, forming a short, narrow middle section of the ventral surface of the frontal region of the neurocranium within the orbital edges of the frontal. The orbitosphenoids are located in a similar position among oviraptoroids. Internally, they form a tubular optic canal separated from the more highly positioned olfactory nerve passage.

Basicranium. The specific features of the basicranium in carnivorous dinosaurs allow us to identify at least three types, distinguished mainly on the degree of development of the basisphenoid capsule.

The first type includes neurocrania lacking a capsule. In general, this was considered characteristic of carnivorous dinosaurs, and was known in variable detail in tyrannosaurids and dromaeosaurids, as well as the earlier allosaurids and possibly coelurids. The second type includes skulls with a capsuled base, whose construction is characterized by the presence of a unique basisphenoidal capsule, first described in Mongolian ornithomimids and saurornithoidids (Osmólska, Roniewicz, and Barsbold, 1972; Barsbold, 1974). The third type, conditionally termed intermediate (between the first and second), does not have a completely formed capsule, and the basicranium is differentiated by a considerable widening, including the frontal part where the basisphenoidal capsule was located in the capsuled type. Even though formation of the capsule did not occur, the frontal part of the basicranium seems to have nearly reached the capsular structure externally. A system of sinuses is developed inside the basicranium. The intermediate type is found in *Erlicosaurus* (Barsbold and Perle, 1980).

The study of the unique features of these neurocrania should begin with the simplest (capsuleless) type.

Capsuleless Type (Fig. 3). The absence of the capsule is [apparent] to a considerable degree in the configuration of the basicranium. First of all, it is not as notably widened, and along with this the basipterygoid and sphenooccipital processes are much more prominent than in other types. Tyrannosaurids and allosaurids are the most sharply delineated, in which the base of the basisphenoid projects strongly anteroventrally, forming two elongated basipteryoid processes with well-developed articular surfaces. The basioccipital is connected behind the basisphenoid, forming the occipital part of the wide, massive sphenooccipital elevation. The cristae ventrolateralis et tuberalis are highly developed. Mongolian dromaeosaurids have a similar basicranial construction, as well as *Itemirus* (Kurzanov, 1976a) and allosaurids (Madsen, 1976a). The increase in height of the basicranium and the entire skull is related to the vertical distance of the basisphenoid. A relatively small skull height is observed in the gigantic carnivores with maximal extension of the basisphenoid. These are primarily tyrannosaurids and allosaurids, secondly are "high-skulled" dromaeosaurids

(*Dromaeosaurus*-type), and the last in the diminishing series of skull height are "narrow-skulled" dromaeosaurids (*Velociraptor*-type).

Notably, the basicranium in oviraptorids is beyond the extent of the studied types. It is formed on a compact platform, elongated anteroposteriorly, and somewhat compressed, which are uncharacteristic for the basicranium of capsuleless types. The greatest deviation is in the unusually strong reduction of the basipterygoid processes, which are almost undifferentiated from the base of the basisphenoid. The pterygoids connect (and possibly fuse) to the two basipterygoid processes. Such fusion must completely block or strongly limit its mobility. Oviraptorids are similar to intermediate types in the degree of reduction of the basipterygoid processes and the absence of a sizeable ventral process of the basicranium. However, the absence of a large degree of basicranial widening, studied in the context of determining "intermediateness", supports placement of the oviraptorid basicranium in the category of the capsuleless type.

The basisphenoid rostrum in the capsuleless type extends anteriorly and above the interpterygoidal cavity in the horizontal plane. In tyrannosaurids and allosaurids, the rostrum consists mainly of the skull base in the vertical plane and approaches the anterior region of the neurocranium. In contrast, dromaeosaurids are characterized by the lower position of the rostrum, and the Mongolian *Velociraptor* most likely shows the extreme condition in this regard. A very low rostrum position is also characteristic of oviraptorids. In addition, the base of the rostrum is highly compressed and widened in the sagittal plane, but without any [overall] widening.

The capsuleless basicranium mostly likely evolved along with the mobile basipterygoid joint necessary for the wide distribution of metakinesis in the carnivorous dinosaur skull. Unique characteristics of the capsuleless skull base, such as the highly developed basipterygoid processes (as evidenced by their elongation), massiveness, the well-developed articular end, etc., reveal a considerable mobility in this joint. Reduction of the basipterygoid processes in oviraptorids is possibly tied to the blocking (or limited mobility) of this single connection. The middle ear in a skull of any given size did not have a defined bony surface and exhibited typically reptilian characters.

Capsuled Type (Fig. 4). The capsular construction of the basicranium was first established in Mongolian ornithomimids and saurornithoidids (Osmólska, Roniewicz, and Barsbold, 1972; Barsbold, 1974). It is possible to distinguish two structural types: in the first, the basisphenoid capsule is open posteriorly (ornithomimosaurs); in the second, the capsule does not have an external opening (saurornithoidids).

In both cases, the basisphenoid capsule appears as a spur-like, pear-shaped POLOE formation in the base of the braincase, with its narrow end directed anteriorly. Posteriorly, the widest region of the capsule exhibits unique characteristics in each subtype. A narrow groove extends dorsally along the capsule midline, which becomes a basisphenoidal rostrum, and delineates the base of the interocular division.

In the ornithomimid subtype, the basisphenoid capsule becomes a short, tall [antechamber] bearing its widest part before the fenestra, which opens to the outside posteriorly by a large, depressed, ventrally-widened opening. The floor and side walls of the [antechamber] threshold, which are formed by the ventral part of the basicranium and also form the lower edge of the opening, are limited by the basipterygoid processes; the ventral processes from the sphenooccipital elevations are connected with the latter, paired, have complex lateral cross-sections, and frame the external opening laterally. The dorsal end of each of the ribs is located slightly anterior to the basioccipital part of the sphenooccipital elevation, sending a convex ventrolateral crest back to them (a similar crest is known in the lizard *Save*; Soderbergh, 1947) that participated in the formation of the elevation. The medial surface of the wall of the threshold along the edge of the inner opening, which actually connects the capsule with the threshold, is analogous in form to the crest that connected with the ventrolateral cross-sectional bridge. As a result of the development of the large, posterior external opening of the basipterygoid process, which limits it ventrally, the sphenooccipital elevations were positioned considerably lower and the base of the basicranium was interrupted in this part.

The saurornithoidid subtype of the capsule is distinguished primarily by the absence of the posterior external opening. As a result of this, the ventral part of the basicranium is formed without any interruption. The basisphenoid capsule supposedly had a connection with the system of sinuses that was developed inside the ventral part of the basicranium. In addition, the capsule in saurornithoidids is connected with the middle ear region by a passage or opening into the rear wall, or by the sinuses. In this manner, the threshold is not formed by the external opening in the saurornithoidid subtype (as it was in ornithomimids). The basipterygoid process and sphenooccipital elevations are located on the same level. The ventrolateral crest of the basicranium does not develop.

Intermediate Type (Figs. 5, 6). In the base of the skull of *Erlicosaurus*, the full, posterior, pear-like basisphenoid capsule is not developed, although this region is highly widened overall. This gives the appearance of a transitional stage in the formation of the capsule. The widening affected not only the anterior basicranium, but to a large degree the posterior, structurally connected with the middle ear region which has characteristics of saurornithoidids. The anterior part is developed to form a convex base of the anterior extension of the basisphenoid, which is weakly delineated from the remainder of the basicranium. A grooved edge extends dorsally along the extension of the process that originates in the interocular partition. The ventral surface continues posteriorly without interruption from the basipterygoid processes to the sphenooccipital elevations. These structures are found on the same horizontal level, as in saurornithoidids.

The inner area of the basicranium is interpreted as a system of sinuses. This means that the basisphenoid capsule is connected to the ventral sinus system in the base of the braincase of the skull. It is also necessary to note that, in comparison with the widened basicranium of *Erlicosaurus*, the post-capsular part at the base of the skull is highly reduced in ornithomimids and saurornithoidids; therefore, the sinus system in the latter is developed, although to a large degree the capsule replaced it.

The construction of the basicranium dimensions described above reflects the "closed" type of basisphenoid capsule position to a certain degree, *i.e.* lacking the posterior external opening. The characteristic features seem to support such a conclusion. First of all, the topographical and structural correlation of the basisphenoid rostrum in the capsules and the basicranial dimensions are identical in both types. Secondly, the capsule lacking the posterior opening is linked to the middle ear by the appearance of a fully formed osseous region, first noted in saurornithoidids (Barsbold, 1974) and also found in *Erlicosaurus* (Barsbold and Perle, 1980). A similar area is absent where the capsule with the external opening was present, as in ornithomimids.

The basisphenoid capsule was first described as possibly related to Rathke's pouch (Osmólska, Roniewicz, and Barsbold, 1972). However, the inner ear region of the capsule is too large to correspond to the purely embryonic formation that Rathke's pouch appears to be. It was noted that the capsuleless basicranium in *Erlicosaurus*, which is enlarged in dimensions by a sinus system but lacks a capsule, suggests that the basisphenoid capsule is connected with pneumatization of the basisphenoid. The system of pneumatic sinuses in the skull base is well-known in crocodiles and birds; in the former, the pneumatic sinuses are connected with the eustachian tube. Very large pneumatic sinuses are also found in the skull base in Protosuchia (Walker, 1972). It is possible that the capsular basisphenoid present in two theropod groups – ornithomimids and saurornithoidids – is [related to] the further pneumatization of the skull that is widely distributed in archosaurian lineages.

Carotid Canal. The development of the carotid canal was first noted in dromaeosaurids and *Itemirus* (Colbert and Russell, 1969; Kurzanov, 1976a), in which openings leading to the internal carotid artery were discovered on the lateral side of the base of the basipterygoid process. In *Itemirus*, the carotid arteries pass through the sinuses in the body of the basisphenoid on the way to the hypophyseal pocket. The foramina for the carotid canals were possibly located in a similar position in allosaurids (Madsen, 1976b). It was not possible to observe these foramina in tyrannosaurids and oviraptorids. With the noted position of the carotid canals, the palatal branches of the internal carotid arteries pass under the skull base on the surface along with the carotid branches of the facial nerve, which is seen in *Itemirus* (Kurzanov, 1976a) and assumed to be present in dromaeosaurids. In this case, the palatal branches of the carotid artery and the facial nerve passed under the base of the basipterygoid process and continued more anteriorly.

Parabasal Canals. Parabasal canals were successfully located in ornithomimosaurs, segnosaurs, and saurornithoidids (Fig. 7). The most complete image of their structure was produced by study of garudimimids, the primitive ornithomimosaur lineage, who filled in the gap that existed in this plan until now.

The entrance into the parabasal canal in garudimimids is an opening located immediately anterior to the shortened, transversely-directed pterygoid process near the posteroventral edge of the capsule, approximately in the area of the transition to the ventral surface of the basicranium. It was previously noted that this transition is uninterrupted in the capsuleless type.

Externally, sutures are not observed in the examined regions between the basisphenoid and the parasphenoid, which covers it ventrally. Pterygoids, displaced to the anterolateral edges of the [incurrent] foramina, apparently line the basicranium and do not participate in the formation of the canals which lead between the basisphenoid and parasphenoid. The incurrent openings of the canals are fairly large and oval in shape, with the long axis directed [at an] angle to the sagittal plane. Openings lead to the short vertical canal that extends [from] the region of the transitional posteroventrolateral edges of the basisphenoid capsule beyond the capsular part of the basicranium. The anterior region of the quadrate flange of the pterygoid is adjacent to the outside of the wall from the departure of the lower edge, where a fissure-like passage is formed that was lined with the main body of the pterygoid and apparently allowed the palatal artery and branch of the facial nerve to proceed anteriorly.

The blockage of the basipterygoid connection, which is related to reduction of the basipterygoid processes and losing the joint-like character of their distal edges, has no small significance in the studied type of parabasal canals. Besides this, the development of a pterygoid that lines the ventral surface of the basicranium in the region of the opening also illustrates the limited mobility of the basicranial articulation. The reduction of the interpterygoid fenestra is quite clear.

Identification of the construction of the basicranial region in ornithomimosaurs allowed [noting] a similar type in the parabasal canals of advanced ornithomimids, the corresponding part of the skull of which was preserved only partially in the collection. In *Gallimimus* there are transversely shortened basipterygoid processes, with which the ventral part of the basisphenoid capsule fuses, and similarly constructed parabasal canals are found in the region of the capsular and trans-capsular part of the basicranium. Only the poor condition of the studied region has, until now, denied the possibility of correctly interpreting these structures in *Gallimimus* (Osmólska, Roniewicz, and Barsbold, 1972). Blockage of the basipterygoid connections is also observed in this case.

Transverse basipterygoid processes are also found in saurornithoidids that are distinguished only by their elongation and width, with which the ventral part of the basisphenoid capsule is connected anteriorly. The transitional region from the capsule to the trans-capsular region of the basicranium is, in general, similar to that of ornithomimids, and provides a basis for assuming similarity in the construction of the parabasal canals. Possibly the position of the pterygoid near the lateral part of the capsule was also similar, allowing supposition of an analogous anterior passage of the palatal artery and branch of the facial nerve.

In many ways, a close similarity is noted in the construction of the parabasal canals of segnosaurids. In *Erlicosaurus*, the basisphenoid capsule is absent, and the basipterygoid processes are highly reduced and seem to have been forced out by the considerably widened basicranium. The entrance into the parabasal canal is limited posteriorly by reduced pterygoid processes, in contrast to the fissure-like opening seen in ornithomimids. The pterygoids also move towards the anterolateral edge of the incurrent opening, apparently lining the basicranium, and do not participate directly in the formation of the canal. As in the case of the capsuled type, incurrent openings lead into short vertical canals that continue into the anterolateral area of the basicranium, which is adjacent to the beginning regions of the quadrate flanges of the pterygoids externally. They form a fissure-like opening as they move away from the anteroventral basicranium, allowing the palatal artery and branch of the facial nerve to pass through anteriorly. Blockage of the basipterygoid connection possibly reaches its highest degree, not only in the maximal reduction of the basipterygoid processes, but also in the additional presence of a hypertrophied connection with the vomer, as studied below. The interpterygoid fenestra is considerably reduced.

Examples of the construction of the parabasal canals in different types of carnivorous dinosaurs allows study of the common conditions of their development. First of all, in general structure the parabasal canals are connected with the development of the basisphenoid capsule in three out of four cases (in garudimimids, ornithomimids, and saurornithoidids). In segnosaurids (*Erlicosaurus*), a fully formed basisphenoid capsule does not exist, but the basicranium is highly developed in dimensions. Parabasal canals are found in the transition region between the capsule and capsuleless part of the basicranium and, upon the absence of externally observed sutures, extends between the basisphenoid and parasphenoid, which cover it ventrally. In *Erlicosaurus*, upon the absence of the capsule, the canals are guided to the anterolateral part of the widened basicranium. The interpterygoid fenestra is highly reduced. Secondly, basipterygoid processes are always directed transversely and, in the majority of cases, reduced to varying degrees – the most highly reduced are in segnosaurids, and to a lesser degree saurornithoidids. Thirdly, blockage of the basipterygoid connection occurs that is mostly expressed by reduction of the basipterygoid processes, whose distal ends lose their joint–like character, as well as the appearance of additional connections between the pterygoid (to the vomer in *Erlicosaurus*) and basisphenoid, which contributed to the blockage. In this manner, parabasal canals in carnivorous dinosaurs are formed [according to] the condition of the basipterygoid connection, analogous to the vidian canals in theriodonts (Camp and Welles, 1956; Tatarinov, 1965, 1966, 1967).

The character of the construction of the parabasal canals in theropods apparently removes the possibility of a vidian canal, which was accepted until now at least in some groups of dinosaurs (Ostrom, 1961; Rozhdestvensky, 1968). Recently, doubt was expressed about its correct identification in hadrosaurs, and the development of the carotid canals shown in *Itemirus* (Kurzanov, 1976a). Now it becomes clear that the assumption about the path of the origin of the palatal artery and palatal branch of the facial nerve, which allows the presence of a vidian canal in ornithomimids and saurornithoidids (Osmólska, Roniewicz, and Barsbold, 1972; Barsbold, 1974), is not supported and was suggested by the skull material existing at that time.

Ear Region of the Endocranium. The construction of the endocranium near the ear capsule was originally illustrated in detail for a specimen of a well-preserved braincase of *Itemirus* (Kurzanov, 1976a). At that time, a whole series of features was recognized as unique to the narrow group to which this form belonged. However, upon study of the ear region in other carnivorous dinosaurs, the general nature of these features immediately [became clear]. For this, cranial specimens from oviraptorids, segnosaurids, and the undescribed carnosaur from Argalant (an isolated cranium) were studied (Fig. 8).

The ear region in the cranium of these carnivorous dinosaurs is particularly highly developed in the considerable concavity of the endocranial base, which is increased in size possibly in relation to the highly developed cerebellum, originally noted in the specimen of *Itemirus* (Kurzanov, 1976a). The lateral wall of this region in all examined cases bears a large, deep pocket that is elongated approximately in the direction of the paroccipital process. The pocket has smooth walls and narrows ventrally, but widens slightly at the bottom. It enters the ear capsule between the semicircular canals that surround it, although there is no direct connection between them. The large opening of the pocket is somewhat compressed. A pocket in a similar position was first noted in the endocranium of *Itemirus*, and was called interotic (Kurzanov, 1976a).

A fairly large process is located slightly posterior to the opening of the pocket and close to the lower part, that is connected to the widened labyrinthine region of the inner ear. The development of the processes, directed opposite to the side walls of the brain region, considerably narrows its upper part immediately above the otic capsule. The anterior semicircular canal curves along the arc of the pocket from the front and top, and was limited posteriorly by the descent of the crus communis process to the level of the top. The semicircular canal is not observed. The horizontal canal must have extended immediately ventral to the pocket. The location of the semicircular canal implies that the widening of the ear capsule, fixed by the above-mentioned process of the endocranium, corresponds to the region of the threshold of the bony labyrinth. The endolymphatic duct was apparently pushed towards the edge of the large foramen magnum by the pocket, as had been supposed in *Itemirus*. The passage for the perilymph canal is not apparent in the studied case.

Several foramina are located ventral to the pocket. In oviraptorids, the lowest and largest two in the anterior group of three openings is the exit for the facial nerve. Two higher, smaller foramina possibly carried vessels. A more posterior group, located closest to the ventral part of the threshold fixed by the process, also consists of three foramina, supposedly allowing branches of the otic nerve into the ear capsule.

Posterior and ventral to the process demarcating the threshold region, a groove-like indentation is located at an angle, and a fairly large jugular foramen is located in its posteriodorsal end, which allowed nerves IX-XI and the posterior cerebral vein to pass through. An elongated series of complete foramina is located little above the bottom of the endocranial region, increasing [in size] caudally and letting pass the branches of XII, which exit externally through the lateral opening of the condyle.

In the undescribed carnosaur from Argalant and *Erlicosaurus*, the location of the foramina for exit of the cranial nerves in this region are similar in many ways to the one noted above. In carnosaurs, large foramina for the exit of the lateral prefacial nerve are located anteroventral to the pocket. In *Segnosaurus*, the foramen for the passage of the prefacial nerve into the thickness of the bone is a free channel, opening separately to the outside. Two smaller foramina are located posterodorsal to it, and the smaller of them is open at both ends and transmits the facial nerve, whereas the posterior one carries the auditory nerve. The large jugular foramen is found in the indentation posterior to the endocranial process, fixing the region of the threshold. The exit for XII is entirely analogous to the one noted in oviraptorid specimens.

The endocranial ear region in representatives of the four groups of carnivorous dinosaurs – *Itemirus* (Kurzanov, 1976a) and, as shown, oviraptorids, segnosaurids, and the carnosaur from Argalant – have one principal plan of construction. In the original description of *Itemirus*, a large pocket in the bone some distance between the semicircular canals was linked to the venous system, and the existence of venous sinuses within it. In addition, the floccular origin of the pocket was also noted. However, flocculi are developed only in mammals, except possibly theriodonts. Only lateral cerebellar lobes are noted in reptiles. The possibility that the cerebellum is the origin of the pocket (from expansion of the lateral lobes, and not the flocculi of the cerebellum) seems more likely than the presence of venous sinuses. It is necessary to note that the walls of the pocket are completely smooth, differing from the walls of the pocket in *Itemirus*, which was used in favor of the existence of some kind of (most likely venous) fluid sac in the pocket. In one theriodont (Tatarinov, 1977), the floccular cavity is located in a closely [similar] condition. Even before the publication of the material of *Itemirus*, a cavity was noticed in American dromaeosaurids (*Dromaeosaurus*) that was entirely identical in position relative to the semicircular canals examined above, and was linked either to a specialized extension of the cerebellum or to the sacculus of the inner ear (Colbert and Russell, 1969). The latter could not be accepted as this became clearer, and similarly the supposed cerebellar pocket is also noted in another representative of carnivorous dinosaurs. The position of the opening in dromaeosaurids, through which pass a number of cranial nerves in this region, is also entirely identical to the one examined here.

The construction of the otic region of the endocranium in several carnivorous dinosaurs reveals the stability of its main features. It shows that the cranium is truly the most conservative part of the skull, which in other respects was changing fundamentally. Therefore, peculiarities in this region, considered unique for *Itemirus* (Kurzanov, 1976) and introduced on this basis into familial ranks, have a much more general character. A similar pocket is also noted in one other group of theropods – avimimids – and is not connected with the development of fluid-carrying sacs (Kurzanov, 1981).

Shape of the Cerebellum. In the only oviraptorid specimen, it is possible to observe a rare example of preservation of the inner layer of the hard membrane of the cerebellum (Fig. 9). In general features, this shows the [size] of the epidural [space] and allows estimation of the size of the space occupied by the brain. The surface of the inner layer clearly fixes the position and shape of the great hemispheres, highly widened and convex relative to the more posterior part of the brain. The hemispheres themselves occupied a little less than one-third of the entire length of the distance occupied by the brain. A wide, gently sloping indentation is noted dorsally between the hemispheres that connects the anterior region to the upper sagittal sinus. The inner layer is perforated by a large circular opening, corresponding to the visual lobes and the base of the olfactory tract. The asymmetric position of the opening is also noted, corresponding to the floccular lobes: the left is directed ventrolaterally, whereas the right one is directed posterolaterally. The roughness or unevenness of the dorsal surface of the inner layer apparently reflected the development of the sinuses of the epidural [space]. Judging from the separate bones of the skull roof, the [space] itself above the brain was considerable, and slightly smaller than the area occupied by the brain itself.

Bony Cavity of the Middle Ear. The middle ear region with bony walls was first discovered in saurornithoidids, and descriptively named the "lateral depression" (Barsbold, 1974). Later, a similar region was found in the skull of *Erlicosaurus* (Barsbold and Perle, 1980). The middle ear region in saurornithoidids has the appearance of a large depression, open to the outside, and occupies a considerable distance in the ventrolateral part of the brain [cavity] behind the basisphenoid capsule, and between the basisphenoid and the base of the paroccipital processes (Fig. 10). Different collaterations participate in the construction of the region that appear only as general features. The anterior part of the region is formed mostly by the basisphenoid, its dorsal edge by the prootic, the posterior edge by the base of the paroccipital process, and the ventral edge by the lateral basioccipital. The medial wall of the region bears the [transverse] crest, apparently connected to the development of the numerous pneumatic sinuses; they are especially apparent in *Erlicosaurus*. The connection between the anterior part of the region and the basisphenoid capsule passed through the sinuses. A passage is also noted as beginning to form through the sinuses of the medial walls, directed dorsally and inward towards the hypophyseal cavity. It is supposed that the channels for the internal carotid artery traveled in the sinuses of the anterior part of the basisphenoid. An elongate foramen, identical with the exit for VII, is located immediately below the dorsal edge of this region. A similar opening, connecting the middle ear region with the pneumatic layers inside the skull, can be found in a similar location in birds. A foramen for the exit of the prefacial nerve is located outside and dorsal to the edge of this region. A large foramen, corresponding to the foramen ovale, occupies the most posterior end, possibly connected outside with the circular foramen from which the shallow stapedial furrow extends along the anterior wall of the paroccipital. Large, well delineated foramina by which the sinuses opened into the middle ear cavity, are located anteroventral to the foramen ovale, closer to the ventral edge of the cavity and considerably limited by it.

The inner ear cavity in *Erlicosaurus* (Fig. 6) is mostly identical to that examined in saurornithoidids. In addition, the preservation of some of its basic elements provides a more complete picture of the modifications in the construction of the bony middle ear cavity in carnivorous dinosaurs. The greatest external difference consists of a considerable widening of the ear region and the base of the braincase, which is not expressed nearly to this degree in saurornithoidids. In addition, the lateral cranial walls are highly widened laterally and become convex, especially in the ventral part. The region of the sphenoccipital elevation is just as widened, and is considerably laterally displaced. In this manner, this part of the basicranium of *Erlicosaurus* seems to fill in the entire distance between the basipterygoid and paroccipital process. The middle wall of the cavity is perforated by the sinuses, which is also noted in saurornithoidids. The sinuses make it difficult to recognize the openings in the basisphenoid through which the canals for the internal carotid artery passed.

The cavity in *Erlicosaurus* is not smaller in size than that in saurornithoidids, [but the edges of the cavity approach each other to a greater degree], which makes it [narrower] than in saurornithoidids. Furthermore, the edge of the cavity in segnosaurids is composed primarily of the basisphenoid. Externally, the opening of the cavity is mostly covered by the area of the quadrate-pterygoid joint (not preserved in saurornithoidids). In this manner, the external roof of the cavity has a double wall almost for its full duration, from the connection of the medial quadrate process and the medial pterygoid flange. This cavity opens only from behind the quadrate shaft as the elongate, oval otic fenestra, approximately marking the position of the external ear. The same is assumed to be true in saurornithoidids. Definite reptilian features appear in this plane in the construction of the cavity, although the high degree of bone formation in both examined cases makes it more similar to the avian middle ear.

Thus, the construction of the middle ear cavity is very similar in saurornithoidids and segnosaurids. Besides the noted differences, it is necessary to mention only the predominant participation of the basisphenoid in the construction of the cavity in the latter. In this case the cavity is distinguished from that of birds mainly by the formation of [lateral neck bones? by] the periotic and exoccipitals. The closure of the majority of the middle ear cavity by the quadrate-pterygoid articulation, as well as both of the main bones fused to its side, should also be noted. The development of the otic fenestra posterior to the quadrate shaft testifies to the presence of a reptilian-type tympanic cavity.

Middle Ear without Bony Walls. The middle ear without osseous walls is seen in different groups of carnivorous dinosaurs, and, judging from the available information, it is not directly linked to the presence of a capsular basicranium as it seemed to earlier upon the first description of such an ear cavity (Barsbold, 1974). This is well illustrated by the presence of a middle ear cavity without osseous walls in ornithomimids and garudimimids, which have a basisphenoid capsule. A middle ear cavity not surrounded by bone is also known in tyrannosaurids, dromaeosaurids, and oviraptorids, all of which are characterized by a capsuleless basicranium. In all of these groups, the middle ear cavity was constructed as it is in contemporary reptiles (Janensch, 1935; Wyeth, 1924). In known specimens the position of the middle ear is usually fixed by the position of the fenestra ovale, from which a clearly-defined vestigial furrow extends on the anteroventral edge of the paroccipital process, accommodating the stapes. Based on the direction of the furrow, it is possible to note that the external ear was located immediately posterior to the rear edge of the quadrate and a little below its dorsal end, as in the case of some carnivorous dinosaur groups.

Conclusion. It is now clearer that some correlations exist in the construction of the braincase in carnivorous dinosaurs. In all possibility, the basisphenoid capsule has a "sphenoid" origin and is actually a hollow swelling related to the development of the basicranial sinus system. However, the function of the capsule is in many ways unclear.

The development of a completely formed basisphenoid capsule, and also the widening of the anterior basisphenoid – which has not yet become a true capsule – is possibly conditional on the presence of parabasal canals; as was noted, their development is tied to the blocking of the basipterygoid articulation, and in this it is similar to turtles and theriodonts. The absence of the capsule (or the widening of the anterior basicranium) and mobility of the basipterygoid articulation – *i.e.* features most clearly expressed in dromaeosaurids and tyrannosaurids – are entirely correlated with the absence of parabasal canals. An avian-type osseous middle ear cavity exists in different carnivorous dinosaur groups. In all of them, a basisphenoid capsule is developed or widening of the anterior basicranium is present. In ornithomimids, an osseous cavity is not developed along with the presence of a true capsule. In the inner ear, the so-called "inner auditory pocket" had a general distribution and was apparently related to the lateral cerebellar lobes.

Palatal Complex. The construction of the palatal complex is clearly divided into three types. At the same time, there is no single criterion on which this division is based. Also, considerable modifications are characteristic of the elements comprising the complex, primarily the vomers, and there are significant variations in each of the types. The construction of other elements comprising the palatal complex is changeable to a great degree, at least part of which is basically correlated with the peculiarities of the vomers. It is quite possible that the modifications of the palatal complex obscure different morphological peculiarities.

First Type (Fig. 11). This is characterized by fused, flattened vomers with elongate, narrow pterygoid processes that divide the choanae. The palatal bones, which are limited posteriorly by the choanae and span a considerable distance between the maxillae and pterygoids, form the basal part of the preorbital wall. The primary and additional palatal openings are large. The pterygoids are of the lamellar type, and the ectopterygoids have hook-like jugal processes. A palatal complex of similar construction has been considered common in carnivorous dinosaurs, and has been described in varying detail in tyrannosaurids, dromaeosaurids, and recently also in garudimimids (Fig. 7a).

Second Type (Fig. 7a). [This type] of palatal complex, typical of oviraptorids, is characterized by strong development of the palatal processes of the maxilla to form a continuous or solid lining for the anterior palate. [The maxilla] bears two longitudinal convex ridges that are separated by a narrow groove and become the palatal processes of the intermaxillary bones. The posterior edge of the maxilla is near the midline and formed by the large bony process from two closely-positioned, medially-flattened, and laterally unevenly convex triangular crests with pointed apices. Fused, laterally compressed, lamellar vomers enter into the narrow [space] between the crests and are considerably displaced posteriorly. The palatines are reduced, forming the basal part of the preorbital wall and occupying an insignificant place on the posterior edge of the choanae in the palatal cavity. The palatal opening is highly reduced and appears to be closed in by the narrow palatal bone a small distance from the hook-like extension of the ectopterygoid. The additional palatal opening is absent. The pterygoid body is very massive, with sharply distended external edges that limit the deep longitudinal ventral cavities. The ectopterygoids are highly displaced anteriorly, with elongate jugal processes that attach to the articulation of the jugal and maxilla.

Third Type (Fig. 7b). [This type] of palatal complex is found in segnosaurids. The vomers, which are fused together, are distinguished by highly elongated processes that almost reach the basicranium. They fuse to it in such a manner as to form a lamellar structure that is V-shaped in cross-section, which divides the elongate and enlarged choanae. At the posterior end of the structure, the V-shape is reduced to nothing, whereas more dorsally it is connected to the pterygoids, and ventrally the V-shaped structure is slightly divided and contains the ventral edge of the basisphenoid rostrum. The pterygoids are reduced, with shortened vomer processes, and closely positioned relative to the basicranium. The palatal bones form the posterior edge of the choanae, and increase [in size] considerably posteriorly, participating in the borders of the additional palatal openings. The primary palatal opening was absent or highly reduced. The ectopterygoids, with shortened jugal processes, were articulated with the region of contact with the jugal and maxilla.

Thus, the greatest deviation from the reptilian norm is expressed in the second and third types of palatal complexes. The deviated features can be summarized as follows. The size and configuration of the vomers [are altered], from those displaced posteriorly beyond the rostral part of the facial region (in oviraptorids), to those extending almost to the basicranium (in segnosaurids). In the first case, increases in the palatal process of the maxilla, articulated with the vomers by means of a special forked, tooth-like process, occur; in the second, additional articulations of the pterygoid process of the vomers with the basisphenoid rostrum [occur]. The palatal openings are reduced in oviraptorids, and the jugal processes of the ectopterygoids are articulated with the region of the jugal and maxilla. All these features create a highly peculiar appearance to the palatal complex, showing the great possibility for changes in it, no less than the palatal modifications known in birds. Features appear in the palatal complex of segnosaurids that are found more fully realized in the palates of ostriches and especially cassowaries, which have paleognathous palates. Judging from everything, paleognathy in segnosaurids has a more primitive character relative to the "true" paleognathy of ratite birds. The features accepted as indicative of paleognathy in segnosaurids are reduced to the following: considerable elongation of the vomers, as a result of which the pterygoid processes are attached to the basisphenoid rostrum (in paleognaths the anterior end of the basisphenoid rostrum is located between the diverging pterygoid processes of the vomers); and reduction of the pterygoids, especially the vomerine processes (in paleognaths the reduction of these processes is even more pronounced). At the same time, a series of typical paleognath features is not expressed in segnosaurids, including articulation of the palatal bones mostly with the pterygoid and divergence of the pterygoid processes of the vomers.

Lower Jaw

As in reptiles, the lower jaw of carnivorous dinosaurs is divided into two basic modifications – toothed and edentulous, of which the latter is characteristic only of a few groups – ornithomimids, oviraptorids, and caenagnathids (Figs. 13, 14). In segnosaurids, the lower jaw lacks teeth in the most anterior part, while it fully corresponds to the normal, toothed type in the remainder. In spite of these great differences, the edentulous type in ornithomimids and garudimimids is also basically similar to the toothed type, whereas in oviraptorids and caenagnathids it represents a more basic deviation. Thus it is proper to group the ornithomimid lower jaw with the toothed (normal) type, and to separately differentiate the lower jaw of oviraptorids, including caenagnathids, for separate examination. In describing it, it is convenient to keep to two structural subdivisions of the lower jaw – anterior and posterior.

Normal Type of Lower Jaw. Anterior Section. The anterior section of the lower jaw occupies a little more than half its length. For a considerable distance, corresponding essentially to the length of the alveolar edge, it is notably narrow, more significantly so in segnosaurids. Widening of the anterior section occurs immediately posterior to the alveolar edge, where the coronoid process is noted to a variable degree but more often comparatively weak, to which is attached the pseudotemporalis muscle, one of the lower jaw adductors.

There are two main elements in the composition of the anterior section – the dentary and splenial. The coronoid is also present, serving as a connection between the two sections and entering topographically into the composition of both parts. The base of the anterior section – the dentary – carries the longitudinal Meckel's canal on the lingual side, which extends to the symphyseal surface. It was noted above that a small section of the anterior end of the lower jaw is toothless in segnosaurids. In ornithomimids and garudimimids, the cavity of the rostral part of the lower jaw rami is rotated externally around the longitudinal axis, so that a notably flattened, hook-like structure is formed on the anterior end, which does not exist in the toothed group. The anterior, pointed end of the splenial partly covers Meckel's canal, carries its ventrally displaced opening, and approaches the symphysis to varying degrees. The angular process of the splenial is considerably developed. The coronoid is represented as a connecting element by various parts in both sections. Its elongate and narrow anterior process extends to the symphysis along the alveolar edge, covering the base (interdental plates) of the dentary tooth row. In the region of the coronoid process on the border of the two sections of the lower jaw, the coronoid is covered lingually by the splenial and opens behind it in the shape of a triangular segment, already within a portion of the posterior section.

The coronoid is the only element that crosses the mobile border of the two sections, and more or less considerably links them together. The coronoid of carnivorous dinosaurs, in contrast to those of ornithischians and lizards, [does not form] the rising coronoid process, which is highly projected above the level of the dorsal edge of the lower jaw. It enters into the composition of the coronoid process beside the posterodorsal region of the dentary and splenial. The connecting function of the coronoid is best expressed in Mongolian tyrannosaurids (*Tarbosaurus*). Previously, its anterior process was usually taken to be a derivative of the dentary, and only its very posterior segment was correctly identified (Osborn, 1906; Romer, 1956; Maleev, 1974). As a result, the connecting role of the coronoid was not taken into consideration. In dromaeosaurids, ornithomimids, and garudimimids, the anterior process of the bone is not as extensive. The coronoid is absent in segnosaurids.

Posterior Section. The predominant part of this section is composed of the surangular, which forms the dorsal edge up to the jaw articulation and the lateral wall of the adductor fossa. The latter is large, as a rule, testifying to the considerable mass of the adductor muscles attached there. Anterior to the jaw articulation, the bone is perforated by the surangular fenestra, which is absent in ornithomimids and oviraptorids. The contact between the angular, surangular, and dentary usually bears an external mandibular fenestra of varying size (usually small). The anterior process of the prearticular is considerably elongated, and its widened end reaches the dorsal edge of the lower jaw near the adductor process, delimiting the border between the anterior and posterior sections on the lingual surface. Ornithomimosaurs are an exception, in which the anterior process does not go beyond the borders of the ventral edge of the adductor fossa. The jaw articulation is located considerably below the dorsal edge of the posterior section. The articular surfaces of the condyles are transversely expanded. The retroarticular process in dromaeosaurids is considerably widened, although it is not noticeably flattened but slightly concave in *Velociraptor*. The posteromedial edge of this widening bears a sometimes pole-shaped extension or process. By analogy with similar structures in some birds (Bock, 1960), it is suggested that this process rested against the quadrate when the lower jaw was highly depressed, thus preventing disarticulation of the jaw articulation (Colbert and Russell, 1969). In ornithomimids, widening of the retroarticular process has considerable height and a deep indentation, the posteromedial edge of which bears a process that controlled dislocation of the lower jaw. However, a similar mechanism may be absent in tyrannosaurids, inasmuch as the retroarticular process is fairly insignificant.

The articulation of the two lower jaw sections corresponds to [point of] definite mobility between them. This is guaranteed by the groove-like articulation that was formed along the ventral edge, and the "slipping" contact with more ventrally-positioned elements. In the dorsal part of the lower jaw ramus, the articulation of elements has the following sequence: labially, the dentary-surangular; next, the coronoid; lingually, the splenial-prearticular. When the coronoid is absent as in segnosaurids, the order of the articulations of the remaining elements is preserved. On the ventral edge, the articulation of the elements is as follows: labially, dentary + splenial-angular; lingually, splenial-prearticular. The articulation of the lingual elements (splenial and anterior process of the prearticular) occurs along an arc corresponding to the posterior edge of the splenial and representing the joint articulation. The character of the articulation of the labial and lingual elements of the dorsal and ventral edges of the jaw ramus guarantees easy rotation (and translation for the separate elements) of the anterior section relative to the posterior.

Oviraptorid Type of Lower Jaw. Anterior Section. The anterior section occupies the lesser half of the length of the lower jaw, and is composed almost entirely of the dentary, which forms the basis for the horny part of the beak (Fig. 13b). The rostral part of the dentary is highly thickened, especially at the symphysis, and has the appearance of a massive, dipper-like structure. Two processes pass from it posteriorly: one rising, widened, and concave, and another lowering, narrowing, and straight, by which means the bones are connected with the remaining elements. These two processes delimit the large mandibular fenestra anteriorly. The lower, lingual edge of the rising process has a longitudinal crest running its entire length. In the posterior rostral part of the dentary, the height of the anterior section increases sharply. The splenial is highly narrowed, lacks the angular process, and participates in the formation of the lingual surface of the ventral edge of the lower jaw ramus. The coronoid is absent.

Posterior Section. The surangular forms the basic part of the lateral surface of this section. It delimits the posterior edge of the mandibular fenestra, sending a narrow, elongate process anteriorly that is divided into two unequal parts. The position of the opening between the two elements of the two jaw sections apparently reflects the primary connection with the external mandibular fossa, which in this case was highly developed. Lingually, the surangular forms a larger internal adductor fossa, while labially it forms the external adductor fossa. A large, laterally-compressed coronoid process for the pseudotemporalis muscle is present on the dorsal edge of the bone. The anterior process of the prearticular is straight and lacks a terminal widening. The angular forms the ventral edge of this region. The jaw articulation is remarkable for its breadth and relief, as well as the sagittal elongation of its central process. The retroarticular process is elongated, narrowed, and slightly concave dorsally, with a small posteromedial process.

The articulation between the two lower jaw sections is groove-like on the dorsal edge. The end of the rising dentary process is divided parasagittally and contains the anterodorsal process of the surangular. The lower dentary process extends along the ventral edge of the jaw, and the splenial accommodates the angular. The nature of the articulation allows rotation of the anterior section relative to the posterior, with more or less simultaneous translation of the ventral edge elements.

Comparison of the Two Types and Peculiarities of the Caenagnathid Lower Jaw. The construction of both sides of the lower jaw in carnivorous dinosaurs is considerably different from the general reptilian form. In spite of some deviation in several features, the normal type (including the edentulous jaw of ornithomimids) is characterized by a relatively elongate anterior section that is narrow for some length, the weak development of the coronoid process, the presence of the coronoid (sometimes it can be absent) and the angular process of the splenial, an insignificantly-sized mandibular fossa, and a frequently widened retroarticular process, all of which guarantee control of maximum displacement of the lower jaw.

The edentulous jaw of oviraptorids is differentiated by its height, the shortened anterior section, the large adductor fossa, absence of the coronoid and the angular process of the splenial, the highly increased and anteriorly displaced external mandibular fossa, and the narrow retroarticular process, all of which limit the ability to control displacement of the lower jaw.

The differentiation in construction of the two types had, in principle, no effect on the articulation between the anterior and posterior sections of the lower jaw ramus. In both cases, the character of the articulation guaranteed rotation of the anterior section relative to the posterior.

The peculiarities of the lower jaw in caenagnathids represent a special case (Fig. 14a) that is most conveniently examined separately. It is differentiated by its elongation, slight height, and moderately developed adductor fossa. The base of the anterior section – the dentary – has an elongated rostral part, a highly elongated symphysis, and parallel, posteriorly-directed upper and lower processes. The occlusal edge is gently concave, while the mandibular fossa is narrow, elongate, and displaced posteriorly. In the posterior section of the caenagnathid lower jaw, the surangular forms the entire upper edge of the mandibular fossa. The anterior process of the prearticular continues anteriorly past the level of the adductor process [as] in oviraptorids.

With the groove-like connection of the two lower jaw sections, dorsally the end of the upper dentary process is deeply forked and accommodates the anterodorsal process of the prearticular. Along the ventral edge, the rami forming it are elongate and also form a slot-like connection. At the same time, the depth of the groove in the dorsal and ventral articulations apparently must have reduced the mobility of the lower jaw ramus.

The type of lower jaw construction is the same in oviraptorids and caenagnathids. However, the lower jaw in caenagnathids is sharply differentiated from that of oviraptorids in detail. The height, correspondence of the length of the anterior and posterior sections, degree of development of the adductor process, shape of the rostral part, depth and linear dimensions, length of the symphysis, dimensions of the mandibular fossa and its position – practically all the basic features of the main part of the lower jaw ramus in oviraptorids and caenagnathids, except for the region of the jaw articulation, are sharply different in character.

Skull Kinesis

Theropods had a kinetic skull that had a great deal in common, relative to mobility, with what is characterized as amphikinesis in lizards (Frazetta, 1962; Iordansky, 1966, 1968). At the same time, metakinetic features are identified in the theropod skull based on consideration of the original basis of internal skull mobility (Versluys, 1910, 1912).

Theropod metakinesis was studied previously in much more limited material (Versluys, 1936). The Mongolian theropod collection removed this absence of information to a certain degree, and allowed, possibly for the first time, [analysis] of general and specific features of kinesis in carnivorous dinosaurs. At the same time, it turned out that peculiar modifications exist in skull construction that led to the almost complete absence of kinesis in separate lineages. Until now, an akinetic skull had been considered characteristic only of herbivorous dinosaurs.

The Metakinetic Structure of the Skull. Two main segments are identified in the metakinetic lizard skull – maxillary and occipital (Versluys, 1910, 1912), the latter sometimes called craniocerebral (Ostrom, 1961). The mobile articulation of segments is characterized by the presence of a basic, metakinetic axis of rotation of the maxillary segment relative to the occipital. Rotation around this axis is limited by the mobile metakinetic articulation, which is positioned dorsally in the skull between the temporal (maxillary segment) and supraoccipital (occipital segment), as well as by the basal articulation between the pterygoid (maxillary segment) and basisphenoid (occipital segment), realized in the basipterygoid articulation (Frazetta, 1962; Russell, 1964). According to the laws of kinetics, the presence or identification of another axis that passes to the basipterygoid articulation besides the metakinetic axis would be completely possible, however the established method of description of kinesis is based mainly on the aforementioned terminology.

An additional metakinetic axis wass identified in the lizard skull roof, located between the temporals and frontals. However, these bones are firmly fused in theropods, even in relatively young specimens. At the same time, mobility seems displaced more anteriorly and fixed at the frontal-nasal contact. This axis may be called prokinetic in birds (Bock, 1964; Derzhinsky, 1972). One other axis of mobility – hypokinetic, located between the palatine and pterygoid – was first identified in the mosasaur skull (Russell, 1964). Mobility between these bones is more or less characteristic of the first theropods.

In the metakinetic theropod skull, the occipital – one of the two main structures of the segments – is composed of the following elements: the occiput complex, squamosal, and elements of the central part of the lateral wall of the cranial skull and basicranium, *i.e.* most of the braincase (without the roof) and the squamosal. The articulations between the maxillary and occipital segments guaranteed mobility in three primary locations, as in lizards (Frazzetta, 1962): dorsally – the metakinetic articulation, posteriorly – the metakinetic axis, and ventrally – the basal articulation. The identification of lower-order structural units (sectors) is possible in the maxillary segment, depending on its relative functional independence in the framework of the basic kinetic structure. The following units are identified in the maxillary segment of theropods:

1. The ***parietal sector***, formed by the parietals, frontals, and postorbitals, has a mobile articulation with the occipital segment by means of the metakinetic articulation and axis; anteriorly it has a mobile articulation with the upper jaw sector along the prokinetic axis.
2. The ***upper jaw sector***, composed of the premaxillae, maxillae, nasals, vomers, lacrimals, prefrontals, jugals, and palatines, has a mobile articulation with the hypokinetic axis of the pterygoid sector.
3. The ***pterygoid sector***, formed from the pterygoids and ectopterygoids, is separated from the occipital segment (basisphenoid) by a mobile basal or basipterygoid articulation; in addition, the mobile pterygoid-quadrate articulation separates it from the quadrate sector.
4. The ***quadrate sector***, formed from the quadrates and quadratojugals, is separated from the occipital segment (squamosals and paroccipital processes) by the quadrate articulation.
5. The ***epipterygoid sector***, formed from the epipterygoids, has a mobile articulation with the pterygoids and is connected to the skull roof. Its kinetic rotation is insignificant relative to that of other sectors.

The composition of the subdivisions of the maxillary segment is usually constant in different theropod groups. However, changes in the position of the mobile boundaries are noted in some lineages, reflected not only in the composition of the sectors but in the basic skull segments. In tyrannosaurids, possibly allosaurids, and also saurornithoidids, the laterosphenoids and orbitosphenoids are not part of the occipital segment but the maxillary segment, because their mobile border is apparently displaced more ventrally along the lateral wall of the [cranium]. The following are signs of this displacement: a strong, almost undetectable fusion of the parietals with the laterosphenoids (in tyrannosaurids and saurornithoidids) and the highly curved fissures between these elements and the orbitosphenoids and parietals (in tyrannosaurids and possibly allosaurids). On the other hand, the fissure line between the laterosphenoids and prootics is more ventrally located, although the mobility of this zone is clearly weakened with age.

The metakinetic skull and corresponding type of mobility are characteristic of most carnivorous dinosaurs, [despite] such seemingly different skull constructions – from the large, high-skulled, huge-toothed tyrannosaurids to the small, low-skulled, edentulous ornithomimids. The basic rotation occurs along the metakinetic axis, which is positioned in the more posterior region of the metakinetic articulation (between the parietal sector and the occipital segment). Motion of the kinetic independent sector of the maxillary segment was also realized along the other [mobile] articulation and axis. Motion of the maxillary sector relative to the parietals and pterygoids occurred on the prokinetic and hypokinetic axes, which was limited along this axis by the mobility between the nasals and parietals, as well as between the palatines and pterygoids. The epipterygoid sector, as noted, did not play an important role in kinesis. The mobility of the quadrate sector defined a somewhat unique form of kinesis – streptostyly. As noted, the quadrate sector of the maxillary segment is articulated in a fixed manner with the pterygoids in the metakinetic theropod skull. The dorsal quadrate articulation has a mobile connection with the occipital segment (squamosals and paroccipital processes), allowing it to rotate around the latter. These motions cause translational and propalinal movements of the lower jaw, accompanied by motions of the pterygoid sector.

Limitations of Kinesis. The skull of a representative segnosaurid, *Erlicosaurus*, apparently shows a process of partial disappearance of kinesis. The construction of this skull preserves kinetic structures in several features. Mobile articulations of the roof and upper occipital bones are noted, which serve as one of the main conditions for metakinesis. However, as noted above, the basipterygoid connections are fused due to the appearance of a connection of the pterygoids and vomers with the basisphenoid, and this naturally reduces the possibility of any kind of motion to almost zero. Even if the connection between the posterior end of the vomers and the base of the basisphenoid rostrum was less rigid, the additional articulation between the basic segment would hardly be conducive to mobility. However, the exhibition of individual occurrences of mobility was more or less preserved. Thus, conditions for prokinesis remain sufficient because of the type of articulation of the roof and rostral bones. With this, the development of a large osseous middle ear cavity and areas of fusion between its external wall, the medial process of the quadrate, and the pterygoid should have fully precluded anteroposterior motion of the pterygoids and mobility of the quadrates, meaning monimostyly in this skull of limited kinesis. Inasmuch as a similarly constructed cavity is seen in the saurornithoidid middle ear, it is reasonable to [infer] monimostyly for them as well.

Akinesis. The absence of internal skull mobility occurs in oviraptorids, even though it was suggested previously that they had the capacity for "infrakinesis" (Barsbold, 1977). More perfectly preserved skull material shows that characteristic modifications of several skull structures first made mobility difficult, and then aided or promoted the appearance of new types of kinesis.

If basic subdivisions are sought in the oviraptorid skull according to the metakinesis model, the separate segments form only small parts of one whole segment, such that the occipital, except for its own [between the] skull and brain, also includes the maxillary elements. These changes in segment composition, that is, the fusion of the upper occipital and roof bones and blockage or fusion of the basal connection (basipterygoid articulation) as noted earlier, accompanied the disappearance, or at least great reduction, of metakinetic mobility (Barsbold, 1977). In the first description of oviraptorid skull mobility, it was noted that the maxillary segment, having reduced the number of its compositional elements, is divided into two additional sectors – the rostral and upper jaw sectors – which seem to be [linked] kinetically (Barsbold, 1977). It is possible that this occurs to some degree in the younger forms. However, in other samples such mobility is excluded by the rigid articulation (fusion) between the posterolateral [intergnathal] bones with the jaw bones. Besides, a free connection between the pterygoids and the tooth-like processes of the vomers in the area of their fusion with the jaw bones should be a prerequisite for mobility of these two sectors. This articulation, which externally is reminiscent of a joint, was initially interpreted as mobile and definitive for [identification] of "infrakinesis" in the oviraptorid skull (Barsbold, 1977). The better-preserved material shows that such a connection was most likely rigid in mature individuals. Prokinesis and most likely rhynchokinesis (mobility between the jaw and rostral bones) were absent in the oviraptorid skull, in spite of the fact that the construction of the beak was bird-like in many ways. The development of a high bony crest in adult forms (or males) must have greatly limited rhynchokinesis, because in reality this crest serves as an additional connection between the intergnathal and ear bones. From this it follows that initial assumptions about the syndesmotic connection of the beak in oviraptorids seem unlikely.

In this manner, the typical oviraptorid skull construction most likely did not leave room for mobility. In all likelihood, the rigid connections in the massive skull complex obstructed protraction and retraction of the pterygoid. Thus, the quadrate bones were quite fixed, and therefore monimostyly occurred within an akinetic skull.

Intramandibular Mobility. True lower jaw mobility most likely does not have any special significance due to its small amplitude, but it should not be neglected [when addressing] the general question of kinesis.

There are some common aspects in the manner of the connection between the two basic subdivisions of the lower jaw – the anterior and posterior sections – which creates a more or less single kinetic structure, in spite of small differences in its structure among different carnivorous dinosaur groups. This commonality exists in the groove-like connection in the dorsal part of the lower jaw, which allows rotation of the anterior section relative to the posterior. The connection of these sections along the ventral edge is also groove-like, allowing rotation along an wide arc, which in practical terms of amplitude also meant a back-and-forth motion. The fact that a lower jaw with a different type of construction retains the ability for this type of motion additionally [is illustrated] by the configuration and location of the end of the anterior process of the prearticular. It is constructed in such a manner as to serve as a joint around which rotation of the corresponding part of the anterior section occurs. Only in oviraptorids (and possibly caenagnathids) is the appearance of this process completely altered – it is straighter and sharpened into a V-shape that still allows back-and-forth movement along its ventral connection with the lower jaw sections.

The development of metakinesis in many groups of carnivorous dinosaurs should be noted when drawing any conclusions about internal skull mobility. Metakinesis is accompanied by streptostyly. In addition to the basic forms of mobility, an additional type is also observed in the form of prokinesis, related to mobility of the facial section between the roof and rostral bones. Metakinesis is known to be common in the skulls of carnivorous lizards, while the appearance of a more advanced form of prokinesis is characteristic of birds.

Typical modifications in theropod skull construction limit kinesis up to and including its complete exclusion. This is achieved not only by simple fusion of [previously] mobile structures. The amount of kinesis is, as a rule, reduced with the age of the animal.

Increased rigidity in skull articulations is acquired in different ways, and directed towards solidifying the connections between the basic kinetic subdivisions – the occipital and maxillary segments. In segnosaurids, showing varying preservation of certain prerequisites for metakinesis, the latter was reduced practically to nothing by connections with the basicranium; prokinesis, however, could have been retained. Limited skull mobility was accompanied by monimostyly, and tied to the development of an osseous middle ear cavity that led to fusion of the bones. In oviraptorids, this was achieved by considerably expanding the composition of the first segment at the expense of the second, and increasing the rigidity of the connection between the facial section and the basipterygoid articulation. Specific changes in the palatal complex contributed greatly to this. Akinesis in this case was accompanied by monimostyly, whereas in hadrosaurs internal skull mobility allows streptostyly (Ostrom, 1961).

In this manner, the carnivorous dinosaur skull included a wide variety of potentials from metakinesis to limited mobility to akinesis. It should be noted that skulls which had akinesis and limited mobility, specifically in oviraptorids and segnosaurids, are the most distinct from those of more typical theropods.

Postcranial Skeleton

Naturally, there appear features with a single origin among the wide variations seen in the postcranial skeletons of carnivorous dinosaurs. Secondly, upon description of excavated materials, either the peculiarities of the postcranium were unjustly [judged] as not having any decided significance, or their actually secondary features were exaggerated in order to base detailed specific studies on similar forms. Currently there are many accumulated facts that testify to the general and specific features of the construction of the theropod postcranium. Particularly wide structural variations were common among later carnivorous dinosaurs, which are now most fully represented by the Mongolian forms. A series of new data helps provide a deeper understanding of these similarities and differences, both of the separate compositional elements and of the whole skeleton, that to a great degree helps to define the evolutionary character of the numerous lineages of carnivorous dinosaurs.

Axial Skeleton. Vertebral Column. The following vertebral counts are known from several later theropod groups: 23 presacrals, 5-7 sacrals, and usually less than 40 caudals. Among the presacrals, 10-11 are in the cervical series, 12-13 in the dorsal series, and the general sum of these apparently does not change, and remains 23. Variation in cervical number depends on the presence of "transitional" vertebrae among them, the definition of which is based on the greater or lesser morphological similarity with the more typical elements of both series. Occasionally, assumptions about the functional role of such "transitional" vertebrae are used for this definition.

On the whole, in later theropod specimens where the number of "transitional" pectoral vertebrate does not exceed one or two, it is fairly clear that their classification as cervical or dorsal is entirely conditional. The stability of the presacral count in different theropods, independent of relative neck lengthening or shortening, is a more significant fact that was noted in a series of studies on theropods (Osborn, 1917; Gilmore, 1920; Romer, 1956; Ostrom, 1973). It is necessary to note that a similar picture is also observed for the border between the dorsal and sacral vertebrae: functionally "transitional" posterior dorsals enter into the composition of the sacrum to a greater or lesser degree, although they are more commonly classified as dorsals (Osmólska, Roniewicz and Barsbold, 1972; Barsbold, 1972; Russell, 1972; Maleev, 1974). In any case, it is more important to identify the dynamic of the transition between the different compositional sectors of the axial skeleton.

Cervical Vertebrae. Cervical vertebrae are usually slightly or moderately platycoelous, including those of many tyrannosaurids that have been mistakenly classified as opisthocoelous (Maleev, 1974). Pleurocoels are present on all of these vertebrae. Three types of cervicals can be clearly differentiated depending on the degree of elongation of the centrum and the width of the neural arch.

The first are highly anteroposteriorly compressed, have large centra with disc-like lateral cross-sections, and have high neural arches. They characterize the relatively short necks of tyrannosaurids and allosaurids. A high degree of displacement of the articular surfaces from the vertical plane is characteristic for these centra, such that the posterior is placed much more ventrally than the anterior in each. [This displacement is seen in a large distance and only a leveling of level.] The zygapophyseal articular surfaces are more or less parallel in most of the vertebrae, and only come together ventrally at an acute angle in the more anterior ones. All epiprocesses are highly developed, and can be distinguished by the degree of their differentiation. The displacement of the zygapophyses and the shortening of the vertebral centra basically approach the vertical in the straighter midsection of the tyrannosaurid cervical region.

The second type of cervicals are moderately elongated and widened with relatively low and small centra, and are most clearly seen in dromaeosaurids, oviraptorids, etc. Vertebrae of this type form a relatively longer neck than those in tyrannosaurids. Posterior elongation of the length of the posterior postzygapophyses relative to those more anterior is characteristic of the centra. In dromaeosaurids, the medial planes of the zygapophyseal articular surfaces are oriented at a different angles to the long axis of the centrum, and reach a relatively distinct differentiation in the same vertebra. At the same time, the prezygapophyses are cut under a smaller angle than the postzygapophyses, and the articular surfaces are dorsal. Angles vary from 40-75° in American dromaeosaurids; similar data are observed in Mongolian dromaeosaurids, with all stages between the extremes (Ostrom, 1969b). The epiapophyses are well-developed and similarly constructed. The cervical series is clearly displaced from the vertical as compared to that of tyrannosaurids, due to the smaller displacement of the articular surfaces and the more elongated centra.

The third type of cervicals include highly elongated vertebrae with low neural arches, and widen and elongate considerably towards the posterior end of the series. Such vertebrae are most clearly observed in ornithomimids. As a result of this elongation, the centra are characterized by the relatively small displacement of the articular surfaces and the different angle at which they meet. The articular [surfaces] of the posterior vertebrae become more nearly parallel. The epiapophyses are clearly reduced. The cervical series formed by these vertebrae is differentiated from the first two by its greater elongation and deviation from the vertical.

Dorsal Vertebrae. The dorsal vertebral centra increase successively in length caudally, although the amount of this increase is relatively weak and may only reach a significant level in ornithomimids. The vertebrae are nearly platycoelous or almost amphicoelous, while in tyrannosaurids the anterior concavity is more pronounced than the posterior. Anteriorly, the ventral surface of the centrum becomes thickened and laterally compressed, with a keel reduced in height; this is more strongly expressed in the anterior four or five vertebrae. The keel is absent in ornithomimids and oviraptorids. Pleurocoels are usually present on all dorsal vertebrae, but are absent in primitive ornithomimids. Additional articulations (hyposphene-hypantrum) are present in the vertebrae of tyrannosaurids, oviraptorids, and dromaeosaurids, but are absent or notably reduced in ornithomimids.

Sacral Vertebrae. Usually the sacral vertebral centra are tightly fused with one another and connected to the ilia by the transverse processes (diapophyses) and the highly modified sacral ribs. The centra are more or less consistently similar in construction. The neural arches are fused with one another at their bases, and the zygapophyses in the central complex of these vertebrae usually [are not apparent]. Pleurocoels are found in nearly all centra. The transverse processes of the central, compact part of the sacral series are fused ventrally with the sacral ribs, and medially with the bases of the neural spines. The sacral ribs are usually highly shortened, especially in the anterior vertebrae, although those of segnosaurids are remarkable in being considerably elongated. Highly reduced ribs are found on the anterior sacrals of primitive ornithomimids, adjacent to the medial iliac surface.

In the literature, the general number of sacral vertebrae is reported differently even for the same group of theropods. For example, the following sacral counts have been reported in ornithomimids: four (Gilmore, 1920), five (Osborn, 1917; Osmólska, Roniewicz, and Barsbold, 1972), and six (Parks, 1933; Russell, 1972). Using the premise that the functional sacrals should be considered as those fused together and connected to the ilium, then they number six in later theropods. This number reaches seven in the oviraptorid *Ingenia*, *i.e.* the tendency to form a synsacrum is evident in later lineages, with its axis of symmetry approaching the horizontal.

Cervical Vertebrae. The caudal vertebrae are modified in several basic features. The first is the most widespread, and is a typical example of theropod caudals, even though they change considerably within the bounds of this modification in different ways. Like the vertebrae of the two subsequent modifications, they are platycoelous, decrease in dimensions, and lack pleurocoels. Although the changes in this vertebral series increase gradually towards the rear, it is still possible to discern the boundary between the anterior and posterior tail sections, and to distinguish different groups based on its location. Features of this transition [include] the absence or great reduction of the transverse processes, relative elongation of the centrum, and a clear lowering of the neural spines. On this basis, the transition is noted between the 15th and 16th vertebrae in tyrannosaurids and ornithomimids. As a rule, the vertebrae are laterally compressed at this transition. The highly elongate prezygapophyses, reaching almost the length of the entire vertebrae in the aforementioned groups, are also characteristic.

The second modification of the caudal series is found in oviraptorids. It is differentiated by a high degree of uniformity, and the gradual change in vertebral features along the entire length of the series. The presence of pleurocoels and transverse processes are evident on almost all vertebrae, with the exception of the most posterior ones. The centrum and prezygapophyses are more shortened than in those described above. As a result of the considerable uniformity of the vertebrae, the exact boundary between the anterior and posterior tail sections is not fixed.

The third modification of the tail was described in *Deinonychus* (Ostrom, 1969a), and is completely corroborated by specimens of Mongolian dromaeosaurids. Starting with the first vertebra of the posterior section (or possibly the last of the anterior section), there is an unusually large, strong elongation of the anterior end of the prezygapophyses, which have the shape of a long, bony rod. The postzygapophyses maintain an entirely normal structure. Each prezygapophysis forms a rod of paired anterior branches that remain closely connected for a long distance. The rod extends anteriorly for no more than 8-10 vertebrae, and the rods of more anterior vertebrae are located dorsal to those of the posterior vertebrae. The anterior ends of the ventral part of the chevron continue as paired branches in analogous bony rods, especially in the posterior section of the tail. In summary, compact ventral channels, composed of very compact ossified tendons, are formed on both sides of the neural arches and chevrons and continue for almost the entire length of the tail. The vertebrae are as though they are [arranged]within the membrane of these tendons, undoubtedly providing strength and rigidity to the tail. The tendons of the postzygapophyses and chevrons appear to be ossified tendons of the caudal muscles (Ostrom, 1969a, b).

It is necessary to note that carnivorous dinosaur vertebrae reflect the characteristic function of the different [vertebral] regions. During modification of the cervicals, the formation of series that differ in length and degree of curvature clearly reflect the amount and manner in which the weight of the head was carried, and to a certain extent the flexibility and orientation of the neck in different groups. In tyrannosaurids, which had a large, and therefore heavy skull, the neck is shortened and the disc-like vertebrae form a [curve] almost approaching the vertical. The semi-curved cervicals with elongate centra of ornithomimids, which carried a smaller weight, appear to be almost completely opposite those of tyrannosaurids. The necks of dromaeosaurids (Ostrom, 1969b) and oviraptorids are apparently [somewhat intermediate] between these two types. The absence of the displacement and slant of the articular surfaces, as well as their parallel orientations, in the dorsal vertebrae indicate a more or less horizontal position to the vertebral column. The caudal vertebrae testify to the fact that the caudal series had a horizontal orientation, [resulting in] the tail being carried and not used as a third support for bipedal animals as was considered originally. Elongation of the prezygapophyses increased the strength of the vertebral articulations, and the absence of any indication of a supporting function for the caudals support this opinion. In dromaeosaurids, the bony tail channels must have imparted a corresponding rigidity, which was very necessary for dynamic balance. The oviraptorid caudal series, with more shortened vertebrae that exhibit elongated transverse processes, was apparently connected to a more powerful tail musculature that guaranteed lateral curvature of the tail. Such a structure in their portion of the distal tail must have considerably decreased relative to the [extent] of the examined modifications.

Sternum. The sternum in theropods, and in dinosaurs as a group, was practically unknown in excavated [specimens]. In the Mongolian collection, this gap has been filled by certain specimens beloning to the families Dromaeosauridae and Oviraptoridae (Fig. 15).

The sternum is a flattened, lamellar, chute-like element with a bilaterally symmetrical structure that is convex ventrally and concave dorsally. The configuration of the sternum is fairly complex, as its cranial edge can be fairly straight like in dromaeosaurids, or form gently sloping, wide [fossae] on both sides of the median process as in oviraptorids. This edge is especially suited for articulation with the periphery of the coracoids, and bears narrow grooves in which the edges of the latter are fitted. In oviraptorids, the coracoid periphery apparently covers the edge of the sternal fossa, and the grooves are located considerably more medially, are highly widened in the region of the median process, and take on the appearance of the periphery of the coracoid. The lateral edge of the sternum is characterized by a more complex outline, but it is possible to note two uneven indentations or fossae in them – anterior and posterior. In dromaeosaurids, these fossae are almost equal in size and depth; in oviraptorids, the anterior one is bounded by an small arc, while the posterior one is deep and wide, [occupying] a large part of the caudal edge of the sternum. The lateral edges are highly [thinned], especially in the caudal region, and apparently turned into a cartilaginous extension, so characteristic of the reptilian sternum. The fossae of the lateral edge are divided by the lobate process of the sternum. The edges of the anterior fossa are similarly thickened, especially in oviraptorids. The caudal edge of the sternum has a circular appearance in dromaeosaurids; in oviraptorids, this end is very short along its length as a result of a very deep posterior fossa, and forms a narrow, lobate process. The lateral edges of the sternum with their fossae serve as an attachment site for the dorsal ribs. At the same time, the meaning of the fossae of the lateral edges of the sternum regarding the attachment of the ribs is not completely clear, as is equally [true of] the presence of the lobate region that separated the fossae. It is possible that their articulation with the ends of the ribs was made possible by cartilage, and that the complexity of the configuration of the edges was related to the bone-cartilage transition.

In one of the oviraptorids, the sternum consisted of two approximately symmetrical halves. The more convex right side covered the peripheral zone of the left side fairly widely. As noted above, the cranial edge has fossae for reception of the coracoid, but the furrows that accommodated its edges are absent, and the cranial median process of the sternum is formed but not strongly raised. Each of the halves has a fossa (possibly fontanelle), and of them the left is very large while the right is not. As is known, the fused ends of the sternal ribs enter into the composition of the sternum and form its paired foundation. In this case, and also probably [elsewhere], the underdevelopment of the sternum can be considered anomalous in a completely mature specimen.

The oviraptorid sternum is more laterally widened, but shorter craniocaudally, than that of dromaeosaurids. The median process of the cranial edge is expressed more strongly and differentiated from the raised [part] of the adjoining sternum. A lengthwise curvature extends along the midline of the ventral surface of the sternum, marked in places by rugosities. The periphery of the median extension also exhibits roughness. These all suggest that highly developed sternal muscles were attached to the wide ventral surface of the sternum.

Cervical Ribs. The first cervical ribs are differentiated by their considerable proximal shortness and width, bearing closely-set articular facets which. On the more posterior ribs, the capitular and tubercular articular surfaces are farther apart, with the first displaced farther than the second; the ribs become elongated and thicker. The epistropheus may already bear the first pair of reduced cervical ribs, because the diapophysis and parapophysis are sufficiently developed.

Dorsal Ribs. The first rib in the series is the shortest, and in contrast to the cervical rib it is characterized by great elongation of the capitular process and widening of the tubercular process, of which the latter is located higher and more lateral to the base than the former. In subsequent ribs, there is a [change in] the proximal part due to the greater elongation of the capitular process and a change in the connection of the angle with the tuberculum. All the ribs are rapidly elongated, with maximum elongation occurring between the sixth and eighth pairs, after which the ribs become shorter relatively quickly. In ornithomimids, the dorsolateral surface of the ribs is very wide, and characterized by a T-shaped transverse cross-section.

In contemporary Reptilia, sternal (abdominal) ribs are found in the ventral part of the trunk at the distal part of the dorsal ribs, and are composed of two segments – lateral and ventral – that are connected to the sternum (Romer, 1956). The remains of sternal ribs are seen in the American *Deinonychus* (Ostrom, 1969b) and the Mongolian *Velociraptor*.

Gastralia. The presence of gastralia is highly characteristic of carnivorous dinosaurs. Gastralia are known in tyrannosaurids, therizinosaurids, dromaeosaurids, oviraptorids, ornithomimids, and segnosaurids. The general number of gastralia includes no fewer than 12-14 pairs. Each rib consists of two segments – lateral and medial – that connect to each other by means of superposition of their ends, which are directed in opposite directions and reduce to nothing. As a rule, the ribs become [thinner] as they progress posteriorly. Frequently the anterior ribs are fused in pairs, and although the number of pairs is not the same in different groups, it is commonly 1-2 pairs. Medial paired fusion of the remaining ribs is the norm, with the left elements covering those on the right. Besides this, each pair articulates with the previous pair by means of joining the rough capitulum (medial end) of the left ribs with the wide capitulum of the right. As a result, [bracing] of the ribs occurs, [as they are] connected not only in pairs but also to contiguous pairs. In all probability, these articulations were characterized by a certain mobility, producing a curvature to the surface of the belly. The articulation of the rib pairs to each other by the described method apparently has not received previous attention, because the ribs are given as disconnected in the description and illustration of the pairs (Maleev, 1974; Romer, 1956).

Pectoral Girdle. Scapulocoracoid. Usually the coracoid comprises approximately one-third or one-fourth of the length of the whole structure. This externally convex element, often thickened in the middle and thinner along the periphery, mostly transforms into cartilage along the edge in several taxa. The scapulocoracoid suture is more or less straight. The coracoid foramen penetrates the bone obliquely. A convexity is located posteroventral to the coracoid foramen on the external surface of the coracoid, with a sharpened top and bearing signs of its attachment with the bony tendons or sinews of the biceps muscles. The glenoid cavity is fairly deep and wide, slightly outturned, and bears convex, wrinkled edges. The supraglenoid thickening is in the shape of a crest or process, and is separated along the top by the scapulocoracoid suture. The internal surface of the scapulocoracoid is broadly concave.

The blade has a ventrally widened part and a dorsally narrowed ramus, the edges of which are almost parallel to one another. A strongly expressed thickening on the inner surface extends from the glenoid cavity, which occupies the lower part of the dorsal ramus. The acromial process is well developed. Its anterior edge is often considerably [thinned], and possibly turned into cartilage.

Considerable differences were observed in the general construction of the scapulocoracoid in different carnivorous dinosaur groups, especially in the shape and proportions of the separate structural elements. Thus, the coracoid is proportionally very large and wide in therizinosaurids, whereas the blade is very short and is even smaller than the coracoid in length, which is unusual for theropods. For example, the scapulocoracoid in deinocheirids is entirely comparable in size to that of therizinosaurids, [but] corresponds completely to the general type and consists of a relatively narrow and elongate blade with a relatively small coracoid. Besides this, a circular fenestra, through which apparently passed blood vessels and nerves, is located near the anterior edge of the wide blade close to the scapulocoracoid suture in therizinosaurids, and not noted in other theropods. Tyrannosaurids characteristically have a highly elongated ramus that slightly widens dorsally. In small theropods – coelurids, dromaeosaurids, and oviraptorids – the scapulocoracoid is of the usual type, with an elongated blade and a relatively small coracoid. However, in oviraptorids, an unusual construction of the anterior edge of the acromial process is noted, which is considerably thickened and flattened anteriorly with the formation of a well-developed, narrow, elongated region (Fig. 16). The ramus of the fused clavicles was, it seems, closely adjacent to it, and in this manner connected to the scapulocoracoid. In other theropods, a similar [structure] is not formed, however an articular area entirely similar in location and shape is noted in the scapulocoracoid region of *Archaeopteryx* (Ostrom, 1976a, c), which provides a serious basis for its consideration as a place for attachment of the clavicles.

Clavicles. Clavicles are found rarely and poorly preserved in excavated dinosaur specimens, particularly among carnivorous forms. In two theropod representatives – *Oviraptor* and *Segisaurus* – the clavicles were initially described as interclavicles (Osborn, 1924; Camp, 1936). Only recent finds of oviraptorids provide a complete picture of the construction of this element in theropods (Fig. 17).

The clavicles in oviraptorids are entirely similar in general features to the wishbone (furcula) in birds, and appear as a V-shaped, fused structure with widely diverging, dorsally concave rami, the ends of which become flattened into a wedge shape. The region of differentiation of the rami from the [body is] widened by a caudally-directed, shortened process. The flattened ends of the clavicular rami (Fig. 18) lie on the acromial process of the blade, connecting to the scapulocoracoids. In this position, the beak-like posterior process was located between the closely placed coracoids, and possibly articulated with them.

In the articulation between the clavicles and scapulocoracoids, the special structure noted above deserves attention – the anterior edges of the acromial process are flattened by the formation of a triangular area that accepted the external end of the clavicle. It is assumed that this area served as a site for preservation of the clavicles in the scapulocoracoids of these dinosaurs. However, in other theropods, the edge of the acromion does not show signs of an articular surface, and often is clearly flattened up to the condition of a thin layer, which may indicate the absence of clavicles or suggest ligamentous connections with them. A similar construction of the furcula should be noted in birds, where the end is articulated with the coracoid, and not with the acromial process of the blade, and bears corresponding articular surfaces.

Clavicles are found in *Archaeopteryx* (Ostrom, 1976a, c) that are extremely similar to those of oviraptorids, but the manner of articulation with the scapular blade and coracoid remains unknown, so that it is not clear whether the specialized unique articulation between the clavicles and acromial process [is present as it is] in oviraptorids.

Forelimb. Humerus. Differentiations in the construction of the humerus once formed the basis for a separation between grasping (relatively well developed) and non-grasping (relatively weakly developed) forelimbs in theropods. In the first case, the presence of a tall, extensive deltopectoral crest is characteristic and found in most theropods. Correspondingly, the deltopectoral crest was weakly developed in non-grasping forelimbs, as is observed in deinocheirids and ornithomimids. The deltopectoral crest in tyrannosaurids is relatively tall but basically shortened, which immediately differentiates it from the developed-type structure. When sufficiently developed, the deltopectoral crest occupies nearly one-third of the entire length of the humerus, and a little more than half in therizinosaurids. When the crest is weakened, it does not extend beyond one-third, and in tyrannosaurids one-fourth, the length of the bone. The degree of sigmoidal curvature of the humerus is also a characteristic feature, most sharply expressed in therizinosaurids and small theropods, and practically lost in non-grasping forelimbs. A well-formed capitulum, especially in theropods with well-developed forelimbs, testifies to high mobility of the shoulder joint. The distal [articular surface] of the humerus is considerably widened and anteroposteriorly flattened. In this case, the distal condyle is sufficiently developed to be characterized by an anterior displacement, as a result of which the epipodium would have been somewhat flexed at the elbow joint. The distal [articular surface] is wide and flattened at its end in the non-grasping type, and the weakly developed condyles are turned more distally and, consequently, the end was characterized by being straighter.

Forearm. The ulna is more massive than the radius and more often straight, [although it is] slightly anteriorly convex in ornithomimids and deinocheirids. The shaft is triangular in cross-section at the articulation with the radius and corresponding muscle groups. The elbow joint fossa is fairly deep: its articular surface is triangular to circular and subdivided into medial and lateral parts, of which the lateral enters between the humeral condyles and has more a supportive rather than articular function; it represents a new archosaur structure, as it is noted in thecodonts, dinosaurs, and crocodiles (Romer, 1956). The olecranon is developed. The distal end of the shaft is often flattened, and its prearticular region shows signs for extensor and flexor muscle attachment.

The radius is sigmoidally curved (therizinosaurids), straight (dromaeosaurids, oviraptorids), or slightly anteriorly concave (deinocheirids, ornithomimids). The proximal and distal ends were flattened and transversely widened in the [cavity of the crossing on the different angles]. Signs of attachment for the radial carpal connections are present on the edge of the distal end.

Manus. The manus in carnivorous dinosaurs tends to reduce the number of digits. In general, a five-fingered manus is characteristic of earlier theropods, and is established as three-fingered (and sometimes two-fingered) for later forms, in connection with reduction of the lateral digits in most cases. Reduction of the number of manual digits can be seen as a general rule in the evolution of the group. It recent years it has been shown that this general tendency occurs in two different types of construction of the carpal elements, providing information on two different modifications of the manus with distinct functional possibilities. As it turned out, carpal structure is determined by the pulley-like and non-pulley-like nature of its composition.

Pulley-like Carpus (Fig. 19). The unique construction of these carpal elements, first described in detail (although not without some specific errors) in a specimen of the manus of the American dromaeosaurid *Deinonychus* (Ostrom, 1969b), plays [a role] in the basis of its classification. It has also been also described in oviraptorids and therizinosaurids (Barsbold, 1976b). The number of carpal elements is reduced in this type of manus, and in the most extreme cases reaches two – distal and proximal. Because of this, the exact identification of the carpal elements is questionable in most forms. In addition, it is not possible to determine whether fusion of the separate carpal elements occurred during their numerical reduction.

Pulley-like carpal elements have a half-pulley shape (Fig. 20): arched, directed towards the forearm by the part bearing the longitudinal groove, and limited by cylindrical edges. The metacarpal side of the half-pulley has two articular surfaces corresponding to the proximal ends of the metacarpals, to which they are solidly attached. The proximal element is notably reduced, has a circular-conical shape, and is attached by an immobile base to the distal end of the radial articulation. Judging by the attachment, the proximal element may be identified as the os radiale. This element enters into the groove of the pulley, thus forming a model connection. The pulley with well-attached mani could move relative to the immobile proximal element along the circumference of the arch, the dimensions of which were limited by the length of the longitudinal groove. Even when the groove seems to limit the motion of the pulley, the predominance of the pulley cavity (Barsbold, 1976b), the width of the groove, and the circular-conical shape of the proximal carpal element testify to the possibility of sufficient degrees of freedom of motion in other dimensions. In all likelihood, the pulley manus articulation also allowed rotary motion of the manus.

The pulley-like construction of the carpus is also found in therizinosaurids, but with a large number of distal carpal elements. In this case, the pulley consists of two distal elements, the large (medial) one of which is possibly homologous to the single pulley studied above. The smaller (lateral) element, which served as an extension of the large, fits snugly into the wide opening of the latter. The arch-like groove is differentiated by its considerable width, and it almost disappears to nothing on the proximal surface of the smaller element. All this should have considerably altered the degrees of freedom of carpal motion. The width of the groove to a certain degree testifies to the sufficient size of the distal elements, which would have numbered more than one.

Non-Pulley-like Carpus (Fig. 19b). This type of carpus structure is defined by the presence of a large number of carpal elements that do not form a pulley. It is known in tyrannosaurids, ornithomimids, and also in more ancient groups. The number of carpal elements in this type is not as greatly reduced as in the pulley structure, and in most cases is between 4 and 6. Exact identification of elements is also difficult in the non-pulley carpus. The carpal elements are usually flattened, more or less similar in shape, and form distal and proximal rows. Often the distal element that begins the row can be identified by its larger size, and corresponds to the first metacarpal by position. In the proximal carpal row, the carpal articular surfaces for the radius and ulna correspond to the flattened elements, which are often identified as the radiale and ulnare. Occasionally the os intermedium is identified among them. Independently from this, the non-pulley carpal structure entirely retains its similarity between different groups, as much as this type of homologizing is possible. The complete carpal structure does not change, and the minimum possible number of elements – four – is found in Mongolian tyrannosaurids (*Tarbosaurus*). The carpus is supposed to contain five elements in ornithomimids (Osborn, 1917).

It is not suspicious that the non-pulley carpal structure is much less compact and guaranteed less mobility than the pulley structure. Supposedly, such a structure is illustrated [by] the rotary motion of the wrist, requiring a greater degree of [development] in the carpal joint articulations.

Metacarpals. Late Mesozoic carnivorous dinosaurs are usually characterized by the presence of three manus elements (Fig. 19). The first is the shortest, most often half the length of the second, and the third is considerably reduced. However, all the metacarpal elements are approximately equal in length among deinocheirids and ornithomimids. Besides that, the metacarpal I is highly flattened mediodorsally in most Cretaceous theropods, whereas a similar flatness is considerably less expressed in ornithomimids and, especially, deinocheirids. The proximal articular surface of metacarpal I has a triangular or triradiate shape, and in addition the central part of this surface has a wide concavity in the two above-mentioned groups, which is absent in other theropods. An asymmetric articulation is often directed somewhat medially, slightly separating digit I from II. The metacarpal II is usually the longest, is fairly robust, and has a moderately asymmetrical distal articular facet. In the oviraptorid *Ingenia,* the metacarpal II is notably reduced and [thinned].

Metacarpal III is usually the most reduced and often shorter than II, although in deinocheirids it is much longer. The greatest degree of reduction is noted in tyrannosaurids, in which metacarpal III is turned into a "claw" bone that lacks a digit. Considerable reduction is also seen in dromaeosaurids and oviraptorids, but the corresponding digit is preserved in its entirety. The proximal articular surface is triangular when it is less reduced, and laterally compressed when more reduced.

As is apparent from the carpus construction, especially the pulley type which was subjected to a considerable reduction, the metacarpal III was practically included in the articulation with it. In any case, the carpus does not articulate with the metacarpal III as it does with I and II, as is especially easy to observe in dromaeosaurid and oviraptorid specimens.

Manual Digits. The general phalangeal formula of the manus is 2-3-4 in late Mesozoic theropods, but the differentiation of the digits has turned out to be fairly great (Fig. 21). At the same time, a series of consistent features is noted throughout the entire differentiation.

Digit I is either shorter than the rest, especially relative to II (dromaeosaurids, saurornithoidids, tyrannosaurids, and some oviraptorids), closely approaches it in length (ornithomimids, deinocheirids), or is longer than all the others (*Ingenia*). Characteristically, the first phalanx of digit I is the longest relative to the others (with the exception of the unguals). Of the remaining manual digits, II is either the longest, is approximately equal to III in length (in this case they are also more or less equal in the degree of reduction), or it is longer than III but shorter than I. [Another sign for] digits I and II of the mentioned group are positioned in equal sequence. Digit III is the most reduced and also considerably [thinned], although the phalanges remain. Another type of reduction of digit III is widely distributed in later theropod groups, however it only proceeds far in two groups. As was noted, tyrannosaurids are nearly lacking digit III (only the proximal part of the first phalanx is present), and in the manus of the oviraptorid *Ingenia* digits II and III were greatly reduced, although they retained all phalanges. Elongation of the penultimate phalanges is fairly widespread, and also occurs in some carnivorous birds. The exception to this rule is *Ingenia*, in which the phalanges become considerably smaller distally, and possibly in therizinosaurids, judging only by digit II with its nearly equal penultimate and first phalanges. With the exception of these groups, the first phalanx of digit II, as well as the first and second phalanges of digit III, are the shortest. The phalanges in many groups are characterized by the well-developed and widened ginglymodal joint. At the same time, the articular surfaces are much less developed in deinocheirids, oviraptorids, and tyrannosaurids.

Against this background of examined general features, sharply noted peculiarities exist that are common to many groups. Dromaeosaurids have the most laterally compressed, hook-like, curved, and sharpened unguals with large flexor tubercles, while in ornithomimids they are straighter and show comparatively weak development of the tubercles. Deinocheirids are notable for their large, massive, and thickened unguals. Therizinosaurids possibly had no equal in the size of their hypertrophied ungual, which in addition are also very wide and slightly curved. In oviraptorids, the unguals entirely correspond to the general theropod design, but in *Ingenia* the unguals are extremely reduced, due to the unusually large reduction of manual digits II and III, and are also noted for their considerable straightness and weakly developed flexor tubercles (Fig. 22).

In conclusion, it is possible that all of the variations in the construction of the manus elements in carnivorous dinosaurs can be reduced to two modifications, at the base of which lie the pulley and non-pulley carpal structures. Earlier, it was noted that the manus with curved unguals performed a prey-grasping function in carnivorous dinosaurs. The slight deviation of digit I was sometimes incorrectly described as opposing the others, apparently according to the example of higher primates, which contributed to the deepening persistence of finding a "grasping" manus in theropods. Now it is possible to refute this idea, even though the theropod manus was initially better suited to tearing apart the body of the prey than to performing a grasping function. If one considers that sharpened, highly curved unguals on an elongated penultimate phalanx help to grasp, *i.e.* to hold the prey by the forearms, then in this sense the dromaeosaurid and saurornithoidid mani unquestionably earn such a definition. It is possible to show that the most sharply expressed grasping hand had a pulley-like carpal structure, which also allowed greater mobility. The connection between a greater degree of "grasping" and a more developed carpal structure seems completely justifiable. However, "grasping" should not always be taken literally. There are some basic deviations, the best example being the therizinosaurid manus. Already, the presence of large unguals, greater than the length of all other manus structures, completely precludes any kind of grasping function. Nevertheless, the pulley structure testifies in favor of the "grasping" basis on which such a manus developed. The distinct pulley of the therizinosaurid carpus, composed of two parts, is very clearly primitive relative to the single pulley in dromaeosaurids and oviraptorids. In this manner, the carpus initially developed in a grasping-type manus on the basis of the pulley structure. It is necessary to note that the forelimb musculature was increased in all the groups with a clearly expressed grasping-type manus, as is clearly reflected in the relief on the humerus (large deltopectoral crest) and forearm bones, and also in the development of their articular surfaces.

The second carpal modification is constructed on the non-pulley basis. It is characteristic of ornithomimids, tyrannosaurids, and possibly deinocheirids. The manus in the first and last of these groups is fairly similar in several features, even though their sizes are completely different. This similarity, noted above, and also such features as the clear weakening of the forearm and the limited mobility for digit flexion (Ostrom, 1969b; Osmólska and Roniewicz, 1970; Osmólska, Roniewicz, and Barsbold, 1972), are insufficient for any kind of grasping, and indicate a non-grasping type of hand in both groups. The weakening of the forelimbs in ornithomimids and deinocheirids is clearly shown by the refinement of the humerus and forearm, and the more poorly-developed articular surfaces between them (Osmólska and Roniewicz, 1970; Osmólska, Roniewicz, and Barsbold, 1972; Barsbold, 1976a). The presence of a non-pulley carpal structure in the ornithomimid manus (the corresponding bones have not been found thus far in deinocheirids) allows a fairly complete characterization of this type of bone in these theropods.

The tyrannosaurid manus is a good addition to what has already been noted. It is distinguished by didactyly, illustrating the further deepening of its forelimb specialization. However, this forelimb is subjected to a progressive reduction that brought with it a weakening. The manus remains non-grasping, as has been noted, and has a non-pulley carpal structure as its basis. The tyrannosaurid manus serves as an example of the preservation of primitive features along with general specializations (Barsbold, 1976a).

Both types of carpus modifications in carnivorous dinosaurs unquestionably reflect the unique evolution of its lineages within different adaptive zones. The non-pulley structure is, apparently, closer to the primitive type, on which basis proceeded a progressive evolution that led to the highly specialized variation of the grasping manus.

Pelvis and Hindlimbs. Pelvis. During the initial era of dinosaur study, taxonomic significance was given to the pelvis (Seeley, 1888) that lent foundation to the present division into Saurischia and Ornithischia. In recent years, attempts have been made to develop a more detailed examination of the two initial types of pelves. In contemporary research, it is necessary to separate out brachyiliac and dolichoiliac in the context of the saurischian pelvis from the number of those deserving attention (Colbert, 1964). The names prepubic and opsithopubic pelves have been introduced, characterizing the two basic subdivisions of dinosaurs (Charig, 1972). New finds in Mongolia have been noted in recent years that greatly expanded existing ideas about pelvic morphology in carnivorous dinosaurs. This refers to the unique morphologies of dromaeosaurids and saurornithoidids (Barsbold, 1976a, 1979; Barsbold and Perle 1979, 1980). These facts were the basis for division of the carnivorous saurischian pelvis into several basic types (Figs. 23, 24) that reflect the main evolutionary tendencies of the group. However, first it is necessary to study and define the meaning of several ideas that will be used later.

Brachyilia is mainly characterized by shortening of the anterior iliac blade, clearly expressed in the more ancient carnivorous dinosaurs (Colbert, 1964) which do not enter into the composition of Theropoda. In this case, brachyilia applies not only to carnivorous dinosaurs and sauropods, but also to some later thecodonts. Representative theropods exhibited dolichoilia, *i.e.* an elongated anterior iliac blade, that was characteristic of more diverse members of the group. In this manner, brachyilia and dolichoilia can be used to demarcate more ancient groups of carnivorous dinosaurs and to establish a more acceptable basis for the identification of theropod and non-theropod lineages among them.

The names prepubic and opisthopubic were introduced upon the examination of the peculiarities of saurischian and ornithischian types of dinosaurian pelves, with the intention of providing a generalized definition of the orientation of the pubis (Charig, 1972). However, the appearance of new Mongolian material provides a basis for using these names just within the confines of the carnivorous saurischian pelvis (Barsbold, 1979). This use of terminology corresponds to their greatest characterization, and reflects the actual positions of elements – the anteroposterior orientation of the pubis in the saurischian pelvis. At the same time, it is necessary to emphasize that the previously noted morphological peculiarities of the dinosaurian pelvis were based on isolated studies. In reality, the picture is probably much more complex, and is expressed in different complexes of structural forms in the saurischian pelvis. Correlation of these forms is difficult so far, but now it is absolutely clear that the pelvis of carnivorous saurischian dinosaurs (prepubic) and several other archosaurs is [actually] divided into prepubic and opisthopubic types. In the context of both these types, it is suitable to identify dolichoiliac, brachyiliac, and also a completely unique form – altiliac (Barsbold, 1979). In connection with this, brachyilia is seen in carnivorous dinosaurs at an early stage of evolution, as well as later thecodonts that were unrelated to the true theropod lineage, as noted. Consequently, true theropods are characterized by three basic pelvic modifications: prepubic dolichoiliac, opisthopubic dolichoiliac, and altiliac, [the latter] possibly connected only with the opisthopubic pelvis. Below, it is necessary to examine these modifications (Figs. 23, 24).

Prepubic Dolichoiliac. The normal theropod pelvis, most widely distributed in more advanced forms, has a very clearly expressed dolichoilia and usually a lower anterior orientation of the pubis. Such a pelvis is common to podokesaurids, coelurids, etc., and several later lineages – tyrannosaurids, ornithomimids, oviraptorids, and saurornithoidids. The ilium has elongated anterior and posterior blades, and is relatively tall in large theropods but low in small forms. The anterior blade, with the exception of the anterior edges, is closely appressed to the transverse processes of the sacral vertebrae, which do not extend above them, while posteriorly the ilia gradually diverge. The anterior edge of the ilium has two sections in tyrannosaurids, but is whole in ornithomimids and oviraptorids. The posterior blade has a different configuration, usually narrowing more than the anterior. The pubic foot is more elongated than the ischial foot. The pubis has an elongated shaft and a variably-shaped distal end, and is more often elongated anteroposteriorly, having the appearance of a boot. In tyrannosaurids, the distal expansion is very large, highly elongated longitudinally, and massive. In ornithomimids, and especially oviraptorids, the distal boot is very reduced and exhibits a [thinner] outline. The presymphyseal edge is narrow in the anterodorsal part of the boot. The ischium is shorter than the pubis to varying degrees; sometimes it is relatively long and straight, with a small, proximally displaced obturator process, characteristic of tyrannosaurids and ornithomimids. Otherwise, the ischium may be short, with a slightly convex shaft and a large obturator process positioned at midshaft, characteristic of oviraptorids and saurornithoidids.

Opisthopubic Dolichoiliac (Fig. 24). This modification was first identified in specimens of the pelvis of Mongolian dromaeosaurids, particularly *Adasaurus* and *Velociraptor*, and also other related types, as a distinct characteristic of the family (Barsbold, 1976a). It is differentiated from the normal type primarily by the anteroposterior orientation of the pubis, which delineates its great peculiarity. Along with this, the ilium is entirely similar in general outline to [smaller] variations in normal (*i.e.* prepubic dolichoiliac) pelves. The edge of the anterior blade has two parts, the posterior being differentiated by its usual thickening. The pubis has an elongated shaft and a circular, laterally compressed distal end, as well as a reversed orientation, that compose its distinctive peculiarities. The ischium is considerably shorter than the pubis, with a distally displaced, large obturator process as in the case of prepubic dolichoilia.

Altiliac (Figs 24b, c). This modification includes the particular type of large pelvis first described in Mongolian segnosaurids (Perle, 1979; Barsbold, 1979). The ilium has a greatly widened, tall, wing-like, and outwardly bent back anterior blade, the configuration and size of which are very unusual for carnivorous dinosaur pelves. The posterior blade is very short, which is also uncommon in other theropods. The bent back anterior blade and reduction of the posterior blade was, until now, known only in sauropods among saurischians.

A large, massive, cube-like process is present along the upper edge of the altiliac pelvis, which in all likelihood served for attachment of the pelvic-caudal muscles and thus compensated for the assumed reduction of the posterior blade. The ilia are [attached to] extensions of the sacral vertebrae that extend higher than the dorsal edge of the ilium. The pubic foot is considerably elongated. The pubis has a large, distal end that is laterally compressed and anteriorly elongated, but highly shortened posteriorly. Another notable variation of the distal end is the appearance of a small, fairly low, boot-like thickening of the upper presymphyseal edge, with an elongate, Y-shaped concavity. The ischium is shorter than the pubis, and has a large, highly extended obturator process that connects or nearly fuses with the pubis above its distal end. The posterior edge of the bone opposite the obturator process has a clearly expressed, sloping convexity. The distal end of the ischium is wide, and straight to differing degrees.

In this manner, the saurischian pelvis was greatly altered in carnivorous dinosaurs. Brachyilia, characteristic of the early evolutionary stages of the group as well as later thecodonts (Colbert, 1964), not only testifies to their phylogenetic similarity, but also to a certain degree reflects the beginning stages of the [evolution] of several "triradiate" saurischian pelves, which became the bases for further changes. The next stage in this progression resulted in the normal, or prepubic dolichoiliac, pelvis, with later stages defined by a variety of pelvic structural shapes in different theropod groups. Until now, the commonly accepted image of the saurischian theropod pelvis was based specifically on this type of dolichoilia. As in normal dolichoilia, brachyilia was expressed in the prepubic orientation of the pelvis, usually among theropods. However, another shape is identified – opisthopubic – that became known among saurischian pelves only recently. In dromaeosaurids, rotation of the prepubis occurs without visible changes in the remainder of the structures, *i.e.* without disturbing dolichoilia. However, altilia already reveals an entirely new modification, reflecting deep morphological changes in the opisthopubic saurischian pelvis of carnivorous dinosaurs. At the same time, altilia shows a certain similarity between the ilia of certain theropods and sauropods, possibly supporting a single origin of these similar structures in both large groups of Saurischia.

Femur. In most cases the femur is longer than the tibia to varying degrees, and is a little shorter only in tyrannosaurids. Among later theropods, the most characteristic feature is the sigmoidal curvature of the femur – it is convexly-anteriorly bent in the sagittal plane. The head is at the proximal end, with a clearly delineated neck, and is directed medially to the shaft and to the distal condyles. This leads to the femur being oriented in the parasagittal plane, which is linked to the fact that the hindlimb articulations are not [very broad]. As a result, the weight of the body passed over the dorsal edge of the pelvic acetabulum onto the femoral articular surface. The fact that the legs were not planted widely apart limited their motion mainly to the vertical plane. The greater trochanter is located on the same line as the head, and in relief is weakly separated from the extension of the dorsal surface of the neck. A vertically-directed cleft is separated from the greater trochanter anteriorly, where the lesser trochanter is located in the shape of a convexly thickened, rugose crest, that reaches proximally to the same level as the greater trochanter. The external surface of the greater trochanter forms a sharply descending, wide, rugose area. The fourth trochanter is located on the medial surface of the shaft, somewhat below the head, and shaped as an elongate crest, or often a slight convexity that is noted by its rugosity. In theropods, the fourth trochanter is usually displaced proximally, and is found at one-fourth or one-fifth the length of the bone, which normally is considered typical of the bipedal group. The greatest deviation is found in oviraptorids, in which the fourth trochanter is located almost at midshaft, in addition to which it is weakly expressed. The distal end has well-developed condyles, and the intercondylar groove is deep, narrow, and often weakly expressed on the anterior surface of the shaft, which may be flattened as in oviraptorids, or strongly convexo-concave as a result of strong development of the intercondylar groove as in tyrannosaurids. In ornithomimids, the anterior surface of the distal end is differentiated from all these forms in having a distal edge without an intercondylar groove, as well as the fact that the midshaft is longitudinally convex, a deep groove extends along its medial edge that is absent in other theropods, and the edge itself is developed into the shape of a highly flattened, rugose crest. This medial edge of the crest is very elongate in tyrannosaurids, short and convex in oviraptorids, and weakly expressed in dromaeosaurids.

Tibia. The tibia is considerably more massive than the fibula, with a straight anterior edge, and widened on the end that is oriented sub-perpendicularly. The proximal end is wider and thicker, with a bent back cnemial crest. The proximal articular surface consists of two convex condyles, the medial one elongated anteroposteriorly and the lateral spherical and extending greatly outwards. Below it, on the upper one-third or one-fourth of the bone, a highly elongated crest is developed where the fibula attaches to or lies against it. The distal rising of the tibia is limited by the unique mesotarsal articulation.

Fibula. The fibula is the same length as the tibia, with a distally tall, narrow shaft. The proximal widening is thickened and slightly concave internally. Crest-like, rugose convexities (attachments for the small pedal flexors) are found along the proximal one-third or one-fourth of the bone, below which the refinement of the shaft becomes more even.

Mesotarsal Ankle. For theropods, as for all dinosaurs, the characteristic ankle articulation is mesotarsal, which is common to archosaurs and many lepidosaurs (Romer, 1956). However, in theropods the structure of the mesotarsal articulation is distinguished by a high degree of specialization. In theropods, this simple and compact structure is formed by two proximal elements (astragalus and calcaneum) and the distal tarsals. The body of the astragalus has the shape of an asymmetrical cylinder, which is characteristic for theropods, and a very tall ascending process. The calcaneum, as a rule, is highly reduced, closely connected with the astragalus, and apparently has a subordinate role in the mesotarsal articulation. Both proximal elements appear as a single structure with a circular articular surface, are immobile, and are fixed onto the distal ends of the tibia and fibula. Such a structure guarantees a firm limitation in the degree of freedom and direction of motion (Krebs, 1965; Charig, 1972; Bakker and Galton, 1974), [which would have been] important during rapid locomotion on a hard substrate. Besides that, the mesotarsal articulation is associated with the digitigrade locomotion, narrow position of the limbs, and bipedalism (Charig, 1972) characteristic of theropods.

The mesotarsal articulation is essentially similar among theropods, *Archaeopteryx*, and birds. Along with this, the nature of its construction varies a great deal in different modifications of the mesotarsal articulation in other Saurischia, as well as in Ornithischia. The mesotarsal articulation in prosauropods and sauropods is more complex, as is the case in most thecodonts. The astragalus is immovably articulated with the calcaneum, as well as with the tibia by means of the large proximal process that entered into a corresponding cavity (Hughes, 1963; Charig, Attridge, and Crompton, 1964). In ornithischians, the astragalus lacks an ascending process, although it is tightly fused to the calcaneum.

In Pseudosuchia and contemporary crocodilians, the astragalus and calcaneum, which had a well-developed tubercle for attachment of the gastrocnemius muscle, are connected immovably (Romer, 1956; Bakker and Galton, 1974). Structurally, the calcaneum enters into the composition of the pes, while the astragalus is functionally related to the tibia, in contrast to theropods where both bones are functionally related to the tibia. The Pseudosuchia-crocodilian type of articulation did not limit mobility, and its character supports plantigrade locomotion with partially- or widely-positioned limbs (Charig, 1972; Ostrom, 1976a). This type served as the basis for construction of the mesotarsal type (Walker, 1964, 1972), but the fact that it is difficult to include the calcaneum in the composition of the tibia without changing the original function of the astragalus in anteroposterior foot motion argues against this (Krebs, 1963, 1965, 1973). Recently it has become known that mesotarsal articulations are present in the pseudosuchians *Lagerpeton* and *Lagosuchus* (Romer, 1971, 1972), as a result of which the question of the original [ankle] type must be posed somewhat differently. In the early stages of saurischian evolution, the evolution of the primitive prosauropod type of mesotarsal articulation, lacking an ascending process of the astragalus, was related [to that of] Triassic theropod saurischians (Huene, 1942; Raath, 1969; Bakker and Galton, 1974).

Pes. It is possible to identify three basic types of pes construction. The first is the normal theropod foot, characterized by its "bird-like" construction, as noted earlier, even though the common name for the group means "beast foot". The second type was discovered fairly recently, and has a unique structure for a predatory ungual. The third type, not very common in carnivorous dinosaurs, in known in segnosaurids.

Normal Pes (Fig. 25). In later theropods, the pes was morphologically four-toed but functionally tridactyl. It is characteristic of most of the group and its numerous variations, such as tyrannosaurids, ornithomimids, oviraptorids, coelurids, etc. This type of pes is very similar to the bird type in general, with a compact, compressed metatarsus and radiating digits with sharpened ungual phalanges.

The metatarsus consists of three fully developed (II, III, IV) and two rudimentary (I and V) metatarsals. Two modifications in this construction are recognized. In the first, metatarsal III is almost uncompressed proximally, while it is highly compressed in the second. In the first case, this bone plays an important part in forming the proximal articular surface of the metatarsus, while in the second it is practically excluded from the articulation. Correspondingly, metatarsals II and IV are either fully separated by metatarsal III proximally, or they are connected. The metatarsus of the first modification is most clearly apparent in oviraptorids and allosaurids, and distinguished by their elongation or even shortening besides that. The metatarsus in tyrannosaurids and ornithomimids serves as the best example of the proximal structural reduction of metatarsal III, and it is also typical for it to be considerably elongated. At the same time, as has been recently established, metatarsal III is practically uncompressed proximally in more primitive Mongolian ornithomimids (garudimimids), and is characterized by being considerably shortened. The distal heads of the main metatarsals are, as a rule, characterized by a convex articular surface. Metatarsals I and V appear only as rudiments corresponding to the proximal and distal ends. At the same time, metatarsal I does not bear a reduced digit, and the digit of V is entirely absent. Metatarsal I is completely absent in advanced ornithomimids, in contrast to primitive forms (garudimimids) (Barsbold, 1981).

The phalangeal formula of the pes is 2-3-4-5-0. Digit I is considerably underdeveloped, and did not reach the substrate. Frequently it has been described as recurved or turned back relative to the other digits, but clearly this is incorrect. The articular surface of the remaining metatarsals completely and clearly denies the possibility of such an orientation, which is more characteristic of modern bird pedes. Digits II, III, and IV are fully developed and serve as supports for the digit III, which is sometimes slightly elongated. The phalanges of digit IV are the shortest. The ungual phalanges are fairly similar in shape. In digit I they are laterally compressed and somewhat ventrally flattened, which is typically at its greatest degree in ornithomimids.

Pes with Recurved Digit (Figs. 26, 27). This initially became known in American dromaeosaurids – *Deinonychus* (Ostrom, 1969a, b) – and has been consistently described in Mongolian materials, from which saurornithoidids are added here (Barsbold, 1974).

In this type it is possible to identify two modifications of the metatarsals: one with an almost uncompressed digit III, characteristic of dromaeosaurids, and one with a highly compacted III, characteristic of saurornithoidids. In both cases the metatarsus is not considerably differentiated by elongation. To these basic peculiarities is added the well-developed distal ginglymodal articular block of metatarsal II, whereas III and IV have convex articular heads.

There are no changes in the phalangeal formula of digit IV. At the same time, digit II is distinguished by its unique construction. Its phalanges are notably shortened, and the first participates in the formation of the ginglymodal joint with its metatarsal – it bears a medial crest on its proximal articular surface, which is normally absent in this digit. This distal block has highly developed and dorsally-directed ginglymodal arches. The construction of the penultimate phalanx deviates the most – its proximal articular surface has a highly developed, tongue-like ventral part that extends posteriorly considerably beyond the level of the shortened and deeply indented dorsal edge. As a result of this, a unique articulation formed that does not resemble the usual one, guaranteeing strong backwards bending of the penultimate phalanx. This also aided dorsal [movement] of the ginglymodal arch of the first phalanx. The ungual phalanx was highly sharpened and laterally compressed, and exceeded two or three times the length of typical ungual phalanges. In all probability, the digit with this predatory ungual did not participate in locomotion, and usually was found in the recurved position, not touching the substrate. Digits III and IV were approximately similar in length and generated the force needed for locomotion. The body weight axis passed between these two digits, which basically are not differentiated in any features from the same digits of the normal theropod foot.

Third Type of Pes (Fig. 28). This type is known in Mongolian segnosaurids (Perle, 1979; Barsbold and Perle, 1979). It is fundamentally distinct from the two other types. No fewer than four elements enter into the segnosaurid-type metatarsus, with a rudimentary metatarsal V. The metatarsus is distinguished by being short and having a relatively thickened composition, practically not expressed in its structural compactness, that immediately separates it from the bird type. Metatarsal I is relatively large and wide, which does not exist in other pedal modifications, and its proximal part has a deep concavity by which it was articulated with the adjoining elements. The distal articular heads are wide and convex. The phalangeal formula does not change. Digit I was the shortest, but it could reach the substrate. The remaining digits were more or less similar in length, and the weight axis passed through digit III. The very unique presence of two very shortened, proximally distally flattened phalanges in digit IV has been noted previously in other dinosaurs. The ungual phalanges are laterally compressed to different degrees.

Conclusion. The three types of pes in carnivorous dinosaurs are differentiated in such a way that the functional possibilities of each must have been quite unique. The normally functionally tridactyl pes of later theropods is the logical culmination of the tendency for digital reduction in the originally functionally five-toed pes of the earlier group. In the second half of the Mesozoic, the compact pes of bird-like construction evolved, most highly specializated in tyrannosaurids, advanced ornithomimids, etc. It is necessary to examine the proximal compression of metatarsal III and elongation of the metatarsus as a further step towards the achievement of an entirely supportive structure, necessary for rapid locomotion on the substrate. Pedes of similar construction evolved in some forms, characteristic of earlier and more primitive types, but lacking the proximal compression of metatarsal III (allosaurids, garudimimids).

The pes with the recurved digit originated from the normal pes, having obtained a very unique new structure in the highly modified digit II with a predatory ungual. In this orientation, the pes became a means for defense and attack (Ostrom, 1969a, b), which apparently did not lessen the ability to maneuver and locomote rapidly in any way. The area of contact with the substrate also decreased as a result of the exclusion of the digit with the predatory ungual.

The segnosaurid pes is the type that is most differentiated from the two other types. First, it is short and not compact, which indicates a distinct, probably less progressive manner of locomotion. This pes is similar to that in several ornithopods, for example hadrosaurids, which is confirmed not only by the general similarity of the structure, but also by the disc-like shortening of the digital phalanges. That is why there is reason to suppose that the segnosaurid pes is linked to a generally similar amphibious lifestyle that apparently did not require very easy and quick flight.

Functional Peculiarities of Postcranial Structures

Cervical Vertebrae. The natural curve of the neck depends a great degree on the size, and consequently the weight, of the head as well as the length and flexibility of the cervical vertebral series (Fig. 29). Along with the characteristic bend, there is differential mobility in certain regions of cervical vertebrae.

The relative length of the neck decreases with an increased size and weight of the skull, and in this regard tyrannosaurids probably had no equals. This is seen not only in the reduction of vertebral number, but of lengths as well. With its great shortening, the tyrannosaurid neck approaches the vertical, a fact that is linked to the sharply distinct levels of the anterior and posterior vertebral articular surfaces. It is clear that a more vertical position of the neck corresponds to carrying a greater load. The neck forms a natural sigmoid curve, and the straight area between the curves approaches the vertical. Judging by the shortening of the first vertebra, the sigmoid character of the natural curve was relatively weakly expressed, and in general the neck was less flexible.

Tyrannosaurids were sharply differentiated from ornithomimids, which had elongate and flexible necks. The very small ornithomimid skull resulted in an insignificant weight atop a presumably muscular neck. Judging by the position of the articular surfaces, the natural curvature of the neck corresponded to a gently sloping sigmoid, and at the same time the anterior and posterior vertebrae, which were sufficiently elongated, were oriented more horizontally, while the basic neck area extended between them and was linked to them by a widely arched curvature. It is assumed that the ornithomimid neck was more flexible, and the possibility of greater mobility is expressed in the considerable elongation of the anterior vertebral prezygapophyses, allowing turns and rotations of the head and neck with greater amplitude. The articular facets of the zygapophyses are oriented at a greater angle to the sagittal plane of the vertebra, bringing them towards the horizontal and contributing to the lateral motion of the anterior cervical region. This is noted in other theropod groups with relatively long necks. The straight region of the sigmoid curvature bears zygapophyses with somewhat medially-directed facets, corresponding to long-axis rotation. The posterior vertebrae show some reduction in prezygapophyseal length along with more horizontally-positioned articular facets, which to a greater degree corresponds to flexion, extension, and lateral motion of the neck, rather than rotation. This is also true of the short neck of tyrannosaurids, but similar features are expressed much more clearly in the elongated neck of ornithomimids. As the material from Mongolian collections shows, ornithomimids reached gigantic proportions, almost the size of tyrannosaurids. Their skulls were proportionally much smaller, [relative to] the increased body dimensions. The cervical ribs were well developed and attached to the vertebrae, testifying to the strong musculature that considerably surpassed the needs of basic head support. This development of neck muscles apparently reflects [enhancement] of neck flexibility and mobility in ornithomimids, [which were] in this sense partly similar to long-necked running birds. Other groups – dromaeosaurids and oviraptorids – are somewhere between the short-necked tyrannosaurids and long-necked ornithomimids in their neck structure and orientation.

Dorsal Vertebrae. The dorsal vertebral series forms a more or less horizontal row, with a convex arch to be more precise (in contrast to the traditional view of bipedal dinosaurs, who supposedly rested on the substrate with their tails), which is additionally proven by the positioning of the vertebral articular surfaces on exactly the same level. The zygapophyseal articular facets are directed more medially, to a great extent limiting the ability to flex and extend the spinal column in the sagittal plane, in contrast to the considerably lateral curvatures along the whole length of the dorsal series. Besides this, the presence of a hyposphene-hypantrum intervertebral articulation in dromaeosaurids and tyrannosaurids (Ostrom, 1969a, b; Maleev, 1974), as well as the development of powerful inter-element articulations whose attachments are located on the edges of the processes in practically all theropods (and also crocodiles), testify to considerable limitations of spinal mobility. Similar articulations are found in extant ostriches, thanks to which the vertebrae are turned into a strong, almost immobile, horizontally-directed shaft, especially in the posterior region of the back (Ostrom, 1969b).

Caudal Vertebrae. Transverse processes are well-developed in the anterior region of the tail in most theropods, which also occurs in mammals while in reptiles they continue over a large extent of the caudal vertebral row (Ostrom, 1969b). The development of transverse processes is linked to the presence of the attached caudal musculature. Besides this, dorsal and ventral muscles are always developed in the anterior part of the tail in terrestrial vertebrates, which play different roles but basically serve to raise and lower the tail (Miller, 1969). Dorsal extensors are identified in the region of the transverse processes in lizards, and the ventral flexors are located near the haemal processes. These muscles are grouped predominately in the anterior part of the tail in theropods, which is particularly indicated by the great development of neural and haemal processes in this area. In most theropods, the most "active" part of the tail occupies less than the first half of its length. Along with this, development of zygapophyses and chevrons along almost the entire length of the tail shows clearly enough that its posterior region had definite intervertebral immobility. The elongation and [closeness] of the prezygapophyses, which are raised towards the dorsal vertebral surface, apparently increased the rigidity of tail construction. Positioning of the articular surfaces on the same level is characteristic of all vertebrae, apparently reflecting either the absence or insignificance of natural curvature.

Oviraptorids are differentiated by substantial development of transverse processes along a considerable part of the tail. Besides this, the spinal processes are considerably elongated, which is usually a characteristic of the tail in aquatic reptiles (Romer, 1956). As noted, transverse processes are linked to development of lateral flexors, and their strengthening in oviraptorids might be linked to conversion of the tail into a swimming organ. Lateral tail flexion in a medium such as water demands not only great bending from the flexors, but it must also actively overcome the resistance of the medium, for which the flexors must extend along the greatest possible number of vertebrae. Only upon [fulfilling] these functional conditions will the tail be sufficiently effective. It is possible that shortening of the vertebral centrum, suited for swimming and characteristic of oviraptorids as well as hadrosaurids, is linked to the increase of the [medial] transverse caudal muscles, which attach to the transverse processes across 1-2 vertebrae. As a result, the frequency of muscle attachment is increased relative to a unit of length, guaranteeing a gain in strength.

Caudal vertebral structure in dromaeosaurids appears to be highly specialized, expressed in the development of ossified tendons that continue as prezygapophyses and chevrons. Densely-packed ossified tendons apparently lend stiffness to the tail, which is not achieved by common means. At the same time, limited intervertebral mobility is permitted, as a result of which the ossified tendons are not fused together, the vertebrae are completely separate from one another even in the distal tail, and there is no fusion between the chevrons and the vertebral centrum. The ossified tendons connect with the caudal flexor and extensor tendons (Ostrom, 1969a, b). The elevators and depressors are also grouped predominately at the tail base. As a result, a very rigid caudal structure is [produced] in the main part of the anterior region in dromaeosaurids. A similarly unique organ is reminiscent of a riding crop with its elastic stiffness, except perhaps that it is more massive and apparently occupies a more or less horizontal position during locomotion, or suspended in the air in any case. John Ostrom suggested that the high moment of inertia of the tail is correlated with maneuverability in dromaeosaurids, and helped with sharp turns during [running]. The similarity in theropod tail structure shows an adaptation to performance of the same function, namely balancing during bipedal locomotion. Understandably, such a function first demands a horizontal position, specifically a position suspended in the air for the balancing organ, to serve as a counterweight to the presacral axial skeleton. On this basis, different specific adaptations are developed, which were studied previously, and the functional and positional differentiation of the weight of the theropod tail figures into common ideas about it as a third supporting structure of the body for a bipedal animal, as was widely accepted in traditional dinosaur reconstructions. However, such a conclusion is far from new: Romer (Romer, 1956) previously described the tail of bipedal dinosaurs as primarily a balancing organ during locomotion.

The most advantageous way of differentiating mobility and flexibility of the axial skeleton [comes] with bipedal locomotion. Naturally, the supportive region – the sacrum, closely connected with the pelvis – is immobile. The dorsal vertebrae seem to form a raised truss structure, supporting the center and oriented horizontally along its mobile base (Ostrom, 1969b). Lateral curvature is not convenient with bipedality, and the back was capable of only limited flexion and extension. A transition from the trunk to the flexible, mobile neck is accomplished by means of [consolidation] along the arch. The tail, usually suspended in the air, served as a balance to counterweight the presacral body. It is quite possible that Bakker's reconstructions of galloping dinosaurs (Bakker, 1975) are not a groundless fantasy, and that theropods, at least, were in fact mobile bipeds, whose tail did not serve as a mere passive support even at rest.

The general orientation of the theropod axial skeleton, which defined the position of the body, appears to be as follows: mobility of the sigmoidally curved neck correspondingly increased, in different degrees, from fairly shortened and near-vertical to elongated and gently sloping; the positions of the barely mobile dorsal vertebrae are almost horizontal, and turn into the compact sacral region that formed the immobile base of the axial skeleton; finally, the flexible tail, was held suspended in the air in most cases and had different degrees of inertia.

Forelimb. Theropod forelimb structure clearly shows a commonality of basic design, suited to the performance of diverse actions. However, the forelimb is quite often differentiated in different groups. One of the best examples of this is the deltopectoral crest of the humerus, which reaches an equally high level in many theropod groups. This indicates considerable development of the pectoral muscles, on which the intensity and strength of forelimb motion in such predators as dromaeosaurids, oviraptorids, and especially therizinosaurids were conditional. As is understood, the pectoral muscles perform an important role in forelimb flexion in concert with other shoulder muscles. The [antagonistic] muscles are also highly developed. These are the flexors, and the others are the extensors, which indicate strengthening of the M. triceps, for example, the attachments of which are particularly notable in therizinosaurids and other above-mentioned predators with highly developed pectoral muscles. The presence of a wide pectoral girdle in oviraptorids and dromaeosaurids testifies to this.

Theropod forelimbs obtain a rather considerable mobility, defined by the nearly perfected construction of the shoulder joint. The glenoid cavity is usually deep and turned outward, the articular head of the shoulder is well-expressed, and all this taken together guarantees a fairly varied motion for the limb, including long-axis rotation. Considerable distal widening of the humerus and turning forward of the condyle are characteristic of theropods with strengthened forelimb function, and they define forelimb bending at the shoulder joint while at rest.

In previous studies, aspects of ornithomimids, deinocheirids, and tyrannosaurids mainly formed the opposing examples to the above-mentioned groups. In tyrannosaurids, this is explained by the extreme reduction of the forelimbs, which are weakened and limited but did not entirely eliminate their function. The large forelimb in ornithomimids, and the hypertrophied forelimb in deinocheirids, seem disproportionately weak and therefore less effective in strength and intensity of action. In this group with weakened forelimbs, the articulation appears less perfect and less capable of rotation, the forelimbs are more or less straight about their axis at rest, [and they are] weakly effective in performing protraction and retraction, with flexion and extension involving an especially large effort.

An important significance is usually given to the manus in defining forelimb function. For this, the pulley character of the carpus clearly defines the functional possibilities of this structure. The main type of manus motion with such a carpus is defined by the pulley groove. The amplitude of lateral manus motion is almost exactly defined by the circumference of the carpus taken along the functional surface of the pulley; in all cases this arc did not exceed 180°. Manus flexion and extension were also defined by the construction of the pulley groove, and basically by its width, which limited the degree of freedom of motion. The pulley mechanism with all its complexity, and the order of structures composing it, guarantee a varied, fixed mobility in the carpus (Ostrom, 1969b, 1974a).

The non-pulley carpus is not as developed as the one already described, either structurally or relative to mobility. It is basically less compact, and correspondingly its mobility is less fixd and less organized.

Tridactyly, common in later theropods, possibly should be studied as well-adapted for the unique "grasping" method. Possibly this digital number reflects the best [design] with which the "grasping" capability of the manus is maintained at a high enough level. Theropod "grasping" itself was not the same as in brachiating mammals – primates and early edentates (sloths). Distinctly from them, the hitting-piercing grasp was dominant in theropods with so-called "grasping", which was very similar to the action of the clawed hindlimbs of carnivorous birds. Only in this specific sense can the theropod manus [be described] as "grasping", [meaning] more precisely a grabbing or clutching structure. Similar carpal ability was more sharply expressed in the construction of the digits, which moved apart during extension, as wellas their endowment with sharpened unguals and elongate penultimate phalanges, also characteristic of some carnivorous or predatory birds (Ostrom, 1969b). The contraposition of manus digit I to the others is now known in theropods, although details about this have been described as linked to its "grasping" capability (Osborn, 1917). The natural separation of digit I is due to the medially-turned distal end of the metacarpal. The ginglymodal joint of digit I did not allow encircling flexion (Ostrom, 1969b; Osmólska and Roniewicz, 1970), as is characteristic for the manus of climbing animals.

The carpi of dromaeosaurids, therizinosaurids, and oviraptorids are found within the context of the "grasping" type, as noted, having developed the construction and size of their digits in a particular manner. The dromaeosaurid manus is unquestionably the best example of this type. The sharpness and curvature of their unguals apparently rendered their piercing and cutting especially effective. With sufficient ungual curvature, the sharpened end recurves even more upon flexion of the penultimate phalanx, helping to [produce] an even greater piercing, and in this manner a more secure grasp. A direct connection is found between the large ungual curvature and the degree of development of the tubercles for the long digital flexors; at the same time, the unguals are highly laterally compressed.

The gigantic, laterally compressed unguals of therizinosaurids are hardly adapted for a piercing grasp as in dromaeosaurids. At the same time, the shortened digital phalanges indicate a possible adaptation for delivering a blow from the gigantic claws (therizinosaurid forelimbs are apparently remarkably strong).

Another derivation is observed in the specialized oviraptorid *Ingenia*, in which the entire manus maintains features of the "grasping" type, although the unusually large reduction of digits II and III must have decreased their participation in these basic functions, giving them a role in supporting a skin membrane. The manual digits are of the normal "grasping" type in more primitive oviraptorids.

The "non-grasping" type of theropod manus, with weakened forelimb function, also showed considerable variety. The weakly flexed unguals of ornithomimids have lower flexor tubercles, in direct contrast to the dromaeosaurid condition. Taking the weakened forelimbs and slight ungual compression into consideration, it is possible to state that the ornithomimid manus is not at all suited for delivering a blow or a piercing grasp. In tyrannosaurids, the general size of the forelimb greatly limits function of the manus, which was additionally lacking digit III. Increased forelimb reduction, observed in earlier large carnivores – allosaurids and megalosaurids – and reaching a maximum in tyrannosaurids, also occurs along with the non-pulley carpus, guaranteeing a lower effectiveness in "grasping". The deinocheirid carpus includes several contradictory features that indicate general forelimb weakening and deviation of the manus from the grasping type, along with development of large, massive, curved unguals. In all likelihood, such a manus could only generally perform the motions required for a hitting-piercing grasp. The large forelimbs have a large moment of inertia, but deinocheirids are not as suited for this grasping as therizinosaurids in terms of muscular strength and the degree of specialization of the general structure for this function. Apparently, the deinocheirid manus retains the ability to perform a hitting motion to some degree, although its effectiveness is not likely to have been great. At the same time, the type of hitting motion of the forelimb was not always restricted to attacking a victim, and it is possible to find quite a few other uses for it that do not require a great deal of strength, such as digging up termites, etc. (Rozhdestvensky, 1970).

Hindlimb. Theropod hindlimb structure reflects the commonality of its basic adaptation for bipedal locomotion. A well-formed femoral head, turned medially and oriented almost perpendicular to the long axis of the shaft, indicates transference of force along the axis and reflects the narrow positions of the limbs. Knee curvature also approaches parasagittal near its [surface], and as a result the femoral head axis is perpendicular (or close to it) to the flexure surface of the knee joint (Ostrom, 1969b). This position of the propodia is usually typical of most birds and mammals. The fixed nature of dinosaur tracks also testifies in favor of similar limb positions in these animals (Ostrom, 1969b, 1972; Bakker and Galton, 1974). It is understood that close positioning of the limbs is one of few anatomical indications of endothermy in dinosaurs (Ostrom, 1969b; Bakker, 1971a; Bakker and Galton, 1974).

In bipedal theropods, the fourth trochanter was considerably proximally displaced in most cases, which is linked to the increased role for caudofemoral retractors, apparently [revealing] a gain in speed at the expense of strength due to shortening of the lever arm, which is essential for mobile forms. Upon stepping down, the impact passes through the limbs to the femoral head, not medially as is the case with a horizontally-positioned femur, but through the upper edge of the trochanteric fossa (Bakker and Galton, 1974), simultaneously creating better transmission for weight support. In this case, parasagittal motion of the pelvis heightens the effectiveness of limb motion upon pushing off from the substrate. It had been considered previously that bipedal locomotion provides an advantage in energy use as opposed to quadrupedal locomotion, but it seems that this does not occur and that the advantage lies in increased maneuverability (Bakker, 1972; Bakker and Galton, 1974). The whole hindlimb structure in theropods, which were completely bipedal animals, is directed towards maximizing this advantage. This is reflected in the construction of the functionally tridactyl pes, initially adapted for movement on a more or less hard substrate with the weight on the digits. Characteristically, the pes in most theropods is distinguished by its compactness and narrowness, which is also typical of birds and many mammals. This pedal specialization is exhibited by several carnivorous dinosaurs; thus, in derived ornithomimids the axis of metatarsal I undergoes a proportionally greater lengthening, as observed in many theropods. These features, along with dorsoventral flattening of the pedal unguals, indicate adaptations for swift running. However, the pes in other groups – dromaeosaurids and saurornithoidids – has sharply distinguishing peculiarities [stemming] from development of a recurved digit II with a predatory ungual (Ostrom, 1969a, b; Barsbold, 1974). The penultimate phalanx and its ungual could bend back strongly, due to the specific construction of the articulation between it and the first phalanx, *i.e.* the digit could be retracted, and in its state of rest did not touch the substrate with its sharpened, highly elongated ungual. Relative to locomotion, the pes became didactyl, and this was possibly a simultaneous adaptation to quick, maneuverable flight through reduction of the pedal support surface. At the same time, the pes obtained an additional function, that of an effective weapon for delivering blows and tearing the body of a victim or enemy. It is possible that the "blow" by the "predatory" ungual was delivered with one limb, while the other performed the function of support. This presupposes a high degree of mobility and equilibrium for the animal (Ostrom, 1969b). However, it is more likely that the unguals of both rear limbs were used simultaneously, for which the predator either had to hang on the victim, grasping it with the forelimbs, or fall on its back, which is done today by some members of the cat family. In the unique "grasping skeletons" of the carnivorous *Velociraptor* and herbivorous *Protoceratops*, the position of the hindlimbs of the predator supports exactly this kind of supposition (Barsbold, 1974).

Conclusion. The natural curvature of the neck depends greatly on the size, and consequently the weight, of the head, as well as the length and flexibility of the cervical vertebral series. An increase in the skull is reflected in a decrease in the relative length of the neck, with its orientation more closely approaching the vertical. With a decrease in the skull, the reverse situation occurs – an increase in neck length and its orientation along a gently sloping sigmoid curve.

The dorsal vertebrae form a series with limited mobility, defining the position of the theropod body, which did not felx and extend or lean on the tail as has been accepted in traditional reconstructions of bipedal dinosaurs. In most theropods, the most active part of the tail occupied less than the first half of its length. To a certain degree, this also contradicts considering the tail as a predominately supportive organ. At the same time, "activity" of the tail in oviraptorids is highly increased along practically its entire length, corresponding to its function as a swimming organ. In dromaeosaurids, a large increase is observed in stiffness and elasticity of the caudal vertebral series, [supporting] it in [effective] dynamic balance.

CHAPTER II

CLASSIFICATION, ECOLOGY, AND EVOLUTION OF CARNIVOROUS DINOSAURS

Examination and handling of collections of a new, broader base becomes possible first of all due to the great increase in the variety of late Mesozoic dinosaurs discovered recently. In this, the Cretaceous Mongolian forms have a decided influence in the majority of cases. The extensive theropod material not only allows demonstration of the exclusive characteristics of the later lineages, but basically extends the limits of comparative anatomy of carnivorous dinosaurs, aiding a deeper understanding of the historical development of the entire group.

CLASSIFICATION OF CARNIVOROUS DINOSAURS

Brief Historical Sketch. The Order Dinosauria was established by Owen more than 100 years ago. With accumulation of facts, some among them pertaining to the carnivorous group, the knowledge of different varieties of dinosaurs kept growing. The number of dinosaur identified on rather insufficient taxonomic factual material also increased, especially of earlier forms. During this hundred years, the field of study described the fauna of western Europe, North America, Africa, and central Asia, creating a constantly growing basis for such a classification. Their publication and identified taxonomy are presented in known references (Romer, 1956; Elements of Paleontology, 1964; Kuhn, 1965, 1966; and also Steel, 1969, 1970; White, 1973; Olshevsky, 1978 and others).

The increasing knowledge about the varieties of dinosaurs, both carnivorous and herbivorous, aided wider generalizations that established two main directions [of study]. The first was narrower in character, and [dealt with] the comparatively particular problem of identifying a new taxonomy of families and orders. This was a consideration of the taxonomic work of the earlier stages of study, but on a higher level. The second direction corresponded more to the creation of a phylogenetic classification (Huene, 1909, 1914a, b, 1915, 1920, 1932, 1956), and defined the basic cast in the classification of the Saurischia and served as the rich basis of opportunities for further studies (Romer, 1956; Elements of Paleontology, 1964; etc.). Although understanding of theropods was excluded in Huene's system, nevertheless it was considered in the schemes of scientists who accepted his basic premises. Huene's perspective [was used for] identification of saurischian infrareds, although the ordinal and supraordinal taxonomy were sometimes interpreted quite differently from the originals. The identification of two major branches of carnivorous dinosaurs – carnosaurs and coelurosaurs, and the relegation of both in general to Theropoda (studied in the context of a suborder) – was the basis of the commonly accepted classification, independent of which place is given to each among Saurischia and which order was given to those of the identified subsection. Theropods had been identified as an independent group long before the work of Huene (Marsh, 1881), and many older authors (Matthew, 1915; Abel, 1919) preferred to accept it.

Huene noted the familial ties between "carnosaurs" *sensu lato* – Triassic and post-Triassic – and the prosauropod-sauropod lineage, which led to a subdivision of sauropods into two groups because they were a specialized lineage. Another concept, which observed the similarities of theropods, left open the question of their connection to early saurischians. Colbert (1964, 1970) made a prospective step towards overcoming the difficulties in classification schemes by [separating] the early carnivorous dinosaurs from paleopods, connected at the familial level with prosauropods and particularly with theropods.

The suggested classification is based on this division and studied the theropods as a single lineage of Saurischia and which evolved progressively during the greater part of the Mesozoic.

The Appearance of New Information. Further improvement in classification was first defined by the considerable broadening of the variety of late Mesozoic theropods, especially those of Mongolia. The material of recent years much more fully reflects the specifics of later lineages. Its distinctiveness narrows in the series of cases where there seems to be too great a gap between the lineages, and seems to suggest connections between different theropod lineages, which is very important. These new materials allow increased discoveries about theropod morphology and to broaden the understanding of their evolution. Ordinal limits within the commonly accepted taxonomy seem too narrow, and new information must widen them.

The great diversification of late Mongolian theropods is clearly expressed in the establishment of several families for them, especially during the late Mesozoic. The insufficiency of the original theropod materials, found during almost half a century [since] the discovery of the central Asian fauna in Mongolia, did not permit sorting these taxa within the current system. Thus, there remain theropods in general – *Oviraptor*, *Velociraptor*, *Saurornithoides*, *Alectrosaurus*, and other forms from neighboring China – the location and relationships of which were not understood within the general taxonomy at the time of their original scientific descriptions by the Central Asiatic Expedition (Osborn, 1924; Gilmore, 1933). The initial ideas about the positions of these genera within theropod systematics, which although clearly new were not known from outside Mongolia and also were based on imperfectly preserved materials, later turned out to be incorrect. Nevertheless, one major work and another continues to detract from one and the same family, to which were a type of later identified forms] (see Piveteau, 1955; Huene, 1956; Romer, 1956; Elements of Paleontology, 1964; Kuhn, 1965, 1966; etc.).

This situation started to change in recent years, in connection with new information about Mongolian theropods. A major role in this was played by the work, not directly related to these taxa, on the description of one of the American dromaeosaurids (Ostrom, 1969a, b), possibly the first to provide a clear concept of this important group of related theropods which earlier had been identified as a subfamily (Matthew and Brown, 1922). Ostrom placed the group in an independent family, a fact affirmed by the Mongolian material (Barsbold, 1976a), while it also became one of the most widespread families, dispersed throughout both North America and central Asia. As new information appeared and accumulated, new genera were united into new families, and the variety of theropods quickly increased. Publications in later years sufficiently reflected this tendency, and simultaneously found a more solid basis for concepts about the type of theropod fauna in central Asia and North America (Rozhdestvensky, 1965, 1970, 1971; Russell, 1967, 1972; Osmólska and Roniewicz, 1970; Osmólska, Roniewicz, and Barsbold, 1972; Barsbold, 1974, 1976a, 1977; Perle, 1979). The position of theropods within Saurischia and their familial ties were also studied (Charig, Attridge, and Crompton, 1964; Walker, 1964), which basically reaffirmed the separate and unique nature of theropods. In this scheme, as has been noted, the best perspective appears to be Colbert's (1964, 1970) idea concerning the separation of theropods from paleopods.

Upon the review of theropod classification, the refinements and completion achieved regarding the families, along with the division of theropods from paleopods, are possibly the most important results.

Theropod Families. A side effect of the new Mongolian material was the consideration of the insufficient revision of the predominately early post-Triassic lineages (Colbert and Russell, 1969), suggesting the following classification of theropods:

- Suborder Theropoda
  - Infraorder Coelurosauria
    - Family Podokesauridae
    - Family Segisauridae
    - Family Coeluridae
    - Family Ornithomimidae
  - Infraorder Deinonychosauria
    - Family Dromaeosauridae
  - Infraorder Carnosauria
    - Family Megalosauridae
    - Family Allosauridae
    - Family Spinosauridae
    - Family Tyrannosauridae

The authors did not present any kind of arguments, but it is possible to suppose that Compsognathidae and Procomsognathidae, earlier taken to be families, are apparently considered invalid, because the types [on which they are based] are divided among Coeluridae and Podokesauridae, which seems acceptable only in part at the level of generic validity.

As it seems from the given scheme, Late Cretaceous groups are represented by a modest number of families. In a systematic sense, the Mongolian theropod collection has considerably widened this interval. In addition to the already existing families, Saurornithoididae, Oviraptoridae, Garudimimidae, Deinocheiridae, Therizinosauridae, Segnosauridae, Elmisauridae, and Avimimidae recently have been added (Osmólska and Roniewicz, 1970; Barsbold, 1974, 1976a, b; Perle, 1979; Osmólska, 1980; Kurzanov, 1981). The number of families of later theropods now exceeds ten, and with this practically all the known Late Cretaceous theropod lineages are widely represented in Mongolia, while outside of this area only 4-5 families are distributed – Dromaeosauridae, Ornithomimidae, Tyrannosauridae, possibly Saurornithoididae, and Caenagnathidae, unknown as yet in Mongolia; all of these families have been described from North America. Earlier theropod groups have not yet been found in Mongolia, and the direction of research in this area presents a serious problem.

Here, it is necessary to note here that among the current number of Mongolian theropod groups, only deinocheirids, garudimimids, segnosaurids, elmisaurids, and avimimids were brought to light in recent times. Representatives of the remaining families had already been found at the time of the Central Asiatic Expedition (1922-1925) and the Mongolian paleontological expeditions of the Academy of Science, USSR (1946, 1948-1949), although the establishment of taxonomic relationships were delayed by several years. Only the addition of new material finally advanced the study of these dinosaurs. It should be remembered that oviraptorids were linked with ornithomimids although the supposition of Osborn (1924), which has survived many decades and many references until the recent new information, did not correct this position. With this, a great deal of work was necessary on ornithomimids, Mongolian as well as North American (Osmólska, Roniewicz, and Barsbold, 1972; Russell, 1972). Therizinosaurids (Maleev, 1954) were referred to the sea turtles (Elements of Paleontology, 1964), and later were recognized as carnivorous dinosaurs (Rozhdestvensky, 1970), although the material that existed at that time was very limited, and only new collections affirmed the correct nature of the latter conclusion (Barsbold, 1976b). Furthermore, only in recent times were saurornithoidids classified as members of a distinct family (Barsbold, 1974), and only recently with dromaeosaurids (Colbert and Russell, 1969; Ostrom, 1969a, b). North American caenagnathids were initially classified with birds (Sternberg, 1940; Cracraft, 1971), and only recently was the supposition expressed that they were theropods, related to Mongolian oviraptorids and in the family Caenagnathidae (Osmólska, 1976). However, it is more correct to consider the caenagnathids as a second, independent family within the single group Oviraptorosauria (Barsbold, 1981).

Infraorders. The use of this rank allows sketching a general direction within the basic theropod lineage. As has been noted, saurischian infraorders were identified by Huene (1914, 1920). In this [scheme] carnosaurs were initially separated from coelurosaurs, and two groups within the infraorder rank were included as uniting sauropods and prosauropods (suborder Pachypodosauria). Coelurosaurs and carnosaurs were among the two basic divisions of theropods that entered into scientific usage, corresponding essentially to their descriptive connotations as "small" and "large" theropods. The two were later given the rank of superfamily (*Elements of Paleontology*, 1964), which in principle did not change the general contents of these two taxonomic groups. However, the adoption of such a rank does not seem completely successful, especially because of the great specific differences between the coelurosaurian and carnosaurian lineages. Their progressive development during the later Mesozoic led to the realization of tendencies towards very narrow specializations that turned out to have been initiated fairly early on. Some lineages, realizing this tendency, developed in a parallel manner. The suggested classification maintains Huene's approach and that of his followers, and is based on the series of infraorders that link families which realize similar tendencies. The number of infraorders has considerably increased, as they reflect large evolutionary changes that occurred in the theropod lineage, and in this sense the use of similar ranks in the classification seems completely justified. The family reflects the evolution of a group within a particular environment, which shows sufficiently clearly the specific adaptations of each one.

Taxonomic Representations of the Classification. A series of earlier families, not found in Mongolia, could not be subjected to a much-needed revision because new facts are not available. Stemming from the generally accepted approach, [before mentioning the] sufficiently valid taxa in the proposed classification, more poorly defined groups should be mentioned – that is, first of all segnosaurids and spinosaurids. Recently, when knowledge about theropods became more profound, the lack of definition with regard to the position of these two groups became more obvious.

The recent inclusion of the first lineage – segnosaurids – among theropods notably broadened the scope of this group. A certain conditionally regarding the segnosaurid condition [within Theropoda] is maintained (Segnosauria); this is possibly a group equivalent to it in rank. On the basis of peculiarities in the pelvis, autopodia, etc., it can be allowed that segnosaurids and spinosaurids represent either a fairly significant deviation in the evolution of the theropod lineage, or generally go beyond the borders of this group. All this leads to the fact that segnosaurids and spinosaurids should most likely be classified a carnivorous dinosaurs of indefinite systematic position.

In many ways, the relationships between megalosaurids, allosaurids, and ceratosaurids and is also unclear. Regarding the type materials, the first are very fragmentarily represented European forms, while the others are well-known and from North America. Often workers identified megalosaurids in a general sense, including allosaurids but separating out ceratosaurids. However, a concrete basis for the acceptance of such positions does not exist, and all three families are maintained in the classification that appears below. Apparently, carnosaurian lineages exhibit new information (Welles, 1970; Madsen, 1974, 1976a, b), and were much more varied than has usually been imagined. The unification of deinocheirids and therizinosaurids into a single infraorder is fairly conditional, and is essentially based on the single peculiarity of hypertrophied forelimbs (Barsbold, 1976b, 1977).

The position of compsognathids became clearer following a detailed second study (Ostrom, 1978), and this family is preserved in the proposed system. Saurornithoidids, conditionally classified within deinonychosaurs (Barsbold, 1976a), are, possibly, more logically included within coelurosaurs. Possibly elmisaurids should also be classified here. The systematic position of Avimimidae, another family of small theropods identified recently, is less definite, and possibly they should also be linked to coelurosaurs, separated approximately from the toothless ornithomimids and garudimimids in this manner, as the original scientist who looked at this group believed (Kurzanov, 1981).

The suggested classification includes 19 theropod families, joined into seven infraorders, of which four are established mostly on Mongolian materials. Carnosaurs and coelurosaurs are maintained in this system, but in a much narrower sense than has usually been taken. This allows maintenance of a "balance" of taxa in this scheme. The deinonychosaurs, identified recently on the basis of predominately American dromaeosaurids (Ostrom, 1969a; Colbert and Russell, 1969), were confirmed by the Mongolian material.

The number of essentially valid theropods, possessing the basic materials for comparative anatomy within the group, hardly exceeds 45-50. Of these, nearly half (approximately 20, including the most basic types) originate in the late Mesozoic (predominately the Late Cretaceous) of Mongolia. For the sake of convenience, the traditional names of "small" and "large" theropods are maintained in the classification proposed below, although they do not have taxonomic significance.

SUBORDER THEROPODA

small theropods:

- Infraorder Coelurosauria Huene, 1914
  - Family Podokesauridae Huene, 1914
  - Family Compsognathidae Huxley, 1870
  - Family Coeluridae Marsh, 1881
  - Family Saurornithoididae Barsbold, 1974
  - Family Elmisauridae Osmólska (in press)
  - Family Avimimidae Kurzanov, 1981
- Infraorder Deinonychosauria Colbert and Russell, 1969
  - Family Dromaeosauridae Matthew and Brown, 1922

        Subfamily Dromaeosaurinae Matthew and Brown, 1922
        Subfamily Velociraptorinae subfam. nov.
Infraorder Oviraptorosauria Barsbold, 1976
    Family Oviraptoridae Barsbold, 1976
        Subfamily Oviraptorinae Barsbold, 1976
        Subfamily Ingeniidae Barsbold, 1981
    Family Caenagnathidae Sternberg, 1940

large theropods:
Infraorder Carnosauria
    Family Ceratosauridae Marsh, 1884
    Family Megalosauridae Huxley, 1870
    Family Allosauridae Marsh, 1887
    Family Tyrannosauridae Osborn, 1906
Infraorder Ornithomimosauria Barsbold, 1976
    Family Ornithomimidae Marsh, 1890
    Family Garudimimidae Barsbold, 1981
Infraorder Deinocheirosauria Barsbold, 1976
    Family Deinocheiridae Osmólska and Roniewicz, 1970
    Family Therizinosauridae Maleev, 1954
Infraorder Segnosauria Barsbold and Perle, 1980
    Family Segnosauridae Perle, 1979
    Family Enigmosauridae fam. nov.

Theropoda *incertae sedis*
    Family Segisauridae Camp, 1936
    Family Spinosauridae Stromer, 1915

Evolution of Carnivorous Dinosaurs

Basic aspects. Three aspects appear basic in the study of the evolution of carnivorous dinosaurs. First is the great variety of theropods, especially of later lineages. The second aspect is related to the early foundation of the basic evolutionary tendencies that defined theropod evolution. The third aspect reflects the genetic commonality of theropod dinosaurs.

The variety of theropods is clearly expressed in the classification presented here. As has been noted, the existing material of Mongolian carnivorous dinosaurs does not permit direct study of the early evolution of this group. However, it has considerably broadened the generally accepted view of the later evolution of carnivorous dinosaurs. In the past, the number of representatives had been limited for a long time because of the apparent relative insignificance in taxonomic variety in late Mesozoic lineages. The Mongolian theropod material allows a study of the later evolution of carnivorous dinosaurs from a broader perspective. The representatives and the breadth of this material is demonstrated by the fact that in includes not only all the currently known Late Cretaceous groups (with the exception of caenagnathids), but an entire series of specifically Mongolian lineages, and the general number of valid theropod families in the given interval now exceeds ten. Of them, one-third are found outside of Mongolia. From this, the variety that characterizes Mongolian Late Cretaceous theropods can be seen.

As a result of the better understanding of the morphological evolution of carnivorous dinosaurs, it becomes clearer that later theropod evolution depends on certain tendencies, which were recognized in their very early evolutionary history. Of course, not all fundamental [evolutionary] tendencies were similarly realized in the course of theropod evolution. This can also be expected of the new, until now undiscovered lineages. However, with an example of a late Mesozoic group of carnivorous dinosaurs, it becomes completely possible to note the essential aspects of historical development, and especially those evolutionary tendencies that were realized towards the end of the Mesozoic. An entirely related idea about the final stage of theropod evolution is [that there is] a certain possibility for following the prospects [based on] the tendencies expressed in their initial status. In this manner, the general character of evolution [of the values back] of carnivorous dinosaurs is shown. This allows the expression of some ideas about the [phylogenetic] connections of ancient saurischians and their place among theropods. Among the aspects of evolution noted above, the genetic commonality of carnivorous dinosaurs and the generally close relationship between theropod lineages are among the most complex and significant.

Familial Relationships of Ancient Saurischia. In the basis developed by Huene (1914, 1920, 1932, 1956), the concepts about early saurischian evolution supported placement of Triassic "carnosaurs" families within prosauropods. It was considered that after the Triassic, there were two main lineages leading to "true" carnosaurs and sauropods of the later Mesozoic. Coelurosaurs, on the other hand, which included sufficiently specialized lineages by the end of the Triassic, evolved completely separately until the end of the Cretaceous. That is why the "carnosaur" and prosauropod-sauropod lineages were studied as phylogenetically linked, and their connection was formalized within the boundaries of the suborder Pachypodosauria. Coelurosauria was represented as an independent taxon of equivalent rank (Huene, 1914, 1932, 1956). This arrangement allows us to deal with these theropods, initially studied as a more or less single lineage of carnivorous dinosaurs, without any additional concepts (Marsh, 1881). However, Huene's concept brings some internal contradictions with it. The doubt that arises from the most important part of it is the acceptance of the direct connection between the Triassic and post-Triassic "carnosaurs" and the distinctness of later Mesozoic "real" carnosaurs and coelurosaurs – that is, negation of Theropoda. Together with that, the relationship between prosauropods and Triassic "carnosaurs" was poorly based, apparently; to an equal degree most authors believed that the post-Triassic carnivorous lineages were tied by a close relationship to the "real" carnosaurs and coelurosaurs.

This contradiction was somewhat circumvented by the acceptance of three main evolutionary lineages in the development of Saurischia: coelurosaurs, "carnosaurs" *sensu lato*, and prosauropod-sauropods. It was considered that they were all established during the Triassic and continued into the Mesozoic, with the exception of prosauropods, which did not pass the Triassic-Jurassic boundary. The coelurosaur and carnosaur lineages, as well as the basal part of the third (actually prosauropods), were accepted as sufficiently closely related (sauropods were studied as a far removed lineage), and were united in the composition of the suborder Theropoda (Romer, 1956). A similar grouping [reflects] the partially "vertical" and partially "horizontal" character, because it connects all three Triassic lineages and two post-Triassic lineages (coelurosaurs and especially carnosaurs). Simultaneously, theropods are given a very broad significance in Romer's system, and along with this his system removes Huene's supposed division between coelurosaurs and "real" carnosaurs, which maintains the archaic idea about the presence of a direct relationship between Triassic and post-Triassic "carnosaurs".

In essence, there are few differences from the scheme studies and that which accepted coelurosaurs and "carnosaurs" *sensu lato* as theropods, with prosauropods given an "intermediate" position between theropods and sauropods, and all three large groups given the rank of suborder (*Elements of Paleontology*, 1964). In the theropod part of this scheme, Triassic and late Mesozoic "carnosaurs" are studied as a single lineage. At the same time, the connection between Triassic "carnosaurs" is recognized, but the use of this is very unclear (in reality it is incorrect in this sense), and the terminology of "intermediate position" for prosauropods only heightens the uncertainty of their position. In this scheme, the echo remains of Huene's idea about the "importance" of carnivorous dinosaurs and the later connections with sauropods through the "intermediate" prosauropods, which can now hardly be accepted (Charig, Attridge, and Crompton, 1964).

In this manner, the problem consists mostly in establishing to some degree the family [identity] of Triassic "carnosaurs" and prosauropods, as well as the "real" late Mesozoic carnosaurs. Apparently, a poor decision involved the recognition of relatively close ties and, as a result, a phylogenetic connection between Triassic "carnosaurs" and prosauropods (Colbert, 1964, 1970). Such a scheme of familial ties in named features takes into consideration the essential peculiarities of the early stages of morphological evolution of carnivorous Saurischia. Colbert's separation of brachyiliac and dolichoiliac pelvic types among carnivorous Saurischia served as a basis for their division into two groups. A similar approach permitted a more basic demarcation of earlier and later carnivorous Saurischia, to a different degree opening up the possibilities for a clearer evaluation of theropods themselves. Colbert's concept about the identification of groups by pelvic structure did not, it seems, inspire a series of scientists (see, for example, Charig, Attridge, and Crompton, 1964), but after the discovery of the most recent Mongolian material this path must be evaluated as unquestionably fruitful. It is understood that even from the earliest period of study of dinosaurs, they were classified according to type of pelvic girdle (Seeley, 1888), and even now this principle preserves the strength of the division between Saurischia and Ornithischia. The aforementioned work by Colbert justified itself along with the traditional approach, and having become more widely known, the variety of pelvic structure in later theropods shows that its possibilities are far from exhausted. In relation to this, the Triassic saurischian groups are differentiated into two pelvic constructions – brachyiliac and dolichoiliac – as seems to be almost the only basis that allows satisfactory evaluation of these dinosaur families both among themselves and with post-Triassic carnivorous groups.

A different view on the possible origin and degree of relationship between Saurischia as a whole, but sufficiently close in part regarding connections of their carnivorous groups, was expressed by Charig *et al.* (Charig, Attridge, and Crompton, 1964). Triassic carnosaurs were linked to prosauropods, while theropods themselves (according the authors' opinion, late Mesozoic megalosaurids and tyrannosaurids, as well as coelurosaurs) were separated from them and composed a single lineage. As was the case with Colbert's Triassic "carnosaurs" are separated from "real" post-Triassic forms. In general, this position is also maintained by Walker (1964), even though other aspects of his interpretations are quite different.

Paleopods and Theropods. As shown by Colbert (1964, 1970), brachyilia is peculiar to prosauropods and Triassic "carnosaurs", providing the basis for [supporting] their familial connections as expressed taxonomically by identification of the suborder Paleopoda. The post-Triassic "real" carnosaurs and the coelurosaurs, already beginning to develop in the Triassic, are characterized by dolichoilia and put into the suborder Theropoda. This division of ancient Saurischia according to pelvic construction is very basic in itself, however it does not answer the entire series of questions connected to the origin and evolution of both groups. That is why it is necessary to turn more carefully to the peculiarities of morphological development in paleopods and theropods.

Both saurischian groups are similar in a number of important features. It is very important to note that similar tendencies had already appeared in their early stages of evolution, as expressed in the development of intercorrelated features in each of the two groups – adaptations to carnivory, shortening of the forelimbs, and bipedalism to varying degrees, as well as the consequences from that. It is noted that these features only have the character of general adaptations to similar demands of the surroundings. They testify to the generality of the very basis on which these early existing similar tendencies were realized, and at the same time they started to differentiate fairly early. At least by the Late Triassic (and currently this time interval includes the basic known materials of ancient saurischians, among them also the carnivorous forms), paleopods and theropods had already reached a considerable level of divergence, which is indicated by brachyilia and dolichoilia along with preservation of the general evolutionary trend towards bipedalism and carnivory. Because [of this] it is very possible to assert that the similarities between paleopods and theropods are merely convergence. In order to accept this opinion, it is necessary to recognize that the polyphyly of Saurischia, an idea expressed a long time ago, would not have a solid foundation. For example, Romer (1956) admits the possibility that Saurischia evolved from two or more thecodont groups. The supposed connection of different saurischians with different pseudosuchians leads to the possibility that the entire group is polyphyletic (Charig, Attridge, and Crompton, 1964). However, brachyilia is known in bipedal Pseudosuchia (Colbert, 1964), which agrees accordingly with the most widespread opinion that these are the ancestors of Saurischia, *i.e.* brachyilia possibly appears to be the original type of pelvic construction in all Saurischia. Among them, it was only [concentrated] in one lineage – paleopods – while theropods were characterized by dolichoilia as derived relative to brachyilia. Apparently, brachyiliac paleopods and dolichoiliac theropods evolved in parallel from a general brachyiliac ancestor. It is necessary to note that dolichoilia was well-suited for many types of modifications, which is testified to by the plasticity of this structure. In all likelihood, dolichoilia was best suited to one of the major tendencies in theropod evolution – the perfection of bipedalism (Colbert, 1964) – and in this it had considerable advantages over brachyilia, which corresponded to the imperfect bipedalism of the supposed saurischian ancestors.

Most of the divergences between paleopods and theropods occurred prior to the Late Triassic, although no evidence of this persists today. The Late Triassic can already considered a stage in the evolution of diverging saurischian lineages. The finds of well-established paleopods and theropods (coelurosaurs) serve as proof of this. In addition to that, the similarity among valid paleopods (brachyilia, proportions of the forelimbs, construction of the autopodia) is sufficiently established in general features and does not heighten the differences, in spite of the currently insufficient fixation that testifies in favor of the Late Triassic divergences within the group. The accepted possibility of adaptation of paleopods to different diets (herbivorous and carnivorous) and different locomotory modes (imperfect bipedalism and possibly locomotory forelimbs) provides a basis to observe the expression of their differentiation. Similar phenomena are sufficiently well known in the early stages of evolution in Paleogene mammals, leading to the formulation of taxonomically clearly specialized groups – carnivorous and herbivorous (Mayr, 1963). In the case of paleopods, certain evolutionary tendencies of theropod character, noted in the carnivorous groups, led to the appearance of unrelated similarities in a series of features, which to a certain degree covered the different bases on which the morphological evolution of paleopods and theropods were realized. The same type of similarity complicates the study of early saurischian types, forcing a supposition of direct genetic continuity in the parallel specialization of groups of differing degrees of kinship – carnivorous paleopods (*i.e.* prosauropods or Triassic "carnosaurs") on one side, and [theropods] on the other (specifically carnosaurs). As Mayr also noted, the experienced systematist should notice in the early differentiation the possible division of a group that at one time was single, and Colbert (1970) made a corresponding step with regard to the paleopods, subdividing them into plateosaurids (tending towards herbivory and quadrupedal locomotion) and teratosaurids (carnivorous and bipedal). The blurred borders of this group, and the fact that each of the separate families clearly belongs to the paleopod group, does not have a decided importance in this case because it is necessary only to note the possible main path of evolutionary progress in Saurischia. Plateosaurids fall beyond the scope of this project, but teratosaurids on the other hand bear directly on the definition of the peculiarities of the early stage in the evolution of carnivorous Saurischia, which also includes theropods.

In this plan, it is necessary to more precisely define the question of the evolutionary lineage of carnosaurs. It was previously noted that Triassic "carnosaurs" are classified among paleopods, and consequently are separated from the basal part of the theropod lineage. The ancestors of carnosaurs were usually located among coelurosaurs, which were already present in the Triassic. Such a position reflects the image of coelurosaurs as the more ancient and specialized group among the early saurischian radiation, the ancestors of which were considered common [to] all the remaining saurischian lineages – prosauropods, sauropods, and "carnosaurs" in the general sense (Huene, 1932, 1956). However, the opinion that carnosaurs evolved from coelurosaurs is based only on the greater antiquity of the latter and the commonality of the features of bipedal carnivores (Colbert, 1964), and it meets with a series of difficulties. Carnosaurs are thus far unknown in the Triassic, but nonetheless the very advanced specialization of their earliest post-Triassic lineages clearly indicates that the direction of their evolution was quite different than that during the Triassic (just as in the post-Triassic) coelurosaurs. Consequently, it can be supposed that the division of the two theropod lineages, which developed over a long period of time, took place in earlier stages of the saurischian radiation than is now accepted according to general finds.

The commonality of a series of evolutionary tendencies among paleopods and theropods is based upon their supposed kinship, *i.e.* their possible origin from common ancestors. Theropod evolution tended to attain a greater perfection of bipedalism and carnivory. To a considerable degree, this is reflected in the construction of the pelvis, in which dolichoilia corresponded more to these theropod adaptations than did brachyilia. Other basic features of skeletal structural similarity affirm the general genetic kinship of the two increasingly divergent groups, the development of which began to occur in a different substrate. In this plan, paleopods possibly appear along the path of "non-adaptive" evolution relative to theropods, which already were on the path of progressive, "adaptive" evolution by the end of the Triassic, as indicated by coelurosaurs. This divergence bore a deep character, which guaranteed not only the survival of theropods after the Triassic, but also the wide radiation during the later Mesozoic. A relative progressiveness of theropod is indicated by their kinship with birds, as has been widely discussed in recent years.

The early radiation of theropods most likely occurred at the end of the Triassic; for example, coelurosaurs were well specialized and their evolutionary direction was sufficiently defined. The early theropod lineages during the Triassic stage of development were already far removed from primitive paleopods, and apparently had fully assimilated into the adaptive zone in which carnivory and perfected bipedalism in the context of dolichoilia became the general basis for their further progress. Such an early entrance into this adaptive zone defined much in the later evolution of coelurosaurs (*sensu lato* – all theropods) during the late Mesozoic under conditions of "a more complicated life" (Colbert, 1964). The carnosaurs, particularly, which had common ancestors with coelurosaurs, evolved in a different adaptive zone but also moved along the path to carnivory and complete bipedalism, which demanded a series of general changes in their structural organization. Specific structural peculiarities, both early and clearly defining in coelurosaurs and carnosaurs – skull size and volume, forelimb proportions, basic elements in the construction of a propubic pelvis – are also directly opposite in the two groups. This supports the opinion that differentiation of a series of parallel lineages occurred much earlier than is though according to the finds of carnosaur remains. The latter could possibly accomplish evolutionary entry into the corresponding [adaptive] zone earlier than somewhere close to the Triassic-Jurassic boundary, if not during the Late Triassic.

These general evolutionary tendencies had a considerable influence on the development of progressive theropod groups throughout the late Mesozoic. Their evolution proceeded according to a complex [pattern], a fact testified to by the finds of new, previously unknown theropod groups in Mongolia – deinocheirids, therizinosaurids, segnosaurids, etc. (Maleev, 1954; *Elements of Paleontology*, 1964; Osmólska and Roniewicz, 1970; Rozhdestvensky, 1970; Barsbold, 1976a, b; Perle, 1979). It is impossible to be limited only to the differentiation of large (carnosaurs) and small (coelurosaurs) theropods. The identification of specific "non-carnosaur" large theropods and "non-coelurosaur" small theropods [undermines] the general understanding of the evolution of carnivorous dinosaurs. Although the understanding of small and large theropods became possibly even more conditional than before in connection with the establishment of new groups, nevertheless to completely deny it is senseless – [for the sake] of brevity it is entirely convenient to use these generalized names.

Parallel Development in Theropod Structural Evolution. At first it is necessary to study the general and specific features in the development of different theropod lineages. In the lineages of small and large theropods, their commonality is based primarily on the formation of dolichoilia. The elongation of the ilium in this type of pelvis, characteristic of the majority of currently-known theropods, is linked to the perfection of the topography of a muscle group, mainly the extensors, which received a great deal of development and participation in locomotor functions (Colbert, 1964). Apparently, a dolichoiliac pelvis represents a more perfects structure, corresponding more closely with the bipedal posture of the body and theropod locomotion, in contrast to the brachyiliac paleopods, which exhibited an imperfect bipedalism. The mechanism of such an improvement is still unknown, and the most accepted reconstruction of the musculature and locomotor structures in theropods (Romer, 1923, 1927; Ostrom, 1969; Russell, 1972), as well as in other dinosaurs, remain suppositions in many ways; the qualitative amount of their perfection and the identification of function with dolichoilia are unclear. However, the lack of definition of the "technical" essence of dolichoilia does not lower its [diagnostic] value. The extinction of paleopods and subsequent slow development of theropods, which were perfectly bipedal carnivores, was due to the functional potential of dolichoilia, the adaptive relevance of which was expressed in the variety of forms of pelvic construction in different late Mesozoic theropod lineages. This modification reached a considerable amplitude in both small and large theropods, but nevertheless retained a series of distinctive features in each of them. For example, in small theropods the ilium remains low, and the ischium experiences a considerable reduction, accompanied by development of a large, widened obturator process positioned low [on the shaft], characteristic of later lineages and linked, in this and other degrees, with coelurosaurs. In carnosaurs and other large theropods, the ilium is relatively high, while the ischium is not shortened, the obturator process is positioned more proximally, and the pubis has a large distal end, of a proportion not seen in small theropods. Simultaneously, dolichoilia is characterized by the tendency to increase the number of sacral vertebrae, which numbered five to seven in later groups, and apparently no fewer than four in earlier ones. With brachyilia, there are no more than three sacrals (Colbert, 1964).

In addition to dolichoilia, a considerable number of other structural features have been discovered that reflect a general tendency in the theropod lineage. A considerable significance should be given to the construction of the autopodia under this plan. It has long been known that, throughout the long history of theropods, there has been a tendency towards reduction of the lateral pedal digits, leading to the formation of an "avian" type of construction, particularly in later stages. This tendency is realized in all known lineages as the considerable reduction of digit I and the complete loss of digit V. In advanced ornithomimids, digit I is also absent, but it remains in primitive forms. Reduction of the external digits occurs in the theropod carpus, as a result of which the tridactyl manus is formed in later evolutionary stages. Manual digit III, as a rule, carries most of the further reduction, although it is preserved in the majority of theropods. In tyrannosaurids this reduction leads to the preservation of only two manual digits.

The increased digit reduction in the pes and manus of different theropod lineages serves as a reflection of their general evolutionary tendency, based on the genetic kinship of the entire group. However, to a certain degree these tendencies are spread among the remaining early saurischian groups, which are not themselves theropods. It is possible to suppose that similar occurrences are also based on genetic kinship (as was noted, theropods and paleopods developed in parallel from common ancestors) and linked to perfection of the general bases for locomotion and grasping for forelimb function. In theropods, this tendency serves as a basis for obtaining many additional and varied specializations that are clearly demonstrated by the examples of morphological variations in the construction of the autopodia, which were reached in [several] evolutionary stages by theropod lineages. It is sufficient to note, however, the highly modified pedal digit II with a "predatory" ungual in some small theropods, and the complete absence of pedal digit I in advanced ornithomimids. Regarding the reduction of the external digits, this tendency is supposed to correspond to the later perfection of the initially "grasping" character, which preserved the general structural plan with the following evolutionary changes. A good illustration of this is the different construction of the tridactyl manus with increased "grasping" ability in dromaeosaurids, compared to its weakening in ornithomimids, its supposed suitability for swimming in oviraptorids (possibly membraned), its huge ungual phalanges in therizinosaurids, etc.

The reduction of pedal digits is correlated with the reduction of the corresponding metatarsals, of which I and V clearly experienced the following tendencies toward reduction, suitable for the formation of the "avian" type pes. Its appearance in several later lineages (Avimimidae) could proceed even further with the formation of proximal fusion of the arctometatarsus, generally similar to the metatarsals or tarsometatarsus in birds (Kurzanov, 1981).

Three basic metatarsals in different lineages preserved a single structural plan, expressed in the relative elongation of the metatarsus and their close positions relative to one other. Two possible variations in support for the epipodia are also discovered. The first consists of a great narrowing of the proximal end of metatarsal III (middle among the basal elements), such that it is nearly excluded from participation in the formation of the epipodial articulation of the pes, which is characteristic of carnosaurs, advanced ornithomimids, and saurornithoidids. In this case, the support is created mostly by metatarsals II and IV. However, even here it does not occur without variation – IV is highly widened proximally in saurornithoidids, as a result of which it forms the basic area of most support, while in most theropods both elements enter into the articulation almost equally. In the second variation, metatarsal III experiences only a relatively small compression, and participated equally in the creation of support along with the two contiguous elements. Such a pedal structure is characteristic of a series of small theropods, starting with the particularly ancient coelurosaurs. The noted appearance of reduction in the pes is accompanied with reduction in the number of tarsal elements. As a rule, only two tarsals are preserved in later stages – medial and lateral, which are entirely similar in construction in different theropod lineages.

The preservation of a single basis in the development of a manus structure suited to such different specializations supports the commonality of the pulley carpus, which allows free movement along different surfaces but probably limited [rotation]. Together with this, in tyrannosaurids the bones in which reached the greatest degree in terms of external digit reduction (up to two), four carpal elements of fairly imperfect topography are present, corresponding to the primitive, non-pulley type characteristic of the earliest as well as certain later carnivorous groups. It is now known that a carnivorous dinosaur with a non-pulley carpus had weakened forelimbs with a non-grasping manus. In some large "non-pulley" theropods (especially carnosaurs), a tendency towards progressive reduction of the forelimbs is clearly seen, while in another theropod group (ornithomimids) the forelimb is not subjected to particular reduction, but is characterized by a considerable functional weakening in all features. At the present time, cases in which the highly developed theropod forelimb had a non-pulley carpus are not known.

Non-reduction of the forelimbs is also among a number of clearly expressed tendencies in the majority of theropods. The currently-known group of small theropods is fairly clearly characterized by similar tendencies; later large theropods were discovered which were developed in an analogous direction – therizinosaurids and deinocheirids. In the evolution of large theropods, this feature is correlated with a different basic [sign], and to this number it is necessary to add the development of the aforementioned pulley carpal structure, which corresponded on the one hand to the functional perfecting and strengthening of the forelimb and manus. On the other hand, a connection is established between the non-reduced forelimbs and the relative elongation of the neck, as well as the relatively small size of the skull. Other directions exited along with this – in deinocheirids, a general weakening of the forelimb and non-pulley wrist structure is noted along with the reduction of the forelimb. The carnosaurs, specifically, were characterized by highly reduced forelimbs (especially in later evolutionary stages), a shortened neck, and a highly enlarged skull, which also became taller. In small theropods with a small skull it is relatively low. Although the tendency to considerably increase the general dimensions is apparent in the later evolutionary stages of distinct groups, such is also true of the height of the skull (the "high-skulled" dromaeosaurids).

It is necessary to note the consistency in the number of cervical and dorsal vertebrae, which is usually subjected to considerable variation in the Reptilia. This established consistency is based on information obtained from later groups of different theropods. However, the possibility that this is violated in earlier groups is not completely excluded.

Peculiarities of Segnosaurid Evolution. In the historical development of later carnivorous groups, a special place belongs to the recently discovered, Late Cretaceous segnosaurids, whose structural evolution was highly specialized in many ways. The development of this group apparently did not proceed along the path of perfecting bipedal locomotion on the basis of dolichoilia, as is so clearly expressed in the majority of theropod lineages. Segnosaurids are characterized by a completely different pelvic type, whose differentiating features fall into the isolated category of altilia. However, the functional characteristics of this pelvis remain unclear. Along with a comparison of brachyilia and dolichoilia, this possibly allows predominately the second over the first in a plan of perfecting bipedal locomotion, which in the case of altilia can be asserted only in its high originality, reflected specifically in the peculiarities of locomotion. Basically, the segnosaurid pes is considerably differentiated from the "avian" pes by its relative shortening and relatively large metatarsal I, in general giving the pes a non-compact appearance. This shortening and this disc-like appearance of the pedal phalanges are also uncharacteristic for theropods, and is seen in ornithopods, as mentioned. All these features, together with altilia, testify in favor of the basic morphological deviation of segnosaurids from the general theropod evolutionary lineage. As a result, segnosaurids were apparently defined by a completely different adaptive zone, in which the achievement of perfected bipedalism was either not a dominant evolutionary [pressure], or was accomplished by different means. At the same time, specific features are apparent in segnosaurids that are expressed in other theropod lineages. Among them, it is necessary to note the peculiarity of the basicranium and middle ear, which also exists in ornithomimids, garudimimids, and saurornithoidids. The currently known facts testify in favor of a non-reduction of the segnosaurid forelimb. Finally, the pubis is retroverted in their highly peculiar pelvis, in other words the pelvis was characterized by opisthopuby as was also the case for dromaeosaurids. Among "true" theropods, the relatively shortened and compact metatarsus is known in earlier groups such as allosaurids. Apparently, all the aforementioned was an expression of one basis from which the development of later carnivorous groups occurred, and among these were segnosaurids, which represent a more distant theropod lineage. With this, the specific features of segnosaurids that differentiate them from most other theropods must have evolved sufficiently early.

The Direction of Theropod Evolution. When studying the path of theropod evolution, it is necessary to differentiate the general tendencies that were achieved on a different basis from those general tendencies realized on a single basis. Along with this point of view, the development of paleopods and theropods, as well as the isolation of different types of theropod groups, gains some validity. The general direction of theropod evolution, conditional on their genetic kinship, was broader than that of paleopods, which did not cross the Triassic-Jurassic boundary. Theropods were present throughout most of the Mesozoic, evolving along a series of parallel lines that seem to have been adapted to achieving several narrow specializations, which lent to them a great variety in their later evolutionary stages. The progression of theropod evolution exhibited deviations, limited by [direction] into special adaptive zones, of which the segnosaurids serve as an example. Nevertheless, precisely this variety shows all the more clearly the singularity of these lineages of the theropod trunk, which were isolated from paleopods early on (Fig. 30).

The coelurosaur groups (podokesaurids, compsognathids, coelurids, saurornithoidids, elmisaurids, avimimids) comprise a single lineage from among the known theropods that crosses the Triassic-Jurassic boundary and continues a later rise towards the acquisition of greater specializations until the end of the Mesozoic. Post-Triassic coelurosaur evolution most likely occurred in the context of the same fairly large adaptive zone in which it started. This is confirmed by the fact that post-Triassic coelurosaurs, which in general contain the same evolutionary lineage as the earlier groups, only more deeply realize those morphological tendencies which were present even in podokesaurids. Thus coelurids, and after them elmisaurids, remained small carnivores with greater reduction of lateral pedal and manual digits than podokesaurids, in which these features had barely begun. In the later Mesozoic, coelurosaur lineages experience a radiation that provided a basis for further divergence of new branches and lineages of more narrow specializations. With the beginning of the Cretaceous, coelurids become extinct and their place in the evolutionary scene is taken by other groups, developing in parallel directions towards specialization with the acquisition and enhancement of a series of perfections. Thus, avimimids appear to exhibit an even greater approximation of the avian-type in the construction of its metatarsus. Saurornithoidids form a different lineage with a middle ear region (as in birds) and the reverted pedal digit with a predatory claw. Apparently this is linked to the appearance of saurornithoidids in a new adaptive zone, where they had an advantage over the less specialized later coelurosaurs. At the same time, if the noted improvement characteristic for all coelurosaurs is considered, then saurornithoidids are differentiated from coelurosaurs only by the strengthening of their rather specifically noted specializations.

The deinonychosaur lineage is currently known in the Cretaceous; it includes a series of specializations that were conditional to its similarity to coelurosaurs. However, differences in the construction of their opisthopubic pelvis testifies to their earlier origin. In addition, deinonychosaurs exhibit specializations obtained in parallel with coelurosaurs, such as the presence of a reverted pedal digit II with a predatory claw. Along with the pelvis, which included a retroverted pubis, these basic changes reflect the development of deinonychosaurs into an adaptive zone that is considerably different from than of coelurosaurs. Among deinonychosaurs, a strong reduction in the pedal predatory claw towards the dimensions of a normal ungual is observed in later evolutionary stages, although the particular phalangeal structure is preserved. Deinonychosaurs were differentiated into several lineages, distinguished by details in pedal construction and relative skull height. All this demonstrates the division of deinonychosaurs along closely parallel directions during the end-Cretaceous.

Oviraptorids are a lineage of highly specialized small theropods supposed to be connected phylogenetically with coelurosaurs. Along with features that testify to their sufficiently early separation, the postcranial skeleton of oviraptorids bears a number of features of coelurosaur organization, albeit subjected to considerable modification. Oviraptorids, like the aforementioned deinonychosaurs, demonstrate the well-known appearance of "mosaic" evolution, in which unquestionably advanced features are found with many of more primitive character. In oviraptorids the greatest changes involve the skull, in contrast to deinonychosaurs. The absence of teeth and presence of a massive beak – both present in ceratopsids – and the considerably modified construction of the palatal complex and lower jaw reflect the transition of these peculiar carnivores into an adaptive zone potentially uncharacteristic of most theropods. The initially "grasping" tridactyl manus was possibly changed into a swimming organ. Apparently oviraptorids achieved entry into an entirely new adaptive zone, and became the first amphibious lineage among theropods. At the same time, the position of caenagnathids is unclear; apparently they were a parallel lineage to oviraptorids and evolved in some widely different adaptive zones.

We proceed now to the study of the evolution of large theropods. As already has been noted, carnosaur evolution (megalosaurids, ceratosaurids, allosaurids, tyrannosaurids) clearly follows both general and highly specific tendencies. However, the general features linked to the improvement of bipedalism and carnivory do not necessarily testify to their direct phylogenetic connection with coelurosaurs. As was shown earlier regarding the background of the achievement of "theropod" tendencies, carnosaurs are distinguished by such basic features as the long-observed forelimb reduction, presence of a non-pulley carpus, a clear increase in skull size, shortening of the neck, etc. All this supposes a fairly early carnosaur divergence due to evolutionary displacement and clear divergence from the small theropod lineages. [In order to understand] the evolutionary tendencies of carnosaurs, it seems completely valid to examine megalosaurids *sensu lato* (*i.e.* including ceratosaurids and allosaurids) and tyrannosaurids as two stages in the evolution of a single lineage, whose evolutionary direction was completely preserved during the entire late Mesozoic. In this understanding, the carnosaur lineages which followed each other are found in the same position in the coelurosaur lineage, also forming a large branch with the acquisition of internal parallel specializations. "Carnosaur" peculiarities received, for the most part, only a deeper expression in tyrannosaurids relative to megalosaurids. The increased reduction of the forelimb and all the constructions of structural complexes in carnosaurs which are supposedly correlated with it reflect the development of these carnivores towards gigantism, already expressed in their early evolutionary stages.

Ornithomimosaurs are the second group of toothless theropods, which were earlier classified with coelurosaurs *sensu lato*, *i.e.* with small theropods. At the appearance of the known ornithomimid families and garudimimids, these edentulous carnivores reflect a combination of "coelurosaur" and partly "carnosaur" tendencies in their construction: one the one hand, a small skull, elongated neck, non-reduced forelimbs, and on the other hand a pelvis constructed according to the "carnosaur" type and primitive non-pulley carpus. Apparently a dominant feature to be considered is that the entire construction of the prepubic dolichoiliac pelvis, inasmuch as other structural complexes sufficiently firmly link this to the others, could be subjected to considerable modification, as was demonstrated by theropods of later evolutionary stages. This is the reason that ornithomimids are supposed to have a closer connection with large theropods than with small forms. The direction of such peculiar specializations could have been established fairly early, and ornithomimid evolution could proceed along a path of greater strengthening, to which the complete loss of digit I in more advanced forms testifies, while it is still present in more primitive forms. The appearance of a single specialization, differentiated only by the extent of its expression, shows the evolution of two parallel lineages of ornithomimosaurs existing simultaneously in the late Mesozoic of Mongolia. Opinions regarding the systematic position of ornithomimids is contradictory – for a long time they were placed with small theropods (Matthew, 1915), and this point of view is considered generally acceptable. However, there have also been attempts to classify them with large theropods (Abel, 1919). Apparently ornithomimids represent an early specialized lineage in which the condition of the adaptive zone answered to the greatest degree, the development of which promoted gigantism. The later representatives of the Mongolian ornithomimids were nearly as large as their contemporary tyrannosaurids. On the other hand, in spite of the non-reduced forelimb (in the sense of reduced dimensions), their functional weakening put ornithomimosaurs closer to carnosaurs than to small theropods. Other clear signs, characteristic of ornithomimosaurs, testify in favor of their evolution in a different direction from carnosaurs. It is acceptable to consider that these structural peculiarities – a small skull, elongated neck, forelimbs, etc. – were evolved in a parallel manner in different small theropod groups under similar environmental pressures and, naturally, on the basis of the phylogenetic relatedness of the theropod lineages.

The study of the deinocheirosaur lineage of large theropods, tentatively including deinocheirids and therizinosaurids, encounters several difficulties due to the absence of more complete morphological information. It is possible, however, to state that as large carnivores, they developed further forelimb reduction according to the general theropod tendency towards formation of a tridactyl manus. In therizinosaurids, the strengthened forelimb is constructed based on the pulley carpal mechanism, while in deinocheirids the bone structure corresponds to the more primitive non-pulley type, similar to ornithomimids, and was characterized by a functional weakening. In this manner, the forelimbs of deinocheirids completely corresponded to two structural modifications of theropod nature, which along with the simultaneous development of a more gigantic claw was a basic characteristic reflected in its very narrow specialization. The studied features of deinocheirids force one to suppose that they evolved in a more or less parallel direction to those theropods with non-reduced forelimbs. However, deinocheirids adopted a specific adaptive zone, as considerably differentiated from carnosaurs as from the zones of small theropods. It is possible to suppose that deinocheirids must have acquired an independent evolutionary path early on. Among large theropods, it stands far from carnosaurs and ornithomimosaurs, although additional information may lead to completely different conclusions in the future.

The segnosaurid lineage now appears possible the most specific. Its representatives do not fall easily into the proposed classification of large and small theropods, even on the basis of general dimensions. In the framework of general theropod tendencies, the features of greatest deviation are characteristic of segnosaurids, most clearly expressed in their altiliac pelvis. At the same time, the position of the pubis testifies towards the partially similar construction achieved in the pelves of deinonychosaurs and segnosaurids, although in this their similarity ends. If at first this reorientation occurred in the context of dolichoilia, then the pelvis suffered basic changes secondarily. Apparently, this not only involved fairly early segnosaurid specializations from the general theropod progression, [but] also a considerable lateral deviation from their basic evolutionary direction. Segnosaurids evolved in the context of a highly narrow adaptive zone, possibly not characteristic of theropods as a whole. The modification in the construction of the segnosaurid pelvis indicates the isolation of at least two lineages, apparently achieving parallel specializations.

Let us make a basic summary. The accumulated information fairly clearly specifies against a "diphyletic" – including only carnosaurs and coelurosaurs – position in understanding theropod evolution. This comment already seems too narrow, and a reexamination can be done based mainly on the material from later theropod evolutionary stages. There is no reason to doubt that the further study of these early stages will provide a great deal of new information. At the present time, one thing is clear – theropod evolutionary relationships were much more complex and varied than had been understood in the context of traditional views about these two "lineages". New information supports a basic concept of multi-lineage parallel evolution of carnivorous dinosaurs.

From their earliest appearance, theropod saurischians stood on the path towards perfecting bipedalism. Carnivorous paleopods did not have such a perspective in this direction, as a result of the "inadaptiveness" of the basic and important structures that defined bipedal locomotion. Morphological evolution of paleopods was accomplished to a certain degree in parallel with theropod evolution. The single theropod trunk divided into a series of lineages, with parallel specializations that occurred throughout the late Mesozoic, limited by the relatively early appearance of the representatives of these lineages within narrow adaptive zones. Some were differentiated by their extreme originality, which brought about the considerable basic deviation of such groups as segnosaurids. The final specificity of these acquired adaptations were accomplished within a single structural basis that was not obscured by all the modifications of later lineages. The last stage in theropod evolution is characterized by adaptive evolution observed in the examples of deinonychosaurs, ornithomimosaurs, and oviraptorids, with the simultaneous parallel evolution within each of these groups of smaller, closely-related lineages. Alongside these, parallelisms of a more general theropod character emphasized the many levels at which parallel evolution occurred. Specializations in later stages were differentiated by their greater depth, corresponding to the conditions of new adaptive zones in which the theropod lineages which had reached a relatively high evolutionary level were located along a broad front.

Phylogenetic Relationships of Theropods

Recently, several interesting interpretations of the problems of dinosaur relationships have been put forward, stemming from different, and often opposite, positions. Briefly, these connections include the basic relationships: thecodonts (among them most often the Pseudosuchia) and dinosaurs; the degree of relationship between Saurischia and Ornithischia; and the supposed relationship between dinosaurs (theropods) and birds.

Thecodonts are distinguished from dinosaurs by the structure of their tarsus and acetabulum, corresponding to the position of their hindlimbs and bipedalism (Walker, 1961, 1964; Charig, 1970; Reig, 1970; Bakker, 1971a, b; Bakker and Galton, 1974). The pseudosuchian crocodyloid tarsus was known [as well as the mesotarsal joint] in dinosaurs (Krebs, 1963, 1965, 1973; Reig, 1970; Thulborn, 1971; Romer, 1972; Charig, 1972; Ostrom, 1976a). The position of the limbs corresponded to the [closed] acetabulum, in contrast to the perforated one in dinosaurs (Romer, 1956; Thulborn, 1975). The earliest thecodonts, including the Pseudosuchia, are very distinct from dinosaurs, although some of their later representatives (such as *Lagerpeton* and *Lagosuchus*) with mesotarsal joints look like "near-dinosaurs" (Romer, 1971; Bakker and Galton, 1974). It seems unlikely that the similar skeletal adaptations and joint articulations in dinosaurs could be the result of convergent evolution of parasagittal limbs in different thecodonts because dinosaurs are apparently a monophyletic group. This is proven by the great similarity between early Saurischia and Ornithischia (Casamiquela, 1967; Bonaparte, 1969; Thulborn, 1970a, b, 1975; Galton, 1970a, 1971, 1972; Bakker and Galton, 1974).

A number of investigators, recognizing this similarity in the general differentiation of dinosaurs from thecodonts, have viewed the origin of dinosaurs as polyphyletic. This refers to Ornithischia and Saurischia (Romer, 1956), as well as the internal subdivisions within both of these groups. It is sometimes supposed than sauropods, theropods, prosauropods, and ornithischians originated from thecodont ancestors (Charig, Attridge, and Crompton, 1964; Thulborn, 1975). The similarities between different early ornithischians and saurischians does not yet indicate the similarity of all Triassic dinosaurs, which evolved in the most varied directions (Romer, 1971). At the same time, this similarity of the different dinosaur groups is connected not with the "prosauropod stage" that is considered to comprise a single basis for dinosaurian lineages, but with the "thecodont-dinosaur transition" in their evolution (Thulborn, 1975).

In recent times, the similarity between theropods and *Archaeopteryx* has been shown in greater detail, as allowed by existing material (Ostrom, 1973, 1974, 1975, 1976a). Separate anatomical (parasagittal limbs), histological (density of the Haversian system), and ecological (predator-prey relationships) data has been interpreted as supporting endothermy in dinosaurs (Ricqles, 1967; Ostrom, 1969, 1972; Bakker, 1971, 1972), a claim countered by a series of investigators (Feduccia, 1973; Bennett and Dalzell, 1973; Thulborn, 1973; Budiko, 1978, *et al.*). The admission of endothermy in dinosaurs and their phylogenetic relationship with birds have been used to support separation of dinosaurs as either a completely independent Class, or one partially joined to Aves (Galton, 1970a, b; Thulborn, 1971, 1975; Bakker and Galton, 1974).

The Mongolian theropod material shows a morphological variety of carnivorous dinosaur skeletal structures in a wide spectrum of modifications. In this region it was possible to increase the factual basis of the aforementioned problem.

Regarding the understanding of dinosaurian monophyly, the possible origin of the opisthopubic ornithischian pelvis from the prepubic saurischian pelvis is usually recognized (Charig, 1972), by means of a posterior reorientation of the pubis. Examples of this were not previously known, not considering the reorientation of the pelvis in *Archaeopteryx*, which itself was the subject of doubt focused mainly on the Berlin specimen. The clear external similarities between the pelves of ornithischians and birds serves as one basis for acceptance of a close relationship between the two. Along with this, the homology of the ornithischian pubic structure were studied in a different manner. The prepubis was occasionally identified with the pubis, and the postpubis considered a new structure (de Beer, 1964). A more widespread, opposing position dictates that the postpubis is the homolog of the reptilian pubis, while the prepubis is a new structure (Huene, 1909; Abel, 1909; Romer, 1927, 1956; Galton, 1970b). The ornithischian postpubis is identified with the avian pubis, and the prepubis with the avian pectineal process. With this, the retroversion of the pubis in ornithischians and birds is linked to the development of bipedalism, and was a momentary feature in the evolution of the group, each having a common ancestor. This position supposes a phylogenetic relationship between ornithischians and birds (Galton, 1970b).

The appearance of a retroverted pubis, as noted, also takes place in the saurischian pelvis, where two completely different types occur – dolichoiliac and archaeopterygian. Instead of this, the possibility of the retroverted pelvis in *Archaeopteryx* receives some support. With this, the pelvis of *Archaeopteryx* fully corresponds to the opisthopubic dolichoiliac pelvis, identified earlier in dromaeosaurids (Barsbold, 1976a). It is necessary to note that only a partially retroverted pubis is accepted in the fifth, Eichstätt specimen of *Archaeopteryx* (Wellnhofer, 1974). Ostrom (1976a), in his most recent article on the origin of birds, also accepts only a partially retroverted pubis in *Archaeopteryx*. Based on study of additional material of the American dromaeosaurid *Deinonychus*, Ostrom (1976a) also accepts partial retroversion of the pubes in this taxon. Giving due to Ostrom in the development of this interesting problem, I must note that the connection between the examples introduced above is not accidental, and in this he reflects his view concerning the close relationship between small carnivorous dinosaurs like *Deinonychus* and *Archaeopteryx* (Ostrom, 1973, 1976a). The insufficient data that Ostrom had on dinosaurs (theropods), and the impossibility of fully denying the retroverted position of the pubes in *Archaeopteryx*, apparently forced him to accept the uncertain decision that the position of the pubes in *Deinonychus* was the same as in *Archaeopteryx*. With this, the most basic obstacle to a phylogenetic relationship between small theropods (like

Deinonychus) and *Archaeopteryx* was overcome, and in the following this is shown with greater conviction.

Another investigator, who held a completely different opinion – that birds and crocodilians were phylogenetically related (Walker, 1977) – suggested artificially retroverting the pubes of an ancient crocodilian (*Hallopus*) according to the position in *Archaeopteryx*, on which he attempted to more firmly base his view. It is entirely clear that both Ostrom and Walker acted in the same manner in their desire to prove the correctness of their concepts, which were highly different from one another – they accepted only that which seemed to correspond to their position (in the given case they went against the facts). However, it is necessary to take into consideration that the appearance of opisthopuby was not yet known to the investigators, who were not familiar with the Mongolian material. Walker (1977) also stressed the fact that it is necessary for the pubes in theropods (saurischians) to be reoriented in order for them to be recognized as related to birds, which seemed impossible to him.

The first doubt regarding pubic retroversion in the pelvis of *Archaeopteryx*, traditionally established on the basis of the Berlin specimen, appears in the study of the Teilorsk specimen (Ostrom, 1970a, 1972a), in which the distal part of the pubis was left in a position parallel to the [ischium]. It is sufficiently clear that the position of the distal pubis in the Teilorsk specimen could reflect a noticeable displacement, and could therefore serve as proof against [retroversion]. Ostrom (1976a) also considered the detail that the X-rayed specimen of *Archaeopteryx* shows the presence of breaks in the base of the pubis and pelvis as a whole, testifying to the possibility of displacement of the separate elements. However, it is typical to have many breaks in the excavated skeletal material, even without any kind of basic displacement or changes, so that the facts or information presented does not appear, in my opinion, sufficiently persuasive. The existing material of *Archaeopteryx* entirely permits not only the acceptance of partial [retroversion] (Ostrom, 1976a), but also more considerable reorientation of the pubis, an analogous position having taken place in the Berlin specimen and also in the pelves of deinonychosaurs and segnosaurids. The position of the saurischian opisthopubic structure in different types of carnivorous dinosaurs, as well as in *Archaeopteryx*, serves as a fair example of their kinship and the possible path of transition of the saurischian pelvis into the ornithischian. It is necessary to note that there was a high degree of variability in the saurischian pelvis. Apparently, modification of the pelvic structure was linked to changes in musculature, and in this manner the opisthopubic saurischian pelvis could be reminiscent of that in ornithischians (Barsbold and Perle, 1979). Galton (1970b) remarked that the ancestors of Ornithischia and birds must have had an elongated anterior iliac blade and a retroverted pubis, which seems not now without interest. This corresponds precisely to the appearance of opisthopubic dolichoilia, found in the pelves of Mongolian dromaeosaurids. Judging by everything, the reorientation of the pelvic region was accomplished repeatedly during saurischian evolution.

A number of other indications that earned characterization should be added, including the development of the bony extension covered by a horny shield in some theropods, and formed by the osseous middle ear, which also exists in a series of birds. Initially the structure of the palatal complex in segnosaurids is noted, supposedly characterized by features typical of the early type of paleognathous palate in cassowaries.

In addition to the pelvis among the conclusions of morphological character, the concept regarding the absence of the clavicle and ossified sternum in theropods was now brought out, usually examined as proof against the acceptance of the theropod origin of *Archaeopteryx*. Already, the presence of a partially preserved clavicle was noted a long time ago in *Segisaurus* (Camp, 1936). Oviraptorids had a huge, V-shaped clavicle that bears a considerable resemblance to a similar structure in Archaeopteryx, and can be compared with the furcula in birds. Basically, the specific method of connection between the V-shaped clavicle and the acromial process first discovered in oviraptorids is almost certainly characteristic of *Archaeopteryx*. The flattened sternum is well known in dromaeosaurids and oviraptorids.

Let us draw some conclusions once again. The orientation of the pubis originated repeatedly in the evolutionary process of different saurischian groups. The realization of such a tendency in different lineages possibly testifies to their relatively close phylogenetic kinship, and therefore their origination from a single ancestral group. Ornithischians with such a pelvis had apparently already appeared in the Triassic, indications of which exist in the discoveries of sufficiently differentiated ornithischians in the Upper Triassic (Crompton and Charig, 1962; Charig , Attridge and Crompton, 1964; Galton, 1972). Ornithischians experienced a deep morphological change brought about by evolutionary displacement, allowing their entry into adaptive zones that corresponded to a specific manner of living, such as herbivory, etc. The evolution of other groups, and the reconstruction that occurred in the context of the saurischian pelvis, went in a characteristic adaptive zone that promoted the realization of parallel specializations of theropod lineages. At the same time, the structural modifications are sometimes characterized by considerable amplitude, clearly demonstrated in deinonychosaurs and segnosaurids by the opisthopubic pelvis. The former, in spite of the small changes, continues to remain similar in many ways to the segnosaurid lineage, while the latter shows a considerable deviation from the main evolutionary direction of theropods. The *Archaeopteryx* lineage remains very close to theropods morphologically. Practically all the features of the different theropod lineages are clearly expressed (Ostrom, 1976a), and this testifies in favor of the close relationship between *Archaeopteryx* and theropods. *Archaeopteryx* could hardly have originated from pseudosuchians, as has been widely accepted (de Beer, 1954, 1964; Bock, 1965, 1969; Piveteau, 1955; Romer, 1966, etc.), without having gone through the dinosaur, or more precisely theropod, stage. An independent lineage, *Archaeopteryx* was supposed to have originated near the Triassic-Jurassic boundary among other parallel lineages of later theropods, although differentiated from related lineages that kept growing by evolutionary replacement, which led them to develop in specific adaptive zones that were not characteristic of theropods.

A series of "avian" features spread diffusely through parallel lineages of post-Triassic carnivorous dinosaurs. There was not a complete collection of similar signs in any lineage of later theropods, in addition to which two aspects are clear: 1) sometimes the general evolution of carnivorous dinosaurs has [combined] these with the basic theropod [nature] of their construction – this includes the avian-type pes and the forelimb construction, etc. characteristic of later lineages (Barsbold, 1977); 2) other signs are more specific – the avian-type middle ear is noted in saurornithoidids and segnosaurids, the V-shaped clavicle in oviraptorids (and *Archaeopteryx*), etc. It is possible to admit that in this lineage, similar to *Archaeopteryx*, the main features of avian character were joined

(Simpson, 1946; de Beer, 1956, 1964). This means that in dinosaurs, more precisely theropods, there was a sufficiently early "ornithization", in the process of which lineages were formed that led, in a sense, to birds even in the early stages of the post-Triassic evolution of carnivorous dinosaurs. It is completely acceptable that *Archaeopteryx* represents only one of them, possible a conservative member, but independent of the degree of deviation from "true" birds, in a sufficient degree it indicates closeness to theropods.

At the same time, the acarinate sternum and the paleognathous palate of some carnivorous dinosaurs apparently testify that a transition to birds could have occurred in more than one parallel lineage, which rose through theropods near the Triassic-Jurassic boundary. In this case, acarinate birds could be a separate lineage that deviated sufficiently early from their common theropod ancestors and developed in many ways parallel to carinate birds, but in a more constantly deviating adaptive zone.

In general form, the phylogenetic arrangement of theropod groups appear as a series of parallel lineages, rising from a single ancestral group and characterized by many varied modifications and unequal degrees of divergent evolution. Apparently, *Archaeopteryx* is not the only link in the following series: Pseudosuchia – Coelurosauria – *Archaeopteryx* – Aves (Ostrom, 1973, 1976a), as it is one of these parallel lineages, aberrantly evolved from the general theropod basis and reflecting kinship between theropods and birds (see Fig. 30).

Intercontinental Connections of Dinosaurian Faunas

Mongolian dinosaur faunas include only the Cretaceous (mainly only Upper Cretaceous) stage of evolution. The short duration of the time interval, the achievement of approximately the same evolutionary level in the majority of forms, and the appearance of the Mongolian dinosaur fauna in the highly worked-over local soil have influenced the depth of the branches of the studied relationships. The limitation of the relatively small number of faunal elements compared (families and genera) shares in this to an equal degree. At the same time, the Mongolian dinosaur faunas have now been studied much more completely than they had been previously, and this places limitations on the necessity of studying their relationships in light of new information (on predominately carnivorous groups). The general view of the evolution and relationships of Asian dinosaur faunas has recently been presented (Rozhdestvensky, 1971, 1974).

In forming associations between the Cretaceous Mongolian dinosaur faunas and recent new elements, an important role was played by the former, which was already highly altered, having native roots, until receiving sufficient [illumination] as a result of blank spots in the geologic history of Central Asia. In other words, the study of the interval being examined was preceded by a long prehistory of population by and further evolution of the original fauna, which experienced considerable changes up until the moment at which it became accessible to investigators.

The limited information regarding the Early Cretaceous Mongolian faunas testifies to the already established relationships between Central Asian and North American theropods (ornithomimids, dromaeosaurids) as well as some ornithopods. At the same time, there are undoubtedly theropod lineages in both regions that, according to the similar degree of specialization, remain for that reason neutral in the scheme of defining phylogenetic and biogeographic relationships, and iguanodontids are studied as a series that begins in North America (Gilmore, 1909) through Europe (Casier, 1960) and into Central Asia, giving rise here to a large ornithopod lineage – hadrosaurids (Rozhdestvensky, 1925a, b, 1961, 1964, 1966, 1974; Brett-Surman, 1979). However, this lineage was very richly developed not only in Central Asia, where the transition from iguanodontids to hadrosaurids occurred in the middle Cretaceous (Rozhdestvensky, 1966, 1974), but also in North America, in which territory a similar transition is unknown although Early Cretaceous iguanodontids are found (Ostrom, 1970b).

Psittacosaurids are another distinct ornithopod group of Central Asian origin, which testifies to the early appearance of primitive types from the main ornithischian evolutionary lineages in this region, giving rise to a series of characteristic Asian lineages. Psittacosaurids and ceratopsids are currently studied as distinct, greatly separated lineages, although rising from a common ancestral group (L. S. Russell, 1970; Maryanska and Osmólska, 1975), in contrast to the widespread opinion favoring close phylogenetic ties between the two (Gregory, 1927; Romer, 1956; Young, 1958; Chao, 1962), although the branching off of protoceratopsians from psittacosaurids had, just as with ceratopsids as a whole, previously been denied on a different basis (Rozhdestvensky, 1955, 1960, 1964; Steel, 1969).

It is also admitted that an early radiation of ankylosaurids also occurred in Central Asia, supposedly having taken place in the Early Cretaceous. In any case, these ornithischians appeared in North America considerably later (Maryanska, 1977).

In this manner, not only do traces of earlier biogeographic connections between Central Asia and North America appear at the end of the Early Cretaceous, which defined the later faunal evolution of the period to a considerable degree, but also a sufficiently earlier foundation in the Central Asian region for the beginning stages of the radiation of several large ornithischian lineages.

The evolution of Late Cretaceous groups points to the existence of faunal ties between the two continents. The [discovery] of new elements – for example pachycephalosaurs, until recently considered a predominately North American group, are now found in Mongolia (Maryanska and Osmólska, 1974) and previously in Europe (Galton, 1971). Later, ankylosaurids appear as valid genera from a common origin, and a comparison of Asian and North American representatives of this family suggests the possibility of immigration of more primitive Central Asian forms into North America, close to *Talarurus* and also *Pinacosaurus* (Maryanska, 1977), although in a position to support different [ideas] (Charig, 1973), the common taxa do not exist on both continents. Closer ties are noted among hadrosaurids, which in several cases are found on both continents (Rozhdestvensky, 1952b, 1957a, b, c). The basic ceratopsian (Lull, 1933) and hadrosaurid lineages are characteristic of the Late Cretaceous of North America, although protoceratopsians were present on both continents and were represented by different genera that do not show phylogenetic connections. The most famous Mongolian representative of the family – *Protoceratops andrewsi* – was for a long time considered a primitive form that gave rise to the North American ceratopsids (Granger and Gregory, 1923; Brown and Schlaikjer, 1940). However, it has recently been shown that it was not so primitive, and could not have been the direct ancestor of the "horned" dinosaurs (Maryanska and Osmólska, 1975). It is possible that their ancestors could have been the more primitive protoceratopsians, more like the Central Asian *Microceratops* (Bohlin, 1953), that could have migrated into North America at approximately the beginning of the Late Cretaceous (Maryanska and Osmólska, 1975).

In this manner, the basic links in the evolution of a series of later ornithischian lineages were apparently [present] on Central Asian soil at the end of the Mesozoic, carried in them the clear imprint of earlier biogeographic connections with North America. The study of Late Cretaceous carnivorous dinosaurs supports this picture in many ways. On both continents, one can follow earlier connections in the evolution of dromaeosaurids. At the same time, a large divergence in Mongolian lineages is observed among dromaeosaurids – the "narrow-skulled" form (*Velociraptor*) is present in addition to the "high-skulled" forms, as well as types with a reduced predatory pedal ungual (*Adasaurus*) that are unknown in North America. The end-Cretaceous tyrannosaurids are also very similar and include closely related genera (*Tarbosaurus* and *Tyrannosaurus*) and possibly also [species] (Maleev, 1955a, b, c). Among the Mongolian forms, Alectrosaurus appears as the earlier and more primitive representative of the family, which had spread to both continents. Advanced ornithomimids continued their evolution, having reached well-known examples of high levels of specialization in North America and Central Asia. However, the discovery of the primitive garudimimid lineage in the first half of the Late Cretaceous of Mongolia testifies in turn to the prolonged evolution, earlier than currently known, of a group that apparently arose in Central Asia. The same is true of saurornithoidids, Late Cretaceous coelurosaurs *sensu stricto*, that apparently seem to be a lineage of Central Asian and North American propagation (Barsbold, 1974).

Along with these reliable links between Late Cretaceous theropods, remains of carnivorous dinosaurs known only from the Late Cretaceous of Mongolia are also found (deinocheirids, oviraptorids, segnosaurids, elmisaurids, avimimids). It is possible that another exclusively Asiatic lineage, chilantaisaurids (Hu, 1964), did not fall into any known carnivorous dinosaur group based on existing information, including deinocheirosaurs, although attempts have been made to approximate them with the latter (Rozhdestvensky, 1970). The discovery of single large ungual phalanges in Nigeria, the trans-Baikal, and Kazakhstan (Ricqles, 1967; Rozhdestvensky, 1970) that are no smaller in size than those of deinocheirosaurs, currently testify only in favor of the evolution and wide distribution of large dinosaurs with non-reduced forelimbs, not necessarily closely related to Mongolian deinocheirosaurs.

The information from Mongolian sauropods (Osborn, 1924b; Gilmore, 1933; Bohlin, 1953; Nowinski, 1971; Borsuk-Bialynicka, 1977) is [insufficient] for any concrete conclusions about the study of their [evolution]. It is possible to affirm only that the evolution of two main sauropod lineages (atlantosaurids and camarasaurids; Borsuk-Bialynicka, 1977) took place in Central Asia, which were spread out earlier in North America as well as on this continent.

A much greater variation, in comparison with the later carnivorous lineages of North America, apparently supports the great degree of native evolution of Central Asiatic theropods throughout the end of the Mesozoic. The carnivorous group that had immigrated relatively recently was not that great in number, which agrees well with ornithischians. The main stages of migration, forming the basis for the evolution of the Central Asian fauna, apparently occurred much earlier, predominately in pre-Cretaceous time when a faunal exchange, mainly with North America at the end of the Mesozoic, did not lead to any great [displacements] in the relatively autochthonous evolution of the

Cretaceous Mongolian faunas. The situation was somewhat different in North America, for here a much more prolonged interval of evolution can be observed, practically starting at the end of the Triassic. It is supposed that hadrosaurids, ankylosaurs, protoceratopsians, and advanced ornithomimids, which comprised a considerable part of the dinosaurian fauna at the end of the Mesozoic, evolved first in Central Asia and reached later peaks on North American soil. And although faunal connections did not bear a single directional character, the relatively autochthonous nature of the Central Asiatic fauna is much higher than that of North America, and was defined to a greater degree by the earlier immigration of ancestral groups, the Late Cretaceous members of which quickly became specifically Central Asian. This, to a great degree, is also true for the carnivorous dinosaur group.

Notes on Theropod Ecology

Basic Theropod Ecological Types. In the area of theropod ecology, just as with dinosaurs as a whole, chance suppositions are often put forth regarding the life habits of the animals. Excluding the more fantastic among them, the general shortcomings of many, even fair, ecological suppositions most frequently concern their weak morphological and functional foundation. New information about later theropods, based on the best knowledge of their morphological and functional characteristics, has partially opened up new possibilities on which suppositions of life habit can be based. This plan, as long as there is no other approach, is to base them on definite morphological structures or complexes with the subsequent attempt towards possible functional interpretation. With this, features of narrow specialization become very useful in comparing with signs of more general character, inasmuch as they highly limit, and in the same manner cement, the bounds of possible functional interpretations.

The carnivorous dinosaurs were unquestionably at the highest trophic level in the food chain. Their general organization testifies clearly enough towards their carnivorous specializations. At the same time, theropods unquestionably occupied a large number of ecological niches within the style of being predatory, in many ways preceding the type that followed them.

In dinosaur ecology, it is unknown whether they were ectothermic animals with a reptilian-level metabolism, as has traditionally been taught, or endothermic and more or less comparable to birds and mammals, a possibility that a series of studies now allows (Russell, 1965; Bakker, 1971a, b, 1972, 1974, 1975a, b; Bakker and Galton, 1974; etc.).

This question is enthusiastically discussed, along with the presentation of often contradictory interpretations (Bennett and Dalziell, 1973; Feduccia, 1973, 1974; Thulborn, 1973; Bennett, 1974; Ostrom, 1974b; Farlow, 1976a, b; Budiko, 1979; etc.). When we study the more particular questions and attempt to analyze some of the better studies on groups of theropods for basing conclusions about the possible mode of life based on new morphological information, at the same time we do not touch on questions about their surrounding environment, climate, etc., and it does not seem necessary to deal with these questions in the framework of the present investigations.

Ecological Types in the Life History of Theropods. Tyrannosaurids could have been scavengers. This possibility contradicts the general tradition of picturing large carnivorous dinosaurs as [active] predators. It is understood that tyrannosaurids completed the lineage of the largest carnivores to ever have appeared in the history of biological evolution on earth. At the same time, similar evaluations often carry accidental, almost impulsive, characters. Specific structural signs of carnosaurs entirely permit carrion-feeding. The features of a noticeably weakened kineticism, signs of which are clearly reflected in skull construction, support this. It is clear that kineticism has become almost excessive with such an inactive (in the sense of overcoming the resistance of a victim) manner of feeding. Blunting of the teeth also partially serves as one of the conclusions to this development. Furthermore, the anterior and posterior jaw sections are connected together rather weakly, by a thin and elongated coronoid region. This imperfect articulation of the largest lower jaw (considerably more than 1 meter in length), in spite of the additional type of articulation in connections, must have severely limited the strength of the lower jaw against fracture from lateral stresses, which are completely unavoidable while overcoming a victim that is attempting to escape from the jaws. In addition to this, the victim, most likely also a dinosaur, would hardly have been small and weak. Therefore, the resistance of a victim grasped by the jaws would have created a great danger of damage to the jaw apparatus, which was practically the only effective attack organ in these carnosaurs. Reduction of the forelimbs and their almost total exclusion from use in any meaningful auxiliary function (the non-pulley carpus is generally poorly suited for grasping) strongly limits the possibility of attack for tyrannosaurids and makes them somewhat similar to predatory birds, for example *Griffon.* In a successful [explanation] by Colbert, tyrannosaurids are the most clearly expressed carnivores in the sense that they represented a jaw attack placed on two limbs. We consider that tyrannosaurids could feed on carrion, but hunting and especially struggling with sufficiently large victims, at least, was hardly within their ability. The increase in skull height could have promoted strengthening of the compressive action of the jaws (through strengthening of the jaw adductors) that would have been useful in eating the corpses of large animals. The head, held high above the ground, and the perfected bipedalism guarantee both a wide view of the vicinity and good locomotor abilities necessary for scavengers to make an effective search for food with a view over a considerable area. In addition, it seems simply fantastic to suppose a method of killing victims by striking with the teeth of the lower jaw, [the force of]which is increased with the inertia of a blow and the body weight of the supposedly attacking tyrannosaurid (Efremov, 1954), inasmuch as the known tooth types in the jaw or skull as a whole [were not able] to have supported the stress that comes about from such a blow. There was probably no lack of scavenger food in the times of dinosaurs, as in recent times, especially if one considers that the contemporaries of tyrannosaurids were sauropods, the largest terrestrial animals. Thus, tyrannosaurids could have managed very well with [sanitary?] functions.

The question arises whether all large carnivores were exclusive carrion feeders. It is possible to suppose that carrion-feeding corresponded to a definite tendency in carnosaur evolution, and that their entry into this narrow adaptive zone was further refined only in the latest of their lineages, that is tyrannosaurids. For example, early allosaurids, as more primitive, may not have been scavengers in a sufficiently refined manner.

Dromaeosaurids could easily have been predators that obtained their food by active hunting. In any case, the entire complex of highly sharpened teeth, perfected metakinesis, curved and sharp unguals, strong forelimbs with grasping, pulley-type mani, and the predatory ungual of the pes clearly supports an attacking method of food acquisition. The unique discovery of two intertwined skeletons of the carnivorous *Velociraptor* and the herbivorous *Protoceratops* (Kielan-Jaworowska and Barsbold, 1972; Barsbold, 1974) allowed a more definitive judgment about the lifestyle of dromaeosaurids. Early suppositions about the method of attack of dromaeosaurids and the use of their means, in particular the grasping ability of their limbs and especially the predatory ungual of the pes, were supported by discovered material. It is notable that this find serves as a clear illustration for discussion of the ecology of dromaeosaurids, given earlier by Ostrom (1969a, b). Dromaeosaurids apparently lead an active search for food, possibly even following it before attacking, and in any case they were animals with maneuverability, proven by such specific structures as the apparently high inertial features such as a tail that served as a dynamic stabilizer, especially during rapid stops and turns (Ostrom, 1969a, b). At the same time, it is possible to suppose that some deviation in feeding methods occurs in later dromaeosaurid lineages. In "high-skulled" representatives, a further increase in skull height is observed, kineticism becomes weaker, and, most remarkably, the predatory ungual of the pes is highly reduced towards more normal dimensions. All this could reflect a lowering of the level of active predation and a transition to scavenging, which evoked a certain similarity to different tyrannosaurid species (Colbert and Russell, 1969). At the same time, the "narrow-skulled" dromaeosaurid lineage, represented by the Mongolian *Velociraptor* (one of the partners in the aforementioned struggle), retained all the features of an attacking predator.

Ornithomimosaurs are represented by two lineages, the ecological possibilities of which were most likely quite specific. At the same time, they were characterized by a series of general features, including a weak jaw apparatus covered by a horny beak that was widened in the rostral part, incomplete connection of the lower jaw segments as in tyrannosaurids, a distinct weakening of the forelimbs with a non-pulley manus, manual unguals distinguished by their considerable straightness, and widened pedal unguals. Apparently, the advanced ornithomimid lineage was remarkable in the ability for fast flight on a hard substrate, supported by highly elongated metapodia and loss of pedal digit I. It is possible that they lived in a relatively dry and open environment, ecologically approaching ostriches. Their food could have included vegetation and small animals (reptiles, mammals, insects) obtained from the ground. The primitive garudimimid lineage, on the contrary, is characterized by shortened metapodia and retention of pedal digit I, which along with other above-mentioned features indicate an equal ability for fast and easy flight. They could have preferred a habitat with more inundated, watery areas, like ciconiiform birds. They may have eaten small vertebrates and invertebrates obtained from land and water. Apparently, a similar mode of life does not demand any special participation of the forelimbs in food acquisition in the two ornithomimosaur lineages.

Oviraptorids, the second group of edentulous theropods, had a characteristic jaw apparatus completely opposite to that of ornithomimids. Their horny beak was remarkably massive, shortened, and curved, in many ways reminiscent of the beak of large parrots or some ornithischians, such as psittacosaurids and protoceratopsians. Judging by everything, the jaw apparatus was suited for generating strong compression, confirmed by the development of an unusually large adductor process for the attachment of the jaw adductor muscles. The strength created by jaw compression must have been considerably increased relative to the rather small jaw dimensions, *i.e.* the reduction in area over which pressure was applied. All this testifies in favor of feeding on fairly hard food items that demand breaking by means of crushing. Since the first discovery of this peculiar theropod, it was supposed to have been a robber of eggs from horned dinosaurs – protoceratopsians – which is reflected in its name, *Oviraptor philoceratops* (Osborn, 1924). However, now there is more basis to consider that the food of oviraptorids must have been harder than eggs. It is much more likely to have been large, freshwater molluscs, such as trigonionids and others with hard shells, which existed in great numbers in Late Cretaceous waters, or, less likely, some type of fruit and the hard sections of plants. The manus in the most specialized oviraptorid is characterized by a high degree of narrowing of digits II and III, but without loss of phalanges, which leads to the suggestion of the presence of a possible skin (swimming?) membrane. The tail, with the elongated processes that widened it, is differentiated by the ability for more lateral curvature along a large section of its length, which could have been an adaptation for performing swimming functions. Oviraptorids could have been amphibious, an uncommon [trait] among carnivorous dinosaurs, and fed on food that demanded the noted adaptations for an aquatic mode of life. Possibly the development in oviraptorids of very large, "open" eyes that guaranteed great eye mobility as in some nocturnal birds (owls) provided an adaptation for either nocturnal life or the ability to see underwater while diving after molluscs.

In this manner, the considerable range of ecological niches occupied, the corresponding peculiarities of lifestyle and behavior, and the use of resources from their surroundings are studied. It is interesting that such ecological variety is based on morphological variety in carnivorous dinosaurs.

Outside this framework, very interesting ecological types remain, about which it is difficult to construct even the most general suppositions. Among them, the "terrible-handed" deinocheirids and therizinosaurids remain the most poorly understood. The huge, laterally compressed, slightly curved ungual phalanges on the shortened digits of the "grasping" manus along with the powerful forelimbs cannot help but arouse an image of therizinosaurids them as carrying on some sort of frightening method of attack that it is possible they may not have had. In deinocheirids, the large, massive ungual phalanges and non-grasping manus seem completely contradictory with their elongated forelimbs, the function of which is just as unknown as in therizinosaurids. The lower jaw of some segnosaurids presents s series of no less surprising structures, [including] a horny beak in the rostral part and small, weakened teeth in the posterior region. As known, a jaw apparatus that simultaneously exhibits both teeth and a beak is a common feature of ornithischians – ceratopsians, ornithopods, ankylosaurs, and stegosaurs. Does the presence of such a jaw apparatus, not characteristic of carnivorous dinosaurs, mean that segnosaurids had shifted to a herbivorous diet? It is expected that all these questions will become clearer with accumulation of more complete material. Whatever the answer may be, it is very clear that the variety of ecological types of carnivorous dinosaurs corresponded to the variety of ecological niches occupied by them.

CHAPTER III

BIOSTRATIGRAPHY OF THE CONTINENTAL CRETACEOUS

AND DISTRIBUTION OF CARNIVOROUS DINOSAURS

The most complete section of continental Cretaceous deposits that contain remains of carnivorous dinosaurs (as well as that of other floras and faunas) are distributed across the Gobi region of the country. Finally, during the first stage of discovery of the Central Asian fauna in the territory of the Mongolian People's Republic (MPR), the question of the stratigraphy of the continental Cretaceous deposits was [put forward] as a result of paleontological exploration, to which were relegated the findings of terrestrial faunas (Berkey and Morris, 1927; Andrews, 1927). The stratigraphic study of the Cretaceous period continued during two stages of paleontological exploration into the Gobi region. It went from the first private scheme of subdividing the Cretaceous continental sequence according to a framework based on the limited number of locations (Berkey and Morris, 1927; Spock, 1930; Morris, 1936) to an attempt towards a wider exposition of the stratigraphic construction (Efremov, 1949, 1954a, b; Maleev, 1952, 1965; Rozhdestvensky, 1954, 1957b; Novozhilov, 1954) that gradually attained an increasingly regional character (Turischev, 1954, 1955, 1956; Marinov, 1957; Vasiliev *et al.*, 1959a, b). This history of the question and evolution of stratigraphic phenomena is [the basis of] sufficiently complete [explanations] (Marinov, 1967; Barsbold, 1972b; Martinson, 1975; Schuvalov, 1975; Gradzinsky *et al.*, 1969, 1977) that permit avoiding any repetition here. The explorations of the last ten years have been especially productive – a very well based and detailed scheme of stratigraphic subdivisions of the Cretaceous deposits of the MPR was created (Martinson, Sochava, and Barsbold, 1969; Martinson, 1973, 1975; Barsbold, 1970, 1972a, b; Schuvalov, 1970a, b, 1975; Sochava, 1969, 1975; Gradzinsky, 1970; Gradzinsky, Kazmierczak, and Lefeld, 1969; Lefeld, 1965, 1971; Kielan-Jaworowska, 1974a, b; Gradzinsky, Kielan-Jaworowska, and Maryanska, 1977).

With consideration of the most recent subdivisions in this region, in the paleontological, and therefore most interesting, studies of the Gobi region the continental Cretaceous of the country can be reduced to the following horizons, which are connected in the following suite (from top to bottom):

Upper Cretaceous	**Approximate Stratigraphic Equivalent**
Nemegtskaya	Upper Senonian (to upper Maastrichtian)
Djadokhtaskaya	Lower Senonian-Campanian (lower part)
Baynshirenskaya	Cenomanian-Turonian
Sainshandinskaya	Albian-Cenomanian (upper Aptian-Albian interval)
Lower Cretaceous	
Khukhtekskaya	Aptian-Albian
Shinekhudukskaya	Hauterivian-Barremian
Tsagantsabskaya	Tithonian-Valanginian

It is necessary to note that identified dinosaur remains below the Tsagantsabskaya horizon, dated as Tithonian on the chart, include the remains of undescribed psittacosaurids that are possibly more ancient than known examples. Regarding the carnivorous dinosaurs, the lowest boundary to date is the Khukhtekskaya horizon, dated as Aptian-Albian on the chart. As a result, the Mongolian theropod fauna occupies only the upper part of the Lower Cretaceous and is distributed mainly within the Upper Cretaceous framework.

Faunal-bearing deposits that are attributed to identifiable horizons have, in part, a definite territorial distribution. The Sainshandinskaya horizon is apparently from the upper part of the Lower Cretaceous, and in the near future it will be necessary to refine this information, which demands a detailed investigation of the paleontological material.

Separation of the horizons has a correlative purpose (Martinson, 1975), and is based on unification of the early or closely-dated age for the stratigraphic correlation within the boundaries of the territory of the whole country; it is constructed on the basis of the biostratigraphic succession of faunal complexes in which the role of the theropod fauna has grown significantly.

It is necessary to note that a series of indefinite difficulties exist inside and outside the country, with regard to the stratigraphic subdivision (Martinson, 1975) and particularly the correlations at different levels. The correlation of the existing series of Lower and Upper Cretaceous horizons often has conditional characters; it is not possible to definitely connect the Upper Cretaceous stratigraphic subdivisions of the southeast and southwest of the country, and finally the most important [issue] is the often highly conditional correlation with the international scale in the suite of subdivisions. The basic complexity that is difficult to overcome and its principal nature apparently consist of the difficulty of correlating the marine and continental faunas, on which is based the corresponding standard and local stratigraphic schemes.

There also exists the necessity for detailing the local geological standard on which the regional stratigraphy is based, and making it more exact. In later articles (Martinson, 1975), isolation of the corresponding horizons in the Upper Cretaceous is apparently not considered necessary, although they are recognized as being expedient in the Jurassic and Lower Cretaceous. Inasmuch as from the point of view of geology and stratigraphy no principal difference exists between the noted intervals and the depositional complexes, in order to better preserve a single approach to the subdivisions which unite them. That is why the Upper Cretaceous horizons are also used (Barsbold, 1970, 1972a, b).

Biostratigraphy and Distribution of Theropod Faunas. The characteristic distribution of theropod faunas, or complexes, is given correspondingly with the importance of the different horizons. Basic locations are noted with this, whose deposits accommodated the fauna. The general composition of the currently known biological complexes has become fairly large due to the appearance of many new groups, and it is not my goal to mention them here inasmuch as a great deal of literature already exists on this question. The literature reference is that in the future and on the basis of the age of the accommodated thicknesses, and therefore their relegation to the selected horizons. It is also necessary to take into account the fact that several stratigraphic levels can be introduced on the exact same horizon. The wide knowledge and fixation of the Cretaceous localities in the literature to which we will refer allows us to act without any reference to their localities.

Khukhtekskaya Horizons. Currently only representatives of the ornithomimids, and also dromaeosaurids, are known and not more precisely identified. According to the construction of the pes and partly the pelvis, the ornithomimids appear to be an advanced lineage, distributed predominately in the later Cretaceous of Central Asia and North America. The Khoren-Dukh (ornithomimids) and Khobur (dromaeosaurids) localities most likely should be correlated with the Lower Cretaceous Khukhtekskaya and Khulsyngolskaya (Vasiliev *et al.*, 1959a, b; Shuvalov, 1970b, 1975; Martinson, 1975).

Sainshanginskaya Horizon. Theropods are this far unknown from this horizon, and it is very poorly characterized by other groups. Contemporaneous suites are distributed in the Khara Khutul, Algu Ulan Tsav, Dzun Bari, Barun Bari, and other regions in the southeastern MPR. The deposits of the near northern regions of the Nogon Tsav, separated out as the Dushiulskaya Svita, can be referred to these horizons (Martinson, 1975).

Baynshirenskaya Horizon. The composition of these complex deposits was established recently. It includes segnosaurids (*Segnosaurus* and *Erlicosaurus*), dromaeosaurids, ornithomimids, and garudimimids. Ornithomimids (*Archaeornithomimus*) and tyrannosaurids (*Alectrosaurus*) are found beyond the borders of the country, near the southeastern border in the Iren Dabasu locality.

The most specific of the complex, segnosaurids, are known so far only from this horizon in the southeast of the country. Dromaeosaurids are represented by the "high-skulled" lineage, distributed among other complexes in Mongolia as well as in the Late Cretaceous of North America. *Garudimimus* is very interesting among the ornithomimids as the first truly primitive representative of the family. The second representative of the group is from the advanced lineage. The remains of *Alectrosaurus* have been found repeatedly in the southeast of the country, not only providing the possibility to more clearly refine its position among later carnosaurs, but also to determine the importance of including *Archaeornithomimus* in the composition of the studied complex, one of the first discoveries of these theropods beyond the borders of North America. *Archaeornithomimus* was regarded as more primitive relative to the North American forms (Russell, 1972), however at that time the features of truly primitive ornithomimosaurs were not as well known as they are now thanks to the example of garudimimids. *Archaeornithomimus* is a rather typical representative of the advanced lineage in general, but it is not as developed as the more advanced Mongolian and North American forms in a series of features.

The theropod fauna of the Baynshirenskaya horizon is peculiar to the region in many features, and does not have a true analog either within or beyond the borders of the country. The presence of such widely distributed forms as dromaeosaurids in no way disguises the unique nature of the horizon, defined primarily by its segnosaurids. In the same manner, a great importance belongs to the ornithomimosaurs. Representatives of their advanced lineage bear greater similarity with end-Cretaceous North American types than with Mongolian forms. The discovery of *Alectrosaurus* provided a basis for comparing this horizon with the Iren Dabasu Formation, even before it was isolated by the Central Asiatic Expedition (Gilmore, 1933; Morris, 1936).

The forms reported from the Baynshirenskaya horizon are from a series of large localities on the southeast border: Khara Khutul, the Tariach region, Mongoin Bulak, Bayshin Tsia, Amtgai, Urilbe, etc. The deposits in the section from the Shiregin Hashun locality can be [assigned] to the southwest horizons. Different authors establish the age correlation of the horizon with a considerable degree of conditionality. Above the faunal deposits of the Baynshirenskaya horizon lay the thicknesses of the Dzhavkhlantskaya Svita, the age of which remains unclarified and, in this case, based on the stratigraphic information belonging to the Baynshirenskaya Svita. The correlation of the Dzhavkhlantskaya Svita with the [compromising] Djadokhtaskaya horizon is taken as highly conditional.

Djadokhtaskaya Horizon. The fauna from this horizon contains the first carnivorous dinosaurs, found more than half a century ago in the territory of the MPR. At the present time, a wider distribution of faunal groups from the horizon has been established, and two complexes are identified in its composition that are closely related but differ in age, and which characterize two suites deposited after it – the Djadokhtaskaya and the stratigraphically higher-positioned Barungoyotskaya. The first of these had already been identified as the Djadokhta Formation at the time of the discovery of the Central Asian fauna in the territory of the MPR (Berkey and Morris, 1927), and this name has been used widely in later works (Gradzinsky, Kazmieczak, and Lefeld, 1969; Gradzinsky and Jerzykiewicz, 1972; Lefeld, 1971; Kielan-Jaworowska and Barsbold, 1972). The goal of consistency for naming in the Russian language corresponds more to the acceptance of this subdivision under the name Djadokhtaskaya Svita.

In the Djadokhtaskaya complex itself, the dromaeosaurid *Velociraptor*, the saurornithoidid *Saurornithoides mongoliensis*, and the oviraptorid *Oviraptor* are known, first discovered by investigators from the Central Asiatic Expedition. In the Barungoyotskaya complex, the oviraptorid *Ingenia* is present, as well as the remains of a dromaeosaurid similar to *Velociraptor*, but not yet identified more precisely.

The Djadokhtaskaya *Velociraptor* is a "narrow-skulled" dromaeosaurid, known so far only from this complex. Oviraptorids characterize both of these complexes, and in the Djadokhtaskaya more primitive oviraptorids are present, while the more specialized *Ingenia* is found in the Barungoyotskaya. Saurornithoidids possibly were more widely distributed stratigraphically, as they are also known from the Nemegtskaya horizon. In this manner, both complexes are characterized by a close connection of the types of forms present, and it is not possible to separate them only on theropod information. However, with consideration of sauropods and the results from studies of mammals, of which both horizon suites are richly endowed (the remains of small mammals are almost unknown in the beds of other Upper Cretaceous horizons), as well as the freshwater fauna (Gradzinsky, Kielan-Jaworowska, and Maryanska, 1977; Maryanska and Osmólska, 1974, 1975), such a subdivision received a more or less weighty and consistent basis. The conclusion regarding the age of the mammals is provided on the basis of comparison with North American forms (Kielan-Jaworowska, 1969, 1970, 1971, 1974a, b, 1975a, b).

Faunal deposits from the Djadokhtaskaya Svita form large localities in the south of the country – Bayn Dzak (Shabarak Usu in American publications), Tugreeken Shira, and the recently discovered Dzamin-Khond. The Barungoyotskaya Svita includes the well-known southwestern localities of Khermeen Tsav and Khulsan.

Nemegtskaya Horizon. The theropod complex consists of tyrannosaurids (*Tarbosaurus, Alioramus*), an ornithomimid (*Gallimimus*), a saurornithoidid (*Saurornithoides*), a dromaeosaurid (*Adasaurus*), and deinocheirosaurs (*Therizinosaurus, Deinocheirus*). The end-Cretaceous Mongolian tyrannosaurids are close to the North American forms. It was noted above that one of the earlier representatives of the family (*Alectrosaurus*) is present in the Baynshirenskaya complex. Ornithomimids are represented by an advanced lineage, also related to the North American forms. Dromaeosaurids are related to the "high-skulled" forms, usually having a wide stratigraphic distribution,, but the Nemegtskaya type represents a specific lineage of the family, with the "predatory" pedal ungual having experienced a great reduction to the level of a normal one. Such dromaeosaurids are known so far only in this complex. The Nemegtskaya saurornithoidids are considerably larger than the Djadokhtaskaya forms. However, the large theropods appear to be a more specific element – deinocheirosaurs with non-reduced forelimbs and gigantic ungual phalanges. They are represented by two families, currently known only in this complex from the southwest of the country. Large ungual phalanges also appear in the trans-Baikal, Kazakhstan, and Nigeria (Rozhdestvensky, 1970; Ricqlès, 1967), however their differentiation from the Mongolian forms is fairly clear, leading to the possibility about several theropod lineages with gigantic claws in different regions that were not contemporaneous.

The Nemegtskaya theropod complex is fairly unique and is actually differentiated from the stratigraphically earlier Djadokhtaskaya and Barungoyotskaya. It is more characteristic of the upper part of the Cretaceous section in Mongolia. Additionally, in recent times it has been suggested that the sediments should be subdivided into two parts, crowned by the Upper Cretaceous section in the area classified with the single Nemegtskaya Svita in the southwest MPR, based on information from the Presnovodikh fauna and its lithologic-taphonomic properties. The lower part of the deposit comprises the main bone layer of the major finds from the Nemegtskaya group (actually Nemegtu, Altan Ula, Tsagan Khushu, Gurilin Tsav, etc.). A large dinosaurian, and partly theropod, fauna is contained exactly in this deposit, which was obtained by the paleontological expeditions of the USSR (Efremov, 1949, 1954a; Rozhdestvensky, 1957b). The upper part is represented by deposits of a somewhat different origin, and is considerably poor with regard to dinosaur remains. A similar thickness has exposures partly in the Nogon Tsav location (here identified under the name Nogon Tsav Svita; Barsbold, 1970, 1972b), and also the upper part of the Cretaceous section at Bugeen Tsav, Khaich, and Naranbulak. The upper part of the Nemegtskaya deposits is differentiated from the lower by a richer fauna, approaching the upper borders with small thicknesses that are covered with paleogenic deposits.

Regional Correlation and Dating. The stratigraphy of the continental Cretaceous of Mongolia is presently fairly developed in this interval, which contained not only invertebrates but also vertebrates, and leads to a wide intercontinental correlation. The conditions and the potential in this respect are highly unequal. With all the wide variety of organic remains in the Cretaceous of the MPR, the wide regional correlation of Cretaceous subdivisions for stratigraphic purposes is often difficult. The reason for this, first of all, is the uniqueness of the continental Cretaceous of Mongolia and the organic groups contained within in as compared to the international stratigraphic standard, which is based mainly on marine deposits and their corresponding fauna. Furthermore, the difficulties of biostratigraphic correlation with far-reaching reasons based on different organic groups leads to a contradictory interpretation. Apparently, in relation to more or less basic correlations the groups refer to the biostratigraphic indications of those groups, whose genetic type would show at least partially, especially in intercontinental plans. In this sense, among Mongolian Cretaceous dinosaur faunas, the dinosaur and mammals that appeared more varied would have a definite advantage, and with this the fauna of the second half of the Cretaceous. The intercontinental correlations of Mongolian Cretaceous subdivisions on the basis of the noted fauna is now oriented mainly towards North

American faunas and their stratigraphic equivalents. With invertebrates, their correlation is more limited on an analogous level, although fairly wide correlations have been worked out in a series of intervals. The already noted information regarding the freshwater fauna (predominately molluscs) of Mid- and Central Asia may serve as an example.

We have now achieved definite progress in the regional and intercontinental correlation of the Cretaceous Mongolian subdivisions. However, the lower part of the Cretaceous of Mongolia is practically excluded from the correlation. The basis for Early Cretaceous layers of Mongolian subdivisions is only conditional in many ways.

In the Lower Cretaceous part, a possible correlation of the Khukhtekskaya horizon is depicted, widely distributed in the MPR (Kalandadze and Kurzanov, 1974), with the Cloverly Formation (Moberly, 1960; Ostrom, 1970) in the Aptian-Albian age interval on the basis of advanced ornithomimids and also dromaeosaurids (Barsbold, Voronin, and Shegallo, 1971; Martinson, 1971, 1975; Martinson and Shuvalov, 1973; Shuvalov, 1970a, b, 1974, 1975). The information on Early Cretaceous mammals does not deny such a correlation (Beliaeba, Trofimov, and Reshetov, 1974; Dashzeveg, 1975). At the same time, the psittacosaurids occasionally found in this horizon are sometimes considered characteristic of a more ancient, Neocomian, age (Rozhdestvensky, 1971, 1974), which apparently is not completely integrated with their relatively wide stratigraphic distribution (Shuvalov, 1974).

In the Upper Cretaceous, correlation with the North American standard is more or less possible only for the second half. This is linked to the fact that the lower part of the Upper Cretaceous is represented most by marine beds in the compared regions of North America (Cobban and Reeside, 1952; L. S. Russell, 1930, 1964; D. Russell, 1967), while the corresponding intervals in Mongolia [either] include dinosaur remains (Sainshandinskaya horizon), or their presence does not provide very much towards biostratigraphic construction within the country (Baynshirenskaya horizon). At the same time, the second half of the Upper Cretaceous contains a varied fauna of both dinosaurs and mammals in both North America and Mongolia.

According to the information from the few collections of freshwater fauna known in northeastern China as well as southern Primoria (Grabau, 1923; Suzuki, 1943; Yakushina, 1964; Martinson, Sochava, and Barsbold, 1969), and the conditional dating of the stratigraphic position of the Sainshandinskaya horizon within the limits of the Albian-Cenomanian, a leaning more towards the Lower Cretaceous interval seems acceptable (Martinson, Sochava, and Barsbold, 1969; Barsbold, 1970, 1972b; Martinson, 1975; Shuvalov, 1975; Sochava, 1975).

The Baynshirenskaya horizon, containing on the southeast specifically faunas of theropods and dinosaurs as a whole, is not very differentiated from the southern and southwestern complexes, characterized by the presence of more primitive ornithomimosaurs. Similar common indications from the theropod fauna as well as the stratigraphic location are in agreement with information from the freshwater groups, supporting the more ancient age of the horizons relative to the Nemegtskaya and possibly the Djadokhtaskaya horizons, in contrast to correlations of earlier works (Maleev, 1952).

The information from ankylosaurs from the Bayashirenskaya and Djadokhtaskaya horizons, as well as protoceratopsians from the Shiregin Gashun localities on the southwest, the deposits of which can be correlated with the Bayashirenskaya on the southeast (Barsbold, 1972a, b; Shuvarov, 1975), is studied as testimony towards the great antiquity of the Bayashirenskaya horizon (Rozhdestvensky, 1971, 1974; Maryanska and Osmólska, 1975; Maryanska, 1977). The freshwater fauna (mostly molluscs) provide a definite possibility for a correlation with analogous formations in Central Asia. Along with this, the correlation of faunal complexes in Fergan and the eastern pre-Urals (Sochava, 1965; Martinson, 1965) correspond to the Tokubaiskaya (Albian-Cenomanian), and also the Yalovakhskaya and Bostobinskaya Svitas (Lower Senonian) that are taken conditionally to mark the interval of the Bayashirenskaya horizon (Barsbold, 1970, 1972b; Martinson, 1973, 1975; Sochava, 1975). Instead of this supposition, basing this horizon correlation with consideration of the stratigraphic position given to it by the suite of the same name corresponds to the wide interval between the Cenomanian and Lower Senonian, in that case narrowed to the Cenomanian-Turonian conditionally.

The primitive mammal fauna in the Djadokhtaskaya horizon allows correlation with more or less closely related North American groups. With this as a basis, the conclusion is taken that the fauna from the lower part of the horizon contained in the Djadokhtaskaya Svita deposits fills the blank between the Albian forms from the Trinity Sandstone of Texas and the Campanian from the Judith River deposits of Montana (Kielan-Jaworowska, 1968, 1969, 1970). From here the age of the Djadokhtaskaya horizon, i.e. actually the Djadokhtaskaya Svita, is defined as within the Coniacian-Santonian interval (Kielan-Jaworowska, 1969, 1970, 1974a, b, 1975a, b).

The dating of the upper part of the Djadokhtaskaya horizon, represented by the Barungoyotskaya Svita, is also based on information from the mammalian fauna of Mongolia and North America and the consideration of the types between the earliest (Djadokhtaskaya) and later (Barungoyotskaya) faunas of the horizon itself. In North America, stratigraphic analogs of the Barungoyotskaya Svita such as the Milk River, Judith River, and [Oldman Formations] will provide information (Cobban and Reeside, 1952; Russell, 1964, 1970; Ostrom, 1965; Morris, 1967; Sloan, 1970; Fox, 1970, 1971, 1971) from which its age was placed within the limits of the Campanian (Kielan-Jaworowska, 1974a, b, 1975a, b; Gradzinsky, Kielan-Jaworowska, and Maryanska, 1977). In this manner, the lower and upper age limits of the Djadokhtaskaya horizon are considered to correspond to the Lower Senonian and Campanian.

The correlation of the Nemegtskaya horizon is built predominately on the information from the relations between the types of dinosaurian fauna, whose evolutionary lineages reach down to the earlier complexes. At the same time, the uniqueness of the theropods and other dinosaurs, the character of the complexes of the freshwater fauna, and the stratigraphic positions of the Nemegtskaya and Nogontsavskaya horizon deposits testify to the fact that the Nemegtskaya horizon crowns the Upper Cretaceous section in the southwestern MPR, and apparently has a higher stratigraphic position in Central Asia (Barsbold, 1969, 1972b). The upper part of the continental Cretaceous of Mongolia, with very rare mammal finds, must be correlated with the corresponding North American subdivisions. The absence of true ceratopsids in the MPR, and the close similarity between the Mongolian and North American tyrannosaurids and hadrosaurids, led to thoughts of the possibility that it was correlated with the Edmonton Formation, which itself is correlated with the lower part of the Lance Formation (Cobban and Reeside, 1952; Russell, 1964; Russell and Chamney, 1967), and the dating of the Nemegtskaya deposits as Maastrichtian (Rozhdestvensky, 1957a, b, 1965, 1968, 1974). Biostratigraphic information from the freshwater fauna also led to the acceptance of a similar age, sometimes bounded by the upper Senonian (Martinson, Sochava, and Barsbold, 1969; Barsbold, 1970, 1972b; Stankevich and Sochava, 1974; Martinson, 1973, 1975; Shuvalov, 1975; Kielan-Jaworowksa and Sochava, 1969). The correlation with the Edmonton Formation (Belly River and others) now seems [supported] by new information about the Mongolian dinosaur fauna (Osmólska, Roniewicz, and Barsbold, 1972). At the same time, the dating of the correlated North American subdivisions have gradually been modified, and the stratigraphic level corresponding to the Edmontonian stage is now defined as belonging to the Upper Campanian-Lower Maastrichtian interval, which is also supported by radiometric information (Morris, 1967). A similar interval is also supported for the Nemegtskaya faunal complex (Osmólska, Roniewicz, and Barsbold, 1972; Maryanska and Osmólska, 1974, 1975; Gradzinsky, Kielan-Jaworowska, and Maryanska, 1977; Maryanska, 1977).

In this manner, the regional and intercontinental correlations of Cretaceous stratigraphic horizons of Mongolia that form the currently identified suites are taken on the basis of various faunas. The lowest of the connecting faunal deposits, that of the Khukhtekskaya horizon within the Aptian-Albian interval, more or less corresponds to the stratigraphic level of the Cloverly Formation of Montana. The following Sainshandinskaya horizon, near the border of the Lower and Middle Cretaceous, is dated as Aptian-Cenomanian based on the similarity of the freshwater molluscs with those distributed in northeastern China and, as has been noted, is similarly relegated to the Lower Cretaceous. The Bayashirenskaya horizon, according to information from the freshwater fauna, also corresponds to the Cenomanian-Lower Senonian interval, established for the Tokubaiskaya, Yalovakhskaya, and Bostobinskaya Svitas in the region of Central Asia (Fergana, trans pre-Urals), and possibly corresponds to the Cenomanian-Turonian interval. The lower part of the Djadokhtaskaya Svita of the horizon of the same name is probably correlated with the Lower Senonian, based on correlation with North America, however its interrelationships with the Bayashirenskaya horizon are not entirely clear. Most likely, the Bayashirenskaya horizon and Svita are actually older than the Djadokhtaskaya Svita, affirming the Cenomanian-Turonian age of the former. The Barungoyotskaya Svita, corresponding to the upper part of the Djadokhtaskaya horizon, is accepted as Campanian by correlation with North America. Analogous correlations lead to the acceptance of the Campanian-Lower Maastrichtian interval for the Nemegtskaya horizon.

SYSTEMATIC SECTION

The systematic section contains descriptions of the carnivorous dinosaurs currently known in Mongolia. This description is built on the Mongolian theropod collection, which represents a wide variety of later lineages of carnivorous dinosaurs most completely. Among those described below, only the exclusively North American caenagnathids, classified with the oviraptorosaurs, are described based on published facts, because they are not present in Mongolia.

The data about the taxonomy of different groups contained in the table are currently the most complete. They include a reexamination of the definition of the suborder Theropoda, as well as the characteristics of the infraorders, families, genera, etc. All the information on carnivorous dinosaurs available in the literature was used for the comparisons. All together, 7 infraorders, 12 families of the 19 known, 4 subfamilies, 14 genera, and 16 species are described.

SUBORDER THEROPODA

Carnivorous bipedal Saurischia of various sizes. Antorbital fenestra present. Basisphenoid capsule and basipterygoid processes of different degrees of development. Basipterygoid articulation from mobile to fused. The middle ear region sometimes has osseous walls. Pterygoid processes of the vomer of different elongations. Vertebrae more often platycoelous. Clavicles and sternum sometimes present. Coracoids often small, scapulae narrow and with well-developed acromial process. The forelimbs are sometimes reduced. The manus is usually tridactyl, and digit III reduced to various degrees. Carpus of pulley or non-pulley construction. The pelvis is of the prepubic and opisthopubic dolichoiliac types, and more rarely altiliac. The hindlimbs are functionally tridactyl, pedal digit I is reduced to different degrees, digit II is sometimes recurved with a predatory claw. Late Triassic – Cretaceous.

Composition. 7 infraorders.

INFRAORDER COELUROSAURIA HUENE, 1914

Coelurosauria: Huene, 1914: p.154; Rozhdestvensky, 1956: 417; 1956: p.610; Tatarinov, 1964: 530; Barsbold, 1976b: p.74.

Coeluroidea: Nopsca 1928: p.183.

Diagnosis. Small, sometimes moderately large theropods. Prepubic pelvis.

Composition. 6 families – Podokesauridae Huene, 1914; Compsognathidae Huxley, 1870; Coeluridae Marsh, 1881; Saurornithoididae Barsbold, 1974; Elmisauridae Osmólska (in press); Avimimidae Kurzanov, 1981*.

The two last families are classified in this infraorder conditionally; their description by these authors was in press at the time of completion of this manuscript and therefore was not included in the systematic part.

Comparisons. The development of the prepubic pelvis appears to be a distinguishing peculiarity of coelurosaurs, with the greatest similarity to the ventral end of the deinonychosaur construction.

Distribution. Late Triassic – Cretaceous; North America, Western Europe, Central Asia.

FAMILY SAURORNITHOIDIDAE BARSBOLD, 1974

Saurornithoididae: Barsbold, 1974: p.7.

Diagnosis. Small to moderately large coelurosaurs. Skull small, with elongated facial region, highly extended antorbital fenestrae, basisphenoid capsule, and osseous middle ear region. Elongate, large maxillary fenestrae. Posterior part of external nares limited by the maxilla. Jugal slightly widened from the deviation of the posterior process. Small teeth, close together, predominately with posterior serrations. Caudal vertebrae lack ossified tendons. Pes with reversed digit II.

Composition. One genus – *Saurornithoides* Osborn, 1924.

Comparisons. Elongate skull with extended accessory antorbital fenestra and reversed pedal digit differentiate saurornithoidids from the similar coelurids and other coelurosaur families.

Discussion. The systematic position of saurornithoidids has remained unclear for some time. They have been supposed to fall with dromaeosaurids, and identified as an independent subfamily within them (Colbert and Russell, 1969; Osborn, 1969a, 1976a), and also classified with Troodontidae (Russell, 1948, 1969). However, the prepubic structure of the saurornithoidid pelvis clearly differentiates them from dromaeosaurids, which also have a pes with a reversed digit II (Barsbold, 1976a). The family Troodontidae, based on highly insufficient material (typical specimens include single teeth, distinct from the teeth of saurornithoidids; see Leidy, 1856), occupies an undefined (if valid at all) systematic position.

Distribution. Late Cretaceous; southern and southwestern Mongolia.

Genus *Saurornithoides* Osborn, 1924

Saurornithoides: Osborn, 1924: p.3; Barsbold, 1974: p.7.

Type Species: *Saurornithoides mongoliensis* Osborn, 1924; Upper Cretaceous, Djadokhta Formation; southern Mongolia.

Diagnosis. As for the family.

Composition. Two species – *Saurornithoides mongoliensis* Osborn, 1924 and *S. junior* Barsbold, 1974.

Distribution. Senonian; southern and southwestern Mongolia.

Saurornithoides mongoliensis Osborn, 1924

S. mongoliensis: Osborn, 1924: p.2; Figs. 3, 4.

Holotype. AMNH 6516; skull poorly preserved, with remains of the postcranial skeleton; Upper Cretaceous, Djadokhta Formation, Bayn-Dzak locality, southern Mongolia.

Diagnosis. Small saurornithoidid with 17-18 teeth in the upper and 27-28 in the lower jaw. 12 serrations along 5 mm of posterior edge of teeth.

Distribution. Lower Senonian; southern Mongolia.

Material. Holotype.

Saurornithoides junior Barsbold, 1974

S. junior: Barsbold, 1974: p. 8; Fig. 1-6, pl. 1, Fig. 1, pl. 2, pl. 3, pl. 4, Fig. 2-3.

Holotype. PST GIN AH MNR 100/1; incomplete skull and part of lower jaw; sacral vertebrae; incomplete series of caudal vertebrae; fragments of right tibia and metatarsus; Upper Senonian, Nemegtskaya Svita; Bugin-Tsav locality, southwestern Mongolia.

Diagnosis. Moderately large saurornithoidid with 19-20 teeth in the upper and 33-35 teeth in the lower jaw. 12 and 15-17 serrations along 5 mm of posterior edge of teeth.

Description. Skull with elongated, narrowing facial region. Maxillary fenestrae widen posteriorly. Premaxilla lacks ventral process. Maxilla limits the posteroventral part of the external nares and forms their ventrally widened, closed edges. In the base of the skull, a large, hollow basisphenoid capsule with a narrow frontal (basisphenoid) process is found, carrying a narrow longitudinal furrow dorsally that marks the base of the sphenethmoid. The hypophyseal cavity is located immediately above the posterior end of the furrow. Shortened, widened, horizontally-directed basipterygoid processes enter into the ventral end of the capsule, supposedly participating in the formation of the incurrent fenestrae for the parabasal canals. The large, elongated middle ear cavity is located in the lower part of the lateral walls of the cranium, and limited posteriorly by the paroccipital processes. At the medial wall, the middle ear cavity bears a series of foramina of which the posterior one borders directly on the closed wall of the paroccipital, and is identified as the foramen ovale. The exit for cranial nerve VII is located in the wall of the upper edge of the cavity, anterior to the foramen ovale. A large opening, supposedly identified with the opening for the basisphenoidal air sinuses, is found anterior and ventral to the foramen ovale, in the middle ear cavity. The large opening in the lateral wall of the braincase is immediately above the upper edge of the cavity, and is identified as the exit for cranial nerve V. The lateral wall is constructed from the prootic and laterosphenoid, which form an immobile articulation with the parietal. A small, unpaired bone is found anterior to the laterosphenoid, in the proximal end of the olfactory nerve passage, supposedly identified as the presphenoid.

The anterior section of the lower jaw is elongated and narrow, and composed mostly of the dentary. The splenial, with a large, posterior lower process and an elongate, V-shaped, narrow anterior end, bears the fenestra for entrance into Meckel's canal and extends to the symphysis. The teeth are small and close, and those most posterior are recurved, with smooth anterior and serrated posterior edges; 12 and 15-17 serrations are found along 5 mm of the upper and lower teeth. There are 19-20 teeth in the upper jaw, 33-35 in the lower.

There are six fused sacral vertebrae. Caudal vertebrae are platycoelous, lack ossified tendons, and are shortened proximally but increase in length distally. The chevrons of the proximal vertebrae are dorsoventrally elongated, while in the distal section they are gradually shortened up to the point of becoming flattened, elongated structures.

There is a mesotarsal joint of typical theropod appearance, represented by an astragalus with a high ascending process and a calcaneum connected to the distal end of the large tibia; this latter is closely adjacent to the end of the small, narrow fibula. The proximal metatarsus is thickened, the end of III is highly laterally compressed and displaced posteriorly, while the adjacent bones contact each other anteriorly.

Comparisons. Differentiated from *S. mongoliensis* by its larger size and greater tooth count.

Distribution. Upper Senonian; southwestern Mongolia.

Material. Besides the holotype, remains of the postcranial skeleton of another specimen, no. 100/2.

INFRAORDER DEINONYCHOSAURIA COLBERT ET RUSSELL, 1969

Deinonychosauria: Colbert and Russell, 1969: p.45; Barsbold, 1976b: p.74.

Diagnosis. Small to moderately large toothed theropods. Opisthopubic pelvis. Pes with reversed digit II.

Composition. Family Dromaeosauridae Matthew and Brown, 1922.

Comparisons. Opisthopubic pelvis and pes with reversed digit II serve as distinguishing signs for future deinonychosaurs from other theropods.

Distribution. Cretaceous; Central Asia, North America.

FAMILY DROMAEOSAURIDAE MATTHEW ET BROWN, 1922

Dromaeosaurinae: Matthew and Brown, 1922: p.367.
Dromaeosauridae: Ostrom, 1969b: p.11.

Type Genus. *Dromaeosaurus* Matthew and Brown, 1922.

Diagnosis. Skull varies in height. Basisphenoid capsule absent. Mobile basipterygoid articulation. Anterior and posterior sections of lower jaw ramus connected by coronoid. Caudal vertebrae with ossified tendons, and without pleurocoels. Clavicle absent. Pubis with laterally compressed, spherical distal end. Short ischium with large obturator process. Manus with pulley carpus. Pes with metatarsal III occasionally compressed.

Composition. Two subfamilies – Dromaeosaurinae Matthew and Brown, 1922 and Velociraptorinae, subfam. nov.

Discussion. The skull structure in dromaeosaurids corresponds completely in many ways to the general type observed in toothed theropods (coelurosaurs, carnosaurs), in which the basisphenoid capsule is usually absent and the basipterygoid articulation is mobile. As in tyrannosaurids, the coronoid connects the anterior and posterior sections of the lower jaw ramus; the clavicle is absent as in the majority of theropods. The pes is characterized by the development of a reversed digit II, also present in saurornithoidids. The greatest differentiating features of dromaeosaurids are related to the pelvic region, and expressed in the retroverted position of the pubis and the laterally compressed configuration of its distal edge. The strong ossification of caudal vertebral tendons is fairly specific, and not seen in other theropods.

Distribution. Cretaceous; North America, Central Asia.

SUBFAMILY DROMAEOSAURINAE MATTHEW AND BROWN, 1922

Dromaeosaurinae: Matthew and Brown, 1922: p.367.

Diagnosis. Moderately large dromaeosaurids with a high, relatively large skull.

Composition. Three genera – *Dromaeosaurus* Matthew and Brown, 1922; *Deinonychus* Ostrom, 1969; *Adasaurus* gen. nov.

Distribution. Cretaceous; North America, Central Asia.

Genus *Adasaurus* Barsbold, gen. nov.

Etymology. From ada, Mongolian – "evil" in national mythology.

Type Species. *Adasaurus mongoliensis* sp. nov.; upper Senonian, Nemegtskaya Svita; southwestern Mongolia.

Diagnosis. Ungual phalanges of reversed digit II highly reduced.

Composition. Monotypic genus.

Comparisons. *Adasaurus* is differentiated from other representatives of the subfamily by the high reduction of the "predatory" pedal ungual.

Distribution. Upper Senonian; southwestern Mongolia.

Adasaurus mongoliensis sp. nov.

Figs. 24a, 27a

Holotype. PST GIN AN MNR 100/20; incomplete skull and remains of the postcranial skeleton; upper Senonian, Nemegtskaya Svita; Bugin-Tsav locality, southwestern Mongolia.

Description. Metatarsal II considerably [thinned], "predatory" claw ungual of reversed digit II reduced to a size comparable to those of the supporting digits.

Discussion. The great similarity of *Adasaurus* to other representatives of the subfamily obviates the need for repeating the general skull features (see Colbert and Russell, 1969; Ostrom, 1969b). Additional distinctions may appear only in the general body proportions of the various dromaeosaurids.

Distribution. Upper Senonian; southwestern Mongolia.

Material. Besides the holotype, the hindlimbs and remains of the postcranial skeleton (lacking the anterior portion) of specimen 100/51.

SUBFAMILY VELOCIRAPTORINAE BARSBOLD, SUBFAM. NOV.

Diagnosis. Small dromaeosaurids with a low, relatively small skull.

Composition. One genus – *Velociraptor* Osborn, 1924.

Comparisons. Differentiated from dromaeosaurines by its smaller size and especially the small, low skull.

Distribution. Upper Cretaceous; Central Asia.

Genus *Velociraptor* Osborn, 1924

Velociraptor: Osborn, 1924: p.1.

Type Species. *Velociraptor mongoliensis* Osborn, 1924; Upper Cretaceous, Djadokhta Formation, southern Mongolia.

Diagnosis. See description of type.

Composition. Monotypic genus.

Distribution. Upper Cretaceous; southern Mongolia.

Velociraptor mongoliensis Osborn, 1924

V. mongoliensis: Osborn, 1924: p.1, Figs. 1-2; Sues, 1977: p.174, Fig. 2.

Holotype. AMNH 6515; partially destroyed skull and manual phalanges; lower Senonian, Djadokhtaskaya Svita; Bayn Dzak locality, southern Mongolia.

Description. Low skull with elongated facial region. Maxillary fenestrae small and spherical. Basipterygoid processes directed anteroventrally. Mobile basipterygoid articulation. Osseous middle ear cavity absent. Lateral walls of the cranium composed of the prootic and laterosphenoid, forming a mobile articulation with the parietal. An elongate furrow diverges from the foramen ovale, limiting the upper posterior part of the middle ear cavity and supposedly containing the stapes. A foramen for the facial nerve is found anteroventral to the foramen ovale. The coronoid bone forms a mobile, groove-like articulation with the articulation of the anterior and posterior jaw ramus. The teeth are relatively large, with large spaces between them, and anterior and posterior serrations. Slender postcranial skeleton. Ten cervicals, 13 dorsals, and five fused sacral vertebrae. With the exception of those most anterior, caudal prezygapophyses and chevrons have elongated ossified tendons, which are the ossified tendons of the caudal musculature. This ossified [sheath] stretches for a length of 8 to 10 vertebrae, and follows a compactly packed course placed symmetrically along the transverse processes. The sternum is flattened, large, and shaped like a shield. Narrow grooves for the articulation of the coracoids are developed on the dorsolateral edges of the sternum. Clavicles absent. Abdominal ribs consist of narrow lateral and medial segments. Scapulocoracoids with a spherical, widened coracoid part and a narrow, elongated scapular blade. Low, elongated ilium with an anterior process that is divided in two, and a thickened posteroventral edge. The pubis is elongated anteriorly, oriented posteroventrally, and has a laterally compressed distal end. Ischium shortened, parallel to the pubis, and has a large obturator process. Forelimbs not reduced, and humerus with a large deltoid crest. Carpus with a pulley construction, manus of "grasping" type. Metatarsal III is thinned along the shaft, and shorter than II and IV. Pedal digit II is of the reversed type, and bears a large "predatory" ungual phalanx.

Discussion. The low skull, widely spaced teeth, and slender postcranial skeleton distinguish *Velociraptor* from the dromaeosaurids and Deinonychus.

Distribution. Lower Senonian, Djadokhtaskaya Svita; Bayn-Dzak and Tugreen-Shire region; southern Mongolia.

Material. Complete skeleton with skull of one specimen (no. 100/25), and partially destroyed skull and remains of postcranial skeleton of another (no. 100/24).

INFRAORDER OVIRAPTOROSAURIA BARSBOLD, 1976

Oviraptorosauria: Barsbold, 1976: p.74.

Diagnosis. Small to moderately large toothless theropods with a shortened, curved beak. Lower jaws with large lateral cavities. Prepubic pelvis.

Composition. Two families – Oviraptoridae Barsbold, 1976 and Caenagnathidae Sternberg, 1940.

Comparisons. The curved shortened beak and low lower jaw with large lateral cavities differentiate oviraptorosaurs from all other theropods.

Distribution. Upper Cretaceous; Central Asia.

FAMILY OVIRAPTORIDAE, BARSBOLD 1976

Oviraptoridae: Barsbold, 1976a: p.685.

Type Genus: *Oviraptor* Osborn, 1924.

Diagnosis. Skull high and highly fenestrated, jaws with shortened occlusal region. Basisphenoid capsule absent. Vomers fused with jaw bones by means of paired, toothlike processes articulated with the pterygoid which separate the choanae. Immobile basipterygoid articulation. Lower jaw with highly convex occlusal edge and high adductor process. Dentary extension participates in the formation of the edge of the completely perforated mandibular fossa. Vertebrae, including caudals, have pleurocoels. Clavicle present. Pubis with small, boot-like distal end. Shortened ischium with a large obturator process. Manus with pulley carpus. In the pes, metatarsal IV is very slightly compressed proximally, and digit I is reduced.

Composition. Two subfamilies – Oviraptorinae Barsbold, 1976 and Ingeniinae Barsbold, 1981.

Discussion. Toothlessness is the only thing that characterizes both oviraptorids and ornithomimids. For the remaining [features], the these two groups are very highly differentiated. As in oviraptorids, the occlusal part of the jaw is shortened, the beak is massive, curved, and highly fenestrated, the basisphenoid capsule is absent, and the basipterygoid articulation was fused, while in ornithomimids the corresponding characters are exhibited in a completely opposite manner. The construction of the palatal complex in oviraptorids appears as that present among theropods and dinosaurs as a whole. The vomers are completely fused with the pterygoids, which is atypical of theropods. The differentiation in lower jaw construction between oviraptorids and ornithomimids is equally contrasting. In the postcranial skeleton, features unknown in other theropods are apparent in oviraptorids – the development of clavicles (posteriorly) of avian type, and also of pleurocoels along the entire vertebral column including the tail.

Distribution. Upper Cretaceous; southern and southwestern Mongolia.

SUBFAMILY OVIRAPTORINAE, BARSBOLD 1976

Oviraptoridae: Barsbold, 1976a: p.685.

Diagnosis. Moderately large oviraptorids with reduced manual digits II and III.

Composition. One genus – *Oviraptor* Osborn, 1924.

Distribution. Upper Senonian; southwestern Mongolia.

Genus *Oviraptor* Osborn, 1924

Oviraptor: Osborn, 1924: p.7; Barsbold, 1976: p.68.

Type Species. *Oviraptor philoceratops* Osborn, 1924; lower Senonian, Djadokhtaskaya and Barungoyotskaya Svita; southern and southwestern Mongolia.

Diagnosis. Oviraptorine with manual digits II and III exhibiting large, laterally compressed ungual phalanges.

Composition. Monotypic genus.

Distribution. Lower Senonian; southwestern Mongolia.

Oviraptor philoceratops Osborn, 1924

Oviraptor philoceratops: Osborn, 1924: p.7, Figs. 6-8; Barsbold, 1976b: p.68.

Holotype. AMNH 6517; incomplete skull and remains of postcranial skeleton; lower Senonian, Djadokhtaskaya Svita (Djadokhta Formation); Bayn-Dzak region (Shabarak-Usu); southern Mongolia.

Description. The premaxilla, comprising the basis of the upper half of a massive horny beak, forms the anterior part of a large, midline longitudinal crest with [ridged] walls, positioned above the external nares. The nasals and frontals participate in the construction of fenestrae in the posterior part. The anterior part of the dorsal crest bears narrow, paired longitudinal pockets (or foramina) that supposedly led to the canal inside the anterior edge of the crest. It is possible that the orbital branch of the facial nerve passed through them, along with the accompanying blood vessels. A tooth-like extension is positioned immediately posterior to the end of the paired, elongate grooves of the palatal surface, in the region of the vomers and palatine process of the maxilla. The extension was composed of paired, lamellar halves that broadened towards the base, pointed towards the top, convex externally, and medially flattened. The huge vomerine processes of the pterygoid enter in between the halves of the processes which separate the choanae. The pterygoids are extremely massive, ventrally concave, and have dropping external edges. The ascending process of the ectopterygoid rested at the bottom near the articular region of the jaw, the jugal, and the lacrimal. The narrow palatines were articulated posteriorly with the ectopterygoid, framing the internal nares anteriorly. From the anterior displacement of the ectopterygoid, the adductor fenestrae were highly longitudinally elongated. The articular surface of the quadrate forms two large, convex condyles, divided by a deep cavity. The basipterygoid processes are weakly developed, the anterior part of the pterygoid region of the articulation directly grasps the anteroventral part of the basicranium, which apparently was connected to it by an immobile articulation. The dentary forms a shortened, massive base for the horny beak with a [distinct] internal thickening, most convex in the symphyseal region and remarkable for its shortness. Two posteriorly elongated dentary processes frame the anterior half of the mandibular fenestra, which is displaced forwards and cord-like in shape. Posteriorly it is limited by the surangular, which extends forwards via a narrow, long process that subdivides the fenestra into two unequal parts. The coronoid process is located approximately midway down the length of the lower jaw, posterior to the mandibular fenestra. The articular joint surface is broadened, rounded in shape, and has a convex, elongate crest that divides the larger external and smaller internal surfaces. The retroarticular process is massive and elongate.

There are six sacral vertebrae. The caudal vertebrae are shortened, and pleurocoels are absent except in the very last. The sternum is composed of paired plate-like elements, connected sagittally. The furcula formed by the clavicles is U-shaped, with widely divergent branches, each of which is connected to the everted edge of the acromial surface of the scapula. The ilium has a widened anterior and narrow posterior process. The pubis has a narrow, strap-like distal end. The obturator process is widened into a U-shape, and is located midway down the bone. Metacarpal I is less than half as long as metacarpals II and III. The manual digits are elongated, with II and III nearly the same size and possessing the longest penultimate phalanges. The ungual phalanges are highly curved, laterally compressed, widened, and pointed distally, with large regions for attachment of the digital flexor ligaments.

Discussion. The specimens that are smaller in size are found in a more western area of the basic region, and the size distribution of *Oviraptor* is conditionally identified with adults in the younger age stages. The best preserved skull of one specimen (no. 100/36) does not show any sign of a wide, developed crest. It is possible that it was weakly expressed and not preserved in the excavated condition. The oviraptorid bony crest does is not reminiscent of the analogous crest in the cassowary, either by its general shape, the elements that comprise it, or its position on the skull. The fenestration of the bony crest wall in oviraptorids testifies to an external covering, composed of hard (horny) material. The friability of the bony crest wall suggests a rich blood supply, as usually exists in birds with the presence of an external horny covering, for example.

Distribution. Lower Senonian, Djadokhtaskaya and Barungoyotskaya (lower part) Svita; Bayn Dzak region (Shabarak-Usu) and Khermeen Tsav; southern and southwestern Mongolia.

Material. Skull and postcranial skeletons of two specimens (one, PST no. 100/42, in good condition), as well as skeletal remains of smaller specimens (supposedly those of younger age stages).

SUBFAMILY INGENIINAE BARSBOLD, 1981

Diagnosis. Small oviraptorids with highly reduced digits II and III.

Composition. One genus – *Ingenia* Barsbold, 1981.

Comparisons. Ingeniines are differentiated from oviraptorines by their considerably smaller size, and a manus with highly reduced digits II and III.

Distribution. Upper Senonian; southwestern Mongolia.

Genus *Ingenia* Barsbold, 1981

Ingenia: Barsbold, 1981: p.35.

Type Species. *Ingenia yanshini* Barsbold, 1981; upper Senonian, Barungoyotskaya Svita; southwestern Mongolia.

Diagnosis. Ingeniine with manual digits II and III bearing reduced, slightly curved ungual phalanges.

Composition. Monotypic genus.

Distribution. Upper Senonian; southwestern Mongolia.

Ingenia yanshini Barsbold, 1981

Ingenia yanshini: Barsbold, 1981: p.35, Fig. 10.

Holotype. PSY GIN AN MNR no. 100/30; lower jaw and incomplete postcranial skeleton; upper Senonian, Barungoyotskaya Svita, Khermeen Tsav locality; southwestern Mongolia.

Description. Metacarpal I less than half the length of II and III, and therefore highly reduced. In the tridactyl manus, digits II and III are progressively shorter than I and highly slender, although the number of phalanges remain complete. The distal phalanges are shortened and the unguals are insignificantly longer than the penultimate ones. The ungual phalanx of digit I is relatively slightly laterally compressed and more curved, while those of II and III are considerably narrower and less curved.

Discussion. The great similarity with *Oviraptor* arises from the repetition of those general features in the construction of the skull and postcranial skeleton that have already been mentioned in the description of the first species. In *Ingenia*, the bones were more massive than would have been expected given their smaller size. As a rule, the epiphyses are broader, wider, and thicker. The bony crest in *Ingenia* is not observed from the degree of preservation of the skull material (possibly it was completely absent).

Distribution. Upper Senonian; Barungoyotskaya Svita (upper part), Khermeen Tsav region and Bugin Tsav; southwestern Mongolia.

Material. Besides the holotype, the remains of the skull and postcranial skeletons of four specimens (nos. 100/30-100/33).

FAMILY CAENAGNATHIDAE STERNBERG, 1940

Caenagnathidae: Sternberg, 1940: p.81; Cracraft, 1971: p.805; Barsbold, 1981: p.36.

Diagnosis. Lower jaw with elongated, curved occlusal region and low coronoid process. The dentary process barely participates in the formation of the mandibular fenestra.

Composition. One genus – *Caenagnathus* Sternberg, 1940.

Comparisons. In caenagnathids, the occlusal region of the lower jaw is low, elongated, and has a curved dorsal edge, as well as a lower coronoid process in a position corresponding to the size of such features in oviraptorids. Besides that, in caenagnathids the dorsal process of the dentary is practically fully excluded from participation in the edge of the mandibular fenestra by the surangular, while in oviraptorids there is no similar phenomenon.

Discussion. In the beginning, caenagnathids were classified as birds (Sternberg, 1940; Russell, 1964; Cracraft, 1971), although their reptilian features were often stressed (Wetmore, 1956, 1960), which seemed sufficient for classifying them with ornithomimids (Romer, 1956). The peculiarity of the type of lower jaw construction, expressed in the features of the jaw articulation, the mandibular fossa, and the occlusal region, elicited controversial discussion surrounding the classification of caenagnathids with birds and also with dinosaurs (Wetmore, 1960; Cracraft, 1971), but the incompleteness of the material did not permit a well-founded conclusion. Only recently was attention focused on the amazing similarity between the lower jaws of caenagnathids and oviraptorids, which became possible through the discoveries of new specimens of the latter in Mongolia (Osmólska, 1976).

This similarity was considered so great by Osmólska that caenagnathids should not only be classified with theropods, but should be included within the oviraptorids. It was allowed that this group maintained a higher taxonomic rank (Osmólska, 1976); however, by the time that Osmólska's article was published, the family Oviraptoridae had already been established, although without consideration of caenagnathids in the infraorder Oviraptorosauria (Barsbold, 1976a, b). Caenagnathids were classified as theropods, and as a second family of oviraptorosaurs.

The elongation of the occlusal region and the lower coronoid process are also characteristic of the ornithomimid lower jaw, but have little in common with the specific features of similar structures in caenagnathids.

Distribution. Cretaceous; Canada.

Genus *Caenagnathus* Sternberg, 1940

Caenagnathus: Sternberg, 1940: p.81, Figs. 1-5; Wetmore, 1960: p.5; Cracraft, 1971: p.806, Figs. 1-2, pl. 92, Figs. 1-2.

Type Species. *Caenagnathus collinsi* Sternberg, 1940; Campanian, Oldman Formation; Alberta, Canada.

Diagnosis. See description of *C. collinsi* Sternberg, 1940.

Composition. Two species – *C. collinsi* Sternberg, 1940 and *C. sternbergi* Cracraft, 1971.

Distribution. Campanian; Alberta, Canada.

Caenagnathus collinsi Sternberg, 1940

Caenagnathus collinsi: Sternberg, 1940: p.81, Figs. 1-5; Wetmore, 1960: p.5; Cracraft, 1971: p.806, Figs. 1-2, pl. 92, Figs. 1-2.

Holotype. NCP 3605/8776; almost completely preserved lower jaw; Campanian, Oldman Formation; Steveville region, Alberta, Canada.

Description. The dentary occupies no more than 2/3 the entire length of the lower jaw. Its occlusal edge is equal and gently curved for its whole duration. As a result of the prolonged symphysis, occupying more than 1/4 the entire length of the lower jaw, its anterior part is elongate and concave, with shallow longitudinal furrows in its symphyseal surface that supposedly connected with a thickened mandibular covering. The low coronoid process is found at the level of the posterior third of the entire lower jaw length, and located approximately above the middle of the elongate, narrow mandibular fossa. Its dorsal external edge is formed by the surangular. The dentary process participates in the formation of the predominately anterior rear edge of the fossa.

The surangular articulation of the horizontally-directed dorsal process of the dentary has a complex forked, grooved character. In the lower jaw articulation, the longitudinal convexity divides the wider medial articular area from the greatly reduced lateral one. The retroarticular process is thickened. The prearticular has a V-shaped anterior process that extends to the level of the posterior end of the occlusal edge.

Discussion. It is expedient to give a more detailed comparison between the lower jaw of caenagnathids and oviraptorids than at the species level, in order to show their similarities and differences. As has been noted, the similarity between them consists of the development of two dentary processes, the presence of large mandibular fenestrae, unique coronoid processes, and also specifically the composition of the lower jaw articulation. In this framework, there are significant differences, which have been mentioned above.

Caenagnathids	**Oviraptorids**
gentle concavity along entire occlusal edge	small concavity along anterior edge, which is mostly convex
extensive symphysis	shortened symphysis
narrow, elongate mandibular fenestra	wide, rounded mandibular fenestra with two posterior sections
upper external edge of fenestra bounded by surangular	upper external edge of fenestra bounded by dentary only
adductor fossa 1/3 of lower jaw length, above middle of mandibular fenestra	adductor fossa on middle of lower jaw, posterior to mandibular fenestra
upper dentary ramus horizontal	upper dentary ramus arches up and back
anterior prearticular process beyond level of front of mandibular fenestra	anterior prearticular process at rear of mandibular fenestra
surangular does not divide mandibular fenestra	narrow, elongate process divides mandibular fenestra
mandibular fenestra displaced posteriorly	mandibular fenestra displaced anteriorly

Distribution. Campanian, Oldman Formation; Steveville region, Alberta, Canada.

Material. Holotype.

Caenagnathus sternbergi Cracraft, 1971

Caenagnathus sternbergi: Cracraft, 1971: p.806, Fig. 2.

Holotype. NMC 2690; posterior end of anterior lower jaw ramus; Campanian, Oldman Formation; Steveville region, Alberta, Canada.

Discussion. The extremely limited information on the second species, *C. sternbergi* Cracraft, 1971, renders its description inexpedient. It was identified according to a fragment of bone with the lower jaw articulation, and differentiated largely on proportions.

INFRAORDER CARNOSAURIA HUENE, 1920

Carnosauria: Huene, 1920: p.211; Romer, 1956: p.613; Barsbold, 1976b: p.74.
Deinodontoidea: Rozhdestvensky and Tatarinov, 1964: p.585.

Diagnosis. Gigantic carnivorous dinosaurs with large, toothed, high skull. Prepubic pelvis. Reduced forearms.

Composition. Four families – Megalosauridae Huxley, 1870; Ceratosauridae Marsh, 1884; Allosauridae Marsh, 1877; Tyrannosauridae Osborn, 1906.

Comparisons. The gigantic body dimensions and large, high skull clearly differentiate carnosaurs from other theropods. Carnosaurs are distinguished from deinocheirids by forearm reduction.

Distribution. Upper Jurassic – Cretaceous; North America, Europe, Asia.

FAMILY TYRANNOSAURIDAE OSBORN, 1906

Tyrannosauridae: Osborn, 1906: p.281.

Diagnosis. Basisphenoid capsule absent. Mobile basipterygoid articulation. Coronoid connects the separate anterior and posterior lower jaw sections. Pubis with large distal end. Ischium with proximally displaced obturator process. Clavicle absent. Highly reduced forearms. Manus lacks pulley carpus, and retains two digits. Metatarsal III highly compressed.

Composition. Eight genera – *Aublysodon* Leidy, 1868 (*Gorgosaurus* Lambe, 1914); *Albertosaurus* Osborn, 1905; *Tyrannosaurus* Osborn, 1906; *Alectrosaurus* Gilmore, 1933; *Tarbosaurus* Maleev, 1955; *Daspletosaurus* Russell, 1970; *Alioramus* Kurzanov, 1976.

Comparisons. Besides tyrannosaurids, absence of the basisphenoid capsule and the mobile basipterygoid articulation are noted only in allosaurids, and are supposed to exist in megalosaurids and ceratosaurids. Connection of the anterior and posterior lower jaw sections via the coronoid is known only in tyrannosaurids, but may be discovered in other carnosaurs. Clavicles are apparently absent in all carnosaurs. The distal ends of the pubis are proportionally greater than in other representatives of the group. The sharpest distinction of tyrannosaurids consists of the highly reduced forearms and two-fingered manus construction, representing [the highest] degree of reduction in this structure among carnosaurs. Tyrannosaurids are distinguished from allosaurids by a series of close features, such as a high proximal compression of metatarsal

III. The absence of horn-like extensions on the skull distinguished tyrannosaurids from ceratosaurids.

Distribution. Upper Cretaceous; North America, Central Asia.

Genus *Tarbosaurus* Maleev, 1955

Tarbosaurus: Maleev, 1955b: p.780, 1974: p.139; Rozhdestvensky and Tatarinov, 1964: p.539; Rozhdestvensky, 1965: p.101.

Type Species. *Tarbosaurus efremovi* Maleev, 1955; upper Senonian, Nemegtskaya Svita; southwestern Mongolia.

Diagnosis. See description of type species.

Composition. Monotypic genus.

Distribution. Upper Senonian; southwestern Mongolia.

Tarbosaurus efremovi Maleev, 1955

Tarbosaurus efremovi: Maleev, 1955b: p.780, Fig. 1.

Holotype. PIN no. 551-2; skull and postcranial skeleton; upper Senonian, Nemegtskaya Svita; southern Mongolia.

Description. Massive, high skull, laterally compressed. Relatively small maxillary fenestra. Premaxilla with ventral process. Large, high maxilla. Basisphenoid capsule absent. Basipterygoid processes massive, elongated, and directed anteroventrally. Mobile basipterygoid articulation. Parabasal canal and osseous middle ear absent. Lateral wall of braincase composed of three auditory bones and the laterosphenoid, which are connected by a complex suture with the temporal. The coronoid almost reaches the lower jaw symphysis, with a groove-like, mobile articulation that connects the anterior and posterior sections of the lower jaw. Large teeth with anterior and posterior serrations, and a blunt apex. The postcranial skeleton is remarkable for its gigantic size. Ten cervical vertebrae, 13 dorsals, and 5 sacrals. Caudal vertebrae with elongate prezygapophyses. Sternum absent. Scapulocoracoid relatively large, mostly at the expense of the elongated scapular blade. Fairly high [ilium], with [bifurcate] anterior and narrower posterior processes. Pubis with massive distal end, whose anteroposterior length reaches 2/3 the length of the shaft. Ischium slightly shorter than pubis, with a proximally placed obturator process and narrow distal end. The manus has a non-pulley carpus, with a reduced metacarpal III and remains of the basal phalanx of digit I. Metatarsal III highly laterally compressed, and practically excluded from the ankle joint.

Comparisons. According to absolute dimensions, *Tarbosaurus* can be completely equated with the American *Tyrannosaurus*, however the skull was less massive and more extended in the former, the configuration of the elements comprising the skull is somewhat different, and the teeth are highly laterally compressed. From the representatives of other closely related tyrannosaurid genera – *Albertosaurus* and *Daspletosaurus* – *Tarbosaurus* is differentiated by the general proportions, the absence of bony extensions from the skull, different relationships and configurations of the rostral and post-rostral skull regions, and the shape and construction of the teeth (Russell, 1970).

Discussion. Rozhdestvensky (1965) placed the various Mongolian tyrannosaurids into a single species, *Tarbosaurus bataar* (Maleev, 1955), which seems to merit attention in the context of new materials. At the same time, types existed that differed greatly from *Tarbosaurus* and also from *Tyrannosaurus*, because they have a larger skeleton and also different limb proportions, numbers of teeth, and details of skull construction, apparently on the example of *Alioramus* (Kurzanov, 1974). All this assumes a considerable variety in tyrannosaurids, and their Mongolian representatives in particular. However, systematic independence of some tyrannosaurids must be refined based on more complete materials.

The brevity of the given characteristics of *Tarbosaurus* is conditional on the details in the existing literature (Maleev, 1974).

Distribution. Upper Senonian; Nemegtu region, Bugin-Tsav, Ingeni-Khobur; southwestern Mongolia.

Material. Complete skull and well preserved postcranial skeleton of one specimen (no. 100/59), and also skull and skeletal fragments of others with varying preservation.

INFRAORDER ORNITHOMIMOSAURIA BARSBOLD, 1974

Ornithomimosauria: Barsbold, 1974: p.74.

Diagnosis. Toothless theropods of large size, with elongate, straight beak. Prepubic pelvis.

Composition. Two families – Ornithomimidae Marsh, 1890 and Garudimimidae Barsbold, 1981.

Comparisons. Differentiated from oviraptorosaurs by their larger size and elongate, straightened beak.

Distribution. Cretaceous; North America, Central Asia.

FAMILY ORNITHOMIMIDAE MARSH, 1890

Ornithomimidae: Marsh, 1890: p.84.

Diagnosis. Moderately large to large ornithomimosaurs. Precaudal vertebrae with pleurocoels. Elongate ischium. Elongate metatarsus, with compressed metatarsal III. Pedal digit I absent.

Composition. Five genera – *Ornithomimus* Marsh, 1890; *Struthiomimus* Osborn, 1917; *Dromiceiomimus* Russell, 1972; *Archaeornithomimus* Russell, 1972; *Gallimimus* Osmólska, Roniewicz, and Barsbold, 1972.

Distribution. Lower (Aptian-Albian) and Upper Cretaceous; North America, Central Asia.

Genus *Gallimimus* Osmólska, Roniewicz, and Barsbold, 1972

Gallimimus: Osmólska, Roniewicz, and Barsbold, 1972: p.105.

Type Species. *Gallimimus bullatus* Osmólska, Roniewicz, and Barsbold, 1972; upper Senonian, Nemegtskaya Svita; southwestern Mongolia.

Diagnosis. See description of species.

Composition. Monotypic genus.

Distribution. Upper Senonian; southwestern Mongolia

Gallimimus bullatus Osmólska, Roniewicz, and Barsbold, 1972

Gallimimus bullatus Osmólska, Roniewicz, and Barsbold, 1972: p.105, Figs. 1-18, pls. 29-53.

Holotype. GIN AN MNR no. 100/11; skull and incomplete postcranial skeleton; Upper Senonian; Nemegtskaya Svita, Tsagan-Khushu locality; southwestern Mongolia.

Description. Skull with basisphenoid capsule open posteriorly, located anterior to the basipterygoid base and covering the interpterygoid cavity dorsally. As a result of this, the basisphenoid is additionally connected to the pterygoid by the ventral part of the capsule, which must have partially dislocated the basipterygoid articulation. Considerably reduced interpterygoid cavity. Incurrent opening of the parabasal canal located anterior to the basipterygoid processes. The bony base of the beak is elongated, and slightly broadened. The splenial does not reach the symphysis. Coronoid absent. 10 cervical, 13 dorsal, and 6 sacral vertebrae. Caudal vertebrae with elongated prezygapophyses. Precaudal vertebrae have pleurocoels. Clavicle and sternum absent. Scapulocoracoid with elongated scapula. [Ilium] with complete anterior and narrower posterior processes, the latter with parallel dorsal and ventral edges. Pubis elongated, with proximally displaced obturator process and hook-like, curved distal end. Humerus with weakened deltopectoral crest. Carpus of non-pulley type, metacarpals nearly subequal in size, and ungual phalanges slightly bent.

Comparisons. Ornithomimids represent a group generally fairly similar in construction, distinctions in which appear mainly in the proportions of skeletal elements. Thus, in *Gallimimus* the ratio of the length of the caudal to dorsal vertebrae (85%) is greater than in other genera (in *Struthiomimus*, for example, this ratio is approximately 76%). The sacrals in *Gallimimus* are also differentiated by their great elongation relative to the length of the femur. Besides these, in the Mongolian form the neural arches of the sacral vertebrae do not completely fuse even in mature specimens, in contrast to those observed in *Ornithomimus* and *Struthiomimus*. The ratio of the forearm to the arm reaches 66% in *Gallimimus*, while in the American forms listed it is 70% and even 91% (in *Dromiceiomimus*).

Discussion. The basisphenoid capsule is established only in Mongolian ornithomimids, but its presence has also been supposed in the American species, and not yet discovered purely because of the degree of preservation of the material.

Distribution. Upper Senonian; Nemegtskskaya region, Bugin-Tsav and Ingeni-Khobur; southwestern Mongolia.

Material. Besides the holotype, skulls and postcranial skeletons (nos. 100/10 and 100/12) and fragmentary remains of several specimens.

FAMILY GARUDIMIMIDAE, BARSBOLD 1981

Garudimimidae: Barsbold, 1981: p.30.

Diagnosis. Fairly large ornithomimosaurs. Precaudal vertebrae lack pleurocoels. Shortened ischium. Shortened metatarsus with metatarsal III almost uncompressed. Digit I present.

Composition. One genus – *Garudimimus* Barsbold, 1981.

Comparisons. Garudimimids are sharply differentiated from ornithomimids by the retention of pedal digit I, the shortened metatarsus, and the barely compressed metatarsal III.

Distribution. Upper Cretaceous; Central Asia.

Genus *Garudimimus* Barsbold, 1981

Garudimimus: Barsbold, 1981: p.30.

Type Species. *Garudimimus breviceps* Barsbold, 1981. Cenomanian-Turonian, Baynshirenskaya Svita; southeastern Mongolia.

Diagnosis. [Ilium] high, with considerably narrowed posterior process. Tarsal 3 presumably connected with the proximal articular surface of metatarsal III.

Composition. Monotypic genus.

Distribution. Upper Cretaceous; southeastern Mongolia.

Garudimimus brevipes Barsbold, 1981

Garudimimus brevipes: Barsbold, 1981: p.30, Figs. 1-4.

Holotype. PST GIN AN MNR no. 100/13; skull, fragments of the axial skeleton, pelvis and incomplete limbs; Cenomanian-Turonian, Baynshirenskaya Svita; Bayshin-Tsav locality; southeastern Mongolia.

Description. Basisphenoid capsule open posteriorly, connected with the medial edges of the pterygoid, covering the reduced interpterygoid cavity dorsally. Basipterygoid articulation supposedly immobile. Incurrent opening of the parabasal canal limited laterally by the ventral edge of the quadrate flange of the pterygoid, posteriorly by the pterygoid process, and medially and ventrally by the basisphenoid capsule. The canal is shortened and directed initially ventrally, then enters into the space between the quadrate flange of the pterygoid and the base of the basisphenoid capsule. From here, there is possibly a passage lining the pterygoid capsule more dorsally, between the front posterior edge of the quadrate flange and the ventrolateral part of the capsule. The ectopterygoid has the appearance of a ventrally widened, V-shaped lamina. In the lower jaw, the splenial has a V-shaped end and does not reach the symphysis. The coronoid is absent. The retroarticular process is widened, with an indentation open dorsally. Dorsal and sacral vertebrae lack pleurocoels. Six sacral vertebrae. In the first sacral, the rib is separated from the diapophysis and contacts the medial surface of the [ilium] with its distal end. The [ilium] is high anteriorly, has a dorsal edge with a rounded, convex shape, and is slightly shorter than the pubis. The posterior process of the ilium is narrowed, with parallel dorsal and ventral edges. Femur slightly shorter than the tibia. Two tarsals (3 and 4), of which 3 rested mostly on the proximal articular surface of metatarsal III and only partly on that of II. Tarsal 4 fully connected with metatarsal IV. Five compositional elements in the pes: three basic (II, III, IV) and two residual (I, V) metatarsals. Metatarsal I with reduced, distally V-shaped shaft, laterally adjoining metatarsal II. The distal head has a convex articular surface, directed ventromedially. Of the three basic elements, metatarsal II is more shortened, its proximal end is widened anteriorly, and it is narrowed posteriorly. Metatarsal III is the most elongated and thickened, slightly curved distally, almost not highly compressed proximally, and fully divides the adjoining metatarsals. Metatarsal IV is intermediate in length between II and III, with a broad proximal end. The distal end of the bone has convex articular surfaces divided weakly by a furrow. Metatarsal V is highly reduced to the condition of a narrow, laterally compressed rudiment, attached to the side of metatarsal IV. Pedal digit I is the most reduced, with its ungual phalanx notably laterally compressed. The phalanges of each digit are progressively smaller distally, a trend most clearly expressed in digit IV. Its ungual phalanx (the ungual phalanges are not known for the other digits) has a flattened ventral surface.

Discussion. The skull of *Garudimimus* is similar in many ways to that of *Gallimimus*, especially in the development and construction of the basisphenoid capsule, open posteriorly. In the latter, the epipterygoids were successfully defined as so-called basipterygoid rami of the pterygoid (Osmólska, Roniewicz, and Barsbold, 1972). The parabasals are similarly constructed in representatives of both families. The shortening of the ischium and metatarsus, the lack of compression of metatarsal III and its complete separation of II and IV (which do not contact each other), and the connection of tarsal 3 mostly with the proximal articular surface of metatarsal III serve as basic differentiating signs of garudimimid features.

The laterally closed basisphenoid capsule, supposedly blocked by the pterygoid articulation, and a similar type of parabasal canal are characteristic of saurornithoidids, in addition to *Garudimimus* and *Gallimimus*. The construction of the pes in *Garudimimus* has many features that are widely spread throughout theropods in general. To them is relegated the development of digit I, the shortened metatarsus, and the lack of proximal compression of metatarsal III. These signs testify to the primitive nature of garudimimids, inasmuch as ornithomimids exhibit features of much higher specialization.

Distribution. Lower Senonian; southeastern Mongolia.

Material. Holotype.

INFRAORDER DEINOCHEIROSAURIA BARSBOLD, 1976

Deinocheirosauria: Barsbold, 1976b: p.7.

Diagnosis. Gigantic theropods (supposedly with a moderately-sized skull) with non-reduced shoulder region, and forearm with large claws.

Composition. Two families – Therizinosauridae Maleev, 1954 and Deinocheiridae Osmólska and Roniewicz, 1970.

Comparisons. Differentiated from other large theropods (particularly carnosaurs) by the non-reduced shoulder region, and forearms with large claws.

Distribution. Upper Cretaceous; Central Asia.

FAMILY DEINOCHEIRIDAE OSMÓLSKA AND RONIEWICZ, 1970

Deinocheiridae: Osmólska and Roniewicz, 1970: p.5.

Diagnosis. Forelimb epiphyses moderately widened, deltopectoral crest weakly developed, manus supported by non-pulley carpus, metacarpals nearly subequal in size and with fairly massive, curved ungual phalanges.

Composition. One genus – *Deinocheirus* Osmólska and Roniewicz, 1970.

Discussion. In their original description, deinocheirids were classified with the superfamily Megalosauroidea Walker, 1964, part of the infraorder Carnosauria, although the authors (Osmólska and Roniewicz, 1970) noted features of considerable differentiation. [Recently] this position has been reexamined, in connection with the refinement of the dimensions of the [theropod] infraorders (Barsbold, 1976b).

The weakening of the forelimbs and the subequal metacarpals are characteristic of ornithomimids, however the large overall dimensions and the massive, curved ungual phalanges serve as distinguishing characters of deinocheirids.

Distribution. Upper Cretaceous; southwestern Mongolia.

Genus *Deinocheirus* Osmólska and Roniewicz, 1970

Deinocheirus: Osmólska and Roniewicz, 1970: p.7.

Type Species. *Deinocheirus mirificus* Osmólska and Roniewicz, 1970; Upper Senonian, Nemegtskaya Svita; southwestern Mongolia.

Diagnosis. See familial diagnosis.

Composition. Monotypic genus.

Deinocheirus mirificus Osmólska and Roniewicz, 1970

Deinocheirus mirificus: Osmólska and Roniewicz 1970: p.8, Figs. 1-4, pls. 1-5.

Holotype. PST GIN AN MNR no. 100/18; right and left humeri, right and left forearm, right and left carpus, manual phalanges (right ungual phalanx is missing).

Description. Scapula length 1190 mm (left side), with moderately widened ventral part, moderately large acromial process, and narrowed, elongated dorsal ramus. The posterior of the thickened edge of the ventral widening becomes thinner anteriorly. The dorsal ramus of the scapula has more or less parallel anterior and posterior edges. The coracoid is 340 mm long and moderately widened; its external edge is slightly convex. The coracoid foramen is rounded on the lateral edge, and has the appearance of a deep furrow on the medial surface. The attachment site for the biceps muscle corresponds to a weakly expressed, gently sloping convexity. The glenoid cavity is shallow, and slightly laterally directed. The supraglenoid thickening has the appearance of a slight concavity.

The humerus is elongated (938 mm), with a relatively thin shaft and moderately widened proximal end. The deltopectoral crest is relatively low, extending approximately one-third the length of the entire bone from the proximal end. The distal end of the humerus is slightly widened, and somewhat flattened anteroposteriorly. The condyles are positioned more distally. The epicondyles are weakly developed. The ulna is elongate (688 mm), relatively slender, and with moderately widened extensions. The proximal articular surface of the bone is slightly differentiated, and participates in the formation of a shallow, weakened elbow joint. The radius is 630 mm in length, slender, weakly curved anteriorly, and has insignificantly widened articular ends. The metacarpus consists of three elements. Metacarpal I is 214 mm long, is the most shortened, massive, flattened dorsoventrally, and has two sections of the proximal articular surface. The distal articular head is asymmetrical, so its cavity is displaced ventrally. Medially, the lateral-connecting cavity is deep, while laterally it is shallow. Metacarpal II is 230 mm long, with a slightly concave proximal articular surface with a quadrilateral outline. The distal articular head is convex, with a ventrally displaced, weakly expressed sagittal cavity. The lateral-connecting cavity is fairly deep. Metacarpal III is 246 mm long and the [thinnest], with a three-sectioned articular surface. The distal articular head has a larger lateral condyle and a deep sagittal cavity. The medial-connecting cavity is more shallow than the lateral one.

Digit I is more massive, with an elongated phalanx 1 (320 mm). Its proximal articular surface is concave, and the distal head is symmetrically divided by a furrow with deep lateral-connecting cavities. The basal phalanges of digits II and III are considerably shortened (140 mm and 110 mm, respectively), and have concave proximal surfaces and symmetrical distal heads with shallow lateral-connecting cavities. Phalanx 2 of digit III is shorter (104 mm) and [thinner] than phalanx 1, with a convex sagittal crest of the proximal articular surface. The penultimate phalanges of digits II and III (226 mm and 186 mm, respectively) have narrow, elongated shafts that form well-developed, ginglymoid articulations. The ungual phalanges are massive, laterally compressed, highly curved, pointed distally, and slightly decreasing in size in digit order. The proximal articular surfaces have convex crests.

Discussion. Presently known large ungual phalanges, found separately (Ricqles, 1967; Rozhdestvensky, 1970), are more or less similar to those of deinocheirosaurs, although they have apparently differences in details of shape and construction. The large sizes of separately found phalanges have not completely decided the question of these similarities and differences. Mostly likely, there existed gigantic carnivorous dinosaurs with unusually large claws and non-reduced forelimbs that were possibly not classified with deinocheirosaurs. *Deinocheirus* probably surpassed *Chilantaisaurus* (Hu, 1964) in the size of the humerus and also in its basic distinguishing features – the configuration and dimensions of the deltopectoral crest, etc.

The supposed absence of the pulley-type carpus in deinocheirids is confirmed by the peculiarities of the construction of the proximal articular surfaces of the metacarpals, as well as in the general functional weakening of the forelimb, which in this is reminiscent of ornithomimids and tyrannosaurids, in which the pulley carpus is [also] not developed.

Distribution. Upper Senonian; Altan-Ula and Ingeni-Khobur regions; southwestern Mongolia.

Material. Holotype.

FAMILY THERIZINOSAURIDAE MALEEV, 1954

Therizinosauridae: Maleev, 1954: p.106; Barsbold, 1976b: p.76.

Diagnosis. Forelimb epiphyses considerably widened, deltopectoral crest highly developed, manus with pulley carpus, metacarpals equal in size and huge, laterally compressed ungual phalanges.

Composition. One genus – *Therizinosaurus* Maleev, 1954.

Comparisons. Based on the large size of the bones of the forelimbs and shoulder region, therizinosaurids are most similar to deinocheirids, but distinguished by the features of functional strengthening of the forelimb (widening of the epiphyses, high development of deltopectoral crest, pulley carpus), as well as the dimensions and peculiarities of the carpus construction and ungual phalanges.

Discussion. Therizinosaurids were originally described on the basis of three ungual phalanges (two of them fragmentary) and supposed identified as gigantic sea turtles, similar to protostegids from the Upper Cretaceous of North America. The "turtle-like lizard", as Maleev called it (1954), earned a classification as a central Asiatic family of turtles in the opinions of the first investigators. Sukhanov (1964) classified *Therizinosaurus* with turtles incertae sedis. Rozhdestvensky (1970), based on the comparison of different types of ungual phalanges, considered it possible to classify therizinosaurids with the carnivorous dinosaurs. The finding of *Deinocheirus* played an important role, as one more representative of large-clawed theropods. In the work dedicated to *Deinocheirus* (Osmólska and Roniewicz, 1970), the classification of therizinosaurids with theropods was also mentioned. The non-reduced forelimbs and shoulder region of therizinosaurids contrasts with those of other large theropods, in which similar structures are subjected to increasing reductions. In this manner, therizinosaurids were similar to small theropods, with evolved without forelimb reduction.

Therizinosaurids are now classified within the present infraorder conditionally, only on the basis of forelimb dimensions. They may form a lineage not closely related to deinocheirids.

Distribution. Upper Cretaceous; southwestern Mongolia.

Genus *Therizinosaurus* Maleev, 1954

Therizinosaurus: Maleev, 1954: p.106; Sukhanov 1964: p.425; Barsbold 1976b: p.78.

Type Species. *Therizinosaurus cheloniformes* Maleev, 1954; upper Senonian, Nemegtskaya Svita; southwestern Mongolia.

Diagnosis. See familial description.

Composition. Monotypic genus.

Therizinosaurus cheloniformes Maleev, 1954

Therizinosaurus cheloniformes: Maleev, 1954: p.106, Fig. 1; Sukhanov, 1964: p.425; Barsbold, 1976a: p.78, Figs. 1-10.

Holotype. PIN no. 551-483; three manual ungual phalanges (two of them incomplete); Upper Senonian, Nemegtskaya Svita; Nemegtu region, southwestern Mongolia.

Description. Scapula 670 mm long (*note*: the measurements here and below were made on the right forelimb elements and the anterior half of the shoulder region, which were almost completely preserved), with a highly widened ventral part, a wide acromial process, and a narrow, relatively short, and flattened dorsal blade. The posterior edge of the ventrally widened scapula is highly thickened, and the acromion is thin, apparently becoming transformed into a cartilaginous framework along its periphery. A rounded foramen is located near the anterior edge of the scapular widening and near the scapulocoracoid fissure, not noted in other theropods, through which blood vessels and nerves supposedly passed. The dorsal blade of the scapula has nearly parallel anterior and posterior edges. The coracoid is 360 mm long, with a widened, convex external surface that forms a gently sloping concavity in the region of the scapulocoracoid fissure which turns towards the scapular widening. Along the periphery of the coracoid, especially near the scapulocoracoid fissure, this edge become very thin and possibly turns into cartilage, as is the case with the scapular edge. The coracoid foramen is large, and cuts across the bony material above the coracoid portion of the glenoid. The attachment point for the biceps muscle is marked by a large tubercle with a shortened top. The glenoid cavity is deep and wide, slightly turned externally, and has convex, thickened, crest-like edges. The supraglenoid thickening, shaped like a convex crest, is divided along the top of the scapulocoracoid fissure.

The humerus is 760 mm long, massive, and has a highly widened proximal end. The deltoid crest is tall and very thickened, and its top is located approximately one-third of the distance from the proximal end of the humerus, while the length of the crest is no less than two-thirds the length of the entire bone. The distal end of the humerus is highly widened, and flattened anteroposteriorly. The condyles are extended onto the anterior side of the distal widening. The epicondyles are highly widened, and extend beyond the limits of the articular block surfaces. The ulna has an elongated shaft (620.2 mm) and a widened ulnar process. The proximal articular surface of the bone is divided into two parts: the lateral has a triangular outline, is limited dorsally by the fossa for the proximal end of the radius, and is slightly concave; the medial forms a semilunar fossa that covers the lunar condyle of the humerus. The widened, thickened distal end of the ulna is inturned approximately 30° relative to the plane of the proximal end. The radius is 550.4 mm long and slightly sigmoidally curved, with a widened, laterally flattened proximal end and a massive, thickened distal end.

The carpus consists of a pulley in which two distal carpals take part. The first distal carpal is 82.3 mm tall and 85.3 mm wide, with two articular surfaces on its distal end. Medially, it is triangular in outline and adjoins the proximal surface of metacarpal I, occupying somewhat less than the lateral area, which is compressed in configuration and adjoins the articular surface of metacarpal II. The two surfaces noted above are divided by an obliquely-oriented process that is formed when they cross. The proximal surface of the first distal carpal is convex, and divided by a wide transverse fossa that forms the articular surface of the pulley trough. The lateral edge of the bone has a right-angled fenestra that closely accommodates the edge of the second distal carpal, which has a height of 56.0 mm and a width of 59.3 mm. For this, the dorsal edge of considerably thickened, while it is narrowed ventrally. The transverse fossa is not expressed on the proximal surface of distal carpal 2. The distal surface is flattened. Upon articulation of the two carpal bones, the articular surface of the pulley continues from the first to the second. The proximal carpal bone that entered the pulley trough is not preserved.

The manus is composed of three elements. Metacarpal I is 145.5 mm long, and is the shortest, highly widened, and flattened obliquely. Its lateral side is wider, particularly the proximal part, and the medial edge is very narrow. The proximal articular surface of metacarpal I has a tripartite construction. The distal articular head is asymmetric, and turns medially from the left, with wide, deep sagittal fossae. The lateral connecting fossae are very weakly expressed. Metacarpal II is 286.8 mm long, is the most elongated and massive, and has a slanted, rectangular, flattened proximal articular surface. The articular surface of the distal head has nearly symmetrical condyles, and is divided by a wide, deep sagittal fossa. The lateral connecting fossae are very weakly expressed. Metacarpal III is 191.6 mm long, has the most slender shaft, and exhibits a tripartite proximal articular surface. The distal articular head is highly asymmetrical, with deep, wide sagittal fossae. The lateral connecting fossae are very weakly expressed.

Only digit II of the right manus, consisting of three phalanges is represented completely in the collection. The basal and penultimate phalanges are subequal in length (141.7 and 143.8 mm, respectively) and shape, as well as massive and shortened. The proximal articular surfaces are nearly symmetrical, and have a convex sagittal crest that is higher in the basal phalanx. The dorsal edge of the sagittal crest is highly protruding and thickened, and is the site for attachment of the extensor tendons. The distal heads of the phalanges are almost symmetrical, and the sagittal fossa is considerably wider and deeper in the basal phalanx compared with the penultimate one. The lateral connecting fossae are weakly expressed, forming crest-like protruding edges for the articular condyles. The ungual phalanges are of gigantic size (approximately 520 mm in length), moderately curved, very wide, highly laterally compressed, narrow in transverse cross-section, and lanceolate in outline. The distal ends are pointed (preserved in a fragment of ungual phalanx PST 100/16). The proximal articulation of the ungual phalanx is symmetrical and has a transverse ridge that divides the surface into two unequal parts, with the upper sagittal crest more convex than the lower. The dimensions of the individual ungual phalanges (PST nos. 100/16, 100/17) testify to the possibility that they belong to manual digits I and III, respectively.

Discussion. Currently finds of large ungual phalanges are known from different regions – Kazakhstan, trans-Baikal, Nigeria (Rozhdestvensky, 1970; Ricqles, 1967) – but these are almost three times smaller in length than those of *Therizinosaurus*. Besides this, there are more than small differences in shape and degree of curvature in corresponding phalanges. The large ungual phalanges, previously identified as belonging to the manus of *Alectrosaurus* (Gilmore, 1933), probably do not belong to this taxon (Perle, 1977) and, therefore, questions about the similarity of this structure in *Therizinosaurus* and *Alectrosaurus* (Rozhdestvensky, 1970) can be entirely put aside. *Chilantaisaurus* also has a similar, large ungual phalanx (Hu, 1964), however its differentiation from those of *Therizinosaurus* is very clear. The specific construction of the forelimb in *Therizinosaurus* testifies to the fact that it cannot be identified with *Chilantaisaurus* and *Alectrosaurus*. Until more complete materials of *Therizinosaurus* were found, this was considered possible (Barsbold, 1970). The discovery of several large ungual phalanges testifies towards the variety of gigantic carnivorous dinosaurs with non-reduced forelimbs, although notable different from *Therizinosaurus*.

Distribution. Upper Cretaceous; southwestern Mongolia.

Material. PST GIN AN MNR no. 100/15; right and left scapulocoracoid (left is poorly preserved), right and left humeri, right forearm and left ulna, two right distal carpals, right manus with phalanges of digit II, among them the ungual phalanx as well. Fragments of dorsal and abdominal ribs. no. 100/17; an ungual phalanx lacking the distal portion. no. 100/16; an ungual phalanx lacking the proximal portion.

INFRAORDER SEGNOSAURIA BARSBOLD ET PERLE, 1980

Segnosauria: Barsbold and Perle, 1980: p.187.

Diagnosis. Toothed theropod of moderate to large size. Opisthopubic, altiliac pelvis. Pes not compact in construction.

Composition. Segnosauridae Perle, 1979 and Enigmosauridae fam. nov.

Comparisons. The altiliac, opisthopubic pelvis and the non-compact, avian construction of the pes sharply differentiate segnosaurs from other theropods.

Distribution. Upper Cretaceous; Central Asia.

FAMILY SEGNOSAURIDAE PERLE, 1979

Segnosauridae: Perle, 1979: p.45.

Diagnosis. Lower jaw compressed anteriorly. Large, elongated cervical vertebrae. Pubis with laterally compressed, ellipsoidal obturator process.

Composition. Two genera – *Segnosaurus* Perle, 1979 and *Erlicosaurus* Perle, 1980.

Distribution. Upper Cretaceous; southeastern Mongolia.

Genus *Segnosaurus* Perle, 1979

Segnosaurus: Perle, 1979: p.45; Barsbold and Perle, 1980: p.188.

Type Species. *Segnosaurus galbinensis* Perle, 1979; Upper Cretaceous, Baynshirenskaya Svita; southeastern Mongolia.

Diagnosis. Mandibular teeth are small, compactly positioned, slightly bent anteriorly, and straight posteriorly. The anterior lower jaw has a small diastema. Pedal ungual phalanges are slightly laterally compressed.

Composition. Monotypic genus.

Comparisons. See comparisons for type species.

Distribution. Upper Cretaceous; southeastern Mongolia.

Segnosaurus galbinensis Perle, 1979

Segnosaurus galbinensis: Perle, 1979: p.46, Figs. 1-7; Barsbold and Perle, 1980: Fig. 1.

Holotype. PST GIN AN MNR no. 100/90; lower jaw, remains of the humerus, forearm, separate manual phalanges and unguals, almost complete pelvis, incomplete right femur, remains of carpus, incomplete caudal vertebrae; Upper Cretaceous (Cenomanian-Turonian), Baynshirenskaya Svita; Amtgai locality, southeastern Mongolia.

Description. Occlusal edge of the lower jaw is slightly concave anteriorly. Dentary with large angular process. Splenial does not reach symphysis, and has elongate, wing-like, narrow anterior and angular processes. Anterior and posterior sections of lower jaw do not have a groove articulation. Weakly expressed coronoid process. Narrow symphysis. 24-25 teeth in each mandibular ramus. Anterior teeth are slightly recurved, while posterior are smaller and slightly straight. Edentulous area in anterior lower jaw corresponds to the width of approximately four presymphyseal teeth. Caudal vertebrae with disproportionately massive centra and low neural arches. Six fused sacral vertebrae with widened centra and highly elongated transverse processes. Unequal, relatively narrow processes reach the dorsal edge of the [ilium] and fuse [to the] top. Proximal caudal vertebrae platycoelous, with large centra, long neural arches, and massive zygapophyses. Prezygapophyses turned dorsomedially and widely separated, postzygapophyses directed somewhat ventrally and externally. Posterior caudal vertebrae have short, massive centra.

Coracoids very wide with [rectangular] outline. Attachment point for biceps muscle clearly indicated by a rise. Small coracoid foramen. Straight, proximally flattened scapula. Acromial process sharply expressed and elongated along the entire contact with the coracoid. Dorsal and distal edges of scapula subparallel. Lower distal end of scapula forms a large part of glenoid cavity, directed posterolaterally.

Forelimbs somewhat shortened. Massive humerus with widened epiphyses. Deltopectoral crest displaced proximally, and moderately developed. Ulna considerably more massive and slightly longer than radius. Olecranon process highly developed. Manus supposed to be tridactyl, with highly curved, laterally compressed ungual phalanges. The ilia are widely positioned, with a tall, laterally curved preacetabular process, and a highly curved exterior. Postacetabular process is highly reduced, with the upper part occupied by a sharply protruding, large process that is tube-like in outline, the upper surface of which corresponds to the dorsal edge of the blade. The pubis is directed posteroventrally, with an elongated, flattened shaft that bears a medial crest on the posterior symphyseal edge. The distal end has an ellipsoidal shape and a protruding anterior portion, is laterally compressed, and has a narrow dorsal symphyseal edge. Ischium parallel to and much shorter than the pubis, with a widened distal end. Obturator process subrectangular in outline, and connected to the posterior medial crest of the pubis above its distal end. A round, low, longitudinal crest-like projection is located on the posterior edge of the ischium, across from the obturator process. Pubic peduncle of ischium shortened. Proximal pubic opening large, with open edges, and formed to a large extent by the ilium and pubis. Femur with weak sigmoidal curvature. It has a massive head and elongated neck. Fourth trochanter found somewhat above midshaft. Tibia slightly shorter than femur. Astragalus with relatively short ascending process that is wide at its base. Calcaneum massive, relatively large, and possibly did not fuse with the astragalus. Pes shortened, metatarsus massive and has wide ends, with the proximal ends forming a very compact structure. Metatarsal I is the most shortened, participating in the formation of the laterally widened proximal articular surface of the pes. Metatarsal V rudimentary. Digit I the most shortened, II and III nearly subequal in size, and IV the [thinnest]. The phalanges of the three main digits are very similar in construction, relatively shortened, and massive. In digit IV, phalanges 2 and 3 are highly shortened, while the ungual phalanges are curved and slightly laterally compressed.

Discussion. In many basic features, *Segnosaurus* is distinct from other carnivorous dinosaurs. The nature of the construction of the lower jaw and teeth, the disproportionately massive and elongated cervical vertebrae, the unusual construction of the pelvis as expressed by altilia and the retroverted pubes, and the shortened and non-compact structure of the tarsus and entire pes all define the great peculiarity of segnosaurids, differentiating them from all other theropods.

Distribution. Upper Cretaceous (Cenomanian-Turonian), Baynshirenskaya Svita; Amtgai region, Khara-Khutul, Bayshin-Tsav and Urilbe-Khuduk, southeastern Mongolia.

Material. Besides the holotype, fragments of postcranial skeletons (including a pelvis) from two specimens (PST GIN AN MNR no. 100/87, 100/88).

Genus *Erlicosaurus* Perle, 1980

Erlicosaurus: Barsbold and Perle, 1980: p.190.

Type Species. *Erlicosaurus andrewsi* Perle, 1980; Upper Cretaceous (Cenomanian-Turonian), Baynshirenskaya Svita; southeastern Mongolia.

Diagnosis. Mandibular teeth are small and closely positioned. Rostral part of lower jaw is edentulous. Pedal ungual phalanges are highly laterally compressed.

Composition. Monotypic genus.

Comparisons. See comparisons for type species.

Distribution. Upper Cretaceous; southeastern Mongolia.

Erlicosaurus andrewsi Perle, 1980

Erlicosaurus andrewsi: Barsbold and Perle, 1980: p.190, Fig. 2.

Holotype. PST GIN AN MNR no. 100/111; skull, individual cervical vertebrae, incomplete hindlimbs; Upper Cretaceous, Baynshirenskaya Svita; Bayshin-Tsav locality, southeastern Mongolia.

Description. Skull with moderately elongated facial region. Highly elongated external nares. Intermaxillary bones in the very anterior part, occlusal edge of the lower jaw edentulous and supposedly covered with a horny beak. Basisphenoid capsule absent, but the anterior part of the basicranium is very wide in dimensions and has a well-developed system of intracranial sinuses. Basipterygoid processes reduced, and basipterygoid articulations blocked. Parabasal canals formed by the basipterygoid processes, the anterior part of the basisphenoid, and the pterygoid. Articulation of the vomers with the basisphenoid is conditionally constructed along a paleognathous line. Posterior processes of vomers are lamellar, ventrally fused along the midline, and form a V-shaped transverse cross-section. Posteriorly, the reach the basisphenoidal rostrum and are connected with it; at the same time, the posterior end of the vomerine processes forks, covering the ventral opening of the rostrum. The lower jaw is narrowed and slightly concave anteriorly. Mandibular fenestra elongated. Dentary with large angular process. Splenial with triangular-ending anterior and angular processes, and does not reach the symphysis. Coronoid absent. Adductor fossa large and elongated. Coronoid process weakly expressed. Symphysis shortened. 31 small, straight teeth in each mandibular ramus, the anterior ones remarkable in being larger in size than those posteriorly.

The cervical vertebrae are disproportionately large, elongated, and have low neural arches. Humerus somewhat shortened, with a moderately large deltopectoral crest. [All] metatarsals are massive, with widened ends (including the proximal end), and form a non-compact structure. Metatarsal I is shortened, and participates in the formation of the laterally elongate proximal articular surface of the pes. Metatarsal [V] is rudimentary. Pedal digit I is the most shortened, II and III are subequal in size, and IV is the most slender. The phalanges of pedal digits I-III are fairly similar in construction, relatively shortened, and have wide articular surfaces. Phalanges 2 and 3 are highly shortened and disc-like in digit I. Ungual phalanges are relatively large, curved, and slightly laterally compressed.

Comparisons. Similarities between *Erlicosaurus* and *Segnosaurus* include the construction of the lower jaw and teeth, the disproportionately large caudal vertebrae, the clear degree of shortening of the forelimbs, and the non-compact pedal structure. At the same time, the smaller and straighter teeth, the large diastema in the anterior lower jaw, the edentulous portion of the lower jaw, and the highly compressed pedal ungual phalanges clearly differentiate *Erlicosaurus* from *Segnosaurus*.

Discussion. The similarities between *Erlicosaurus* and *Segnosaurus* show their undoubtedly related nature, and clearly distinguish them from other carnivorous dinosaurs. It is not possible to compare them exactly based on the materials of both genera, and it is possible that in reality the differences between *Erlicosaurus* and *Segnosaurus* may turn out to be more basic, as supported by such characteristic signs as the shape of the pedal ungual phalanges, etc.

Distribution. Upper Cretaceous; southeastern Mongolia.

Material. Holotype.

FAMILY ENIGMOSAURIDAE BARSBOLD ET PERLE, FAM. NOV.

Diagnosis. Pubis with narrow, shoe-like distal end, and ischium with narrow obturator process.

Composition. One genus – *Enigmosaurus* Barsbold et Perle, gen. nov.

Comparisons. The unique shoe-like shape of the distal pubis and the narrow obturator process clearly distinguish enigmosaurids from segnosaurids.

Distribution. Upper Cretaceous; southeastern Mongolia.

Genus *Enigmosaurus* Barsbold et Perle, gen. nov.

Etymology. From ενιγμα, Greek – mysterious.

Type Species. *Enigmosaurus mongoliensis* Barsbold et Perle, sp. nov.; Upper Cretaceous (Cenomanian-Turonian), Baynshirenskaya Svita, southeastern Mongolia.

Diagnosis. Pubis and ischium narrow, anterior presymphyseal region of distal pubis has an elongated indentation.

Composition. Monotypic genus.

Comparisons. See the "Discussion" section in the description of the type species.

Distribution. Upper Cretaceous; southeastern Mongolia.

Enigmosaurus mongoliensis Barsbold et Perle, sp. nov.

Holotype. PST GIN AN MNR no. 100/84; pelvis lacking ilia (only bases are preserved); Upper Cretaceous (Cenomanian-Turonian), Baynshirenskaya Svita; Khara-Khutul locality, southeastern Mongolia.

Description. Pelvis moderately large. Ilia widely positioned. Anterior iliac blades bent externally, posterior blades reduced, a large cubic process present in the posterior dorsal region. Pubic peduncles of ilium are elongated, [ischial] peduncles are shortened. Pubis reoriented posteroventrally, with elongated, laterally narrow, but not flattened shaft. Distal end of pubis elongated and shoe-shaped, narrowed anteriorly and posteriorly. Presymphyseal region of distal end with wide longitudinal (sagittal) indentation that continues onto the anterior portion of the shaft. Ischium parallel to pubis, slightly shorter, and with a narrow shaft. Obturator process displaced distally, elongated, highly narrowed, fuses tightly to the pubis, and is considerably higher than the distal end. Posterior edge of ischium has a weak longitudinal process across from the obturator process. Trochanteric fossa is large, with open edges. No more than six sacral vertebrae present, with highly elongate transverse processes.

Discussion. Similar features in the pelvis of enigmosaurids and segnosaurids include the following: elongated anterior and posterior [iliac blades] (basic indications of altilia), development of a large shoe-like process on the posterior [distal pubis], widely positioned [ilia] with an outward curvature, highly elongated sacral transverse processes, orientation of the pubes (opisthopuby), and the distal position of the obturator process. These features support a single type of construction for both pelvic structures. Differentiating features of the pelvis of *Enigmosaurus* include the absence of lateral flattening of the pubis and ischium, and the entirely different construction and shape of the distal end of the pubis; highly unique characteristics include the considerable narrowing of the anterior and posterior part of the distal pubis, the longitudinally widened indentation in the presymphyseal region of the anterior shaft and the dorsal edge of the distal end; the highly narrowed and elongated obturator process is also characteristic. The noted features of the pelvis of *Enigmosaurus* in many ways sharply distinguish it not only from segnosaurids, but also from other theropods. The differences in the pelvis of *Enigmosaurus* are entirely sufficient to warrant its classification within an independent taxon of family rank.

It has been suggested that the studied pelvis may belong to an erlicosaurid, because this structure is unknown so far. It is difficult to deny such a possibility, however the established similarity between *Segnosaurus* and *Erlicosaurus* is so great that it does not permit considering the presence of a different pelvic construction among them.

Distribution. Upper Cretaceous; southeastern Mongolia.

Material. Holotype.

SUMMARY

A detailed, comparative anatomical analysis of the most important elements that comprise the skull and postcranial skeleton of the later carnivorous dinosaurs is presented in this work, and this study is based on the rich new materials of Mongolian dinosaurs that have contributed to the wide comparative study of Central Asian theropods and the classification of their place and historical evolution in worldwide dinosaurian communities. First, this analysis has a representative, comparative morphological basis that allows examination of a series of phenomena in order to determine the construction of the various major lineages of carnivorous dinosaurs. Attention is paid to the expressions of similarity among a wide variety of theropods, with the goal of developing a more general morphological characterization of the entire group throughout their long evolutionary history.

1. Specific features are identified in the construction of the skull that reflect the wide variety within the framework of theropod structural types: the varying degrees of development of the basisphenoid capsule are linked genetically to the system of sinuses in determining the construction of the basicranium; the osseous structure of the avian-type middle ear; the construction of the palatal complex, deviating from the common reptilian plan in the formation of supposedly derivative paleognathous features; and the construction of the parabasal canals, often connected with the development of the basisphenoid capsule.

Modifications of the theropod lower jaw are characterized, among which the oviraptoroid, segnosauroid, and partial segnosauroid types are distinguished according to the high degree of uniqueness that sets them apart from other theropod groups.

2. The peculiarities of skull construction in theropod types defines their inner cranial mobility as presumably metakinetic, with corresponding deviations in a large series following the complete exclusion of mobility.

3. The following differentiations are found in the postcranial skeleton of carnivorous dinosaurs: a sternum constructed similarly to that of acarinate birds; modification of the forelimbs characterized by pulley and non-pulley carpus constructions; avian-type clavicles, specifically connected with the pectoral girdle (as in *Archaeopteryx*).

4. Among theropods the prepubis and opisthopubic types of pelvis construction, based on the dolichoiliac type, are identified along with the altiliac type, which represents a significant deviation from the theropod norm. The pelvis of *Archaeopteryx* is characterized by opisthopubic dolichoilia. Basic modifications of the theropod pes are also examined.

5. The functional characteristics of the axial skeleton of carnivorous dinosaurs are presented, defining the distinct mobility of the forelimbs which perform the basic "grasping" function to a varying degree and effectiveness, as well as that of the hindlimbs which are bipedal throughout their construction. The more dynamic position of the body in carnivorous dinosaurs, relative to what has been previously accepted, is also examined.

6. The classification of carnivorous dinosaurs offered in this work is based on the division into paleopods and theropods, studying the latter as a single saurischian lineage that evolved progressively throughout the greater part of the Mesozoic. This scheme

includes seven infraorders that link 19 families (plus two families of indeterminate position), of which four infraorders and nine families are identified predominately on the Mongolian materials.

7. Aspects of evolution in carnivorous dinosaurs are analyzed, along with identification of family type of the most ancient Saurischia – paleopods and theropods – that evolved in a parallel manner in a series of features. The early foundations of the main evolutionary tendencies in theropods is based on the perfection of bipedalism, and the evolution of other predatory features is connected with it. Morphological evolution in theropods lineages was defined as [a series of] parallel specializations that led, in later stages, to a variety that amazes the imagination. There are also many deviations in the evolution of small theropods, conditional to their displacement into special adaptive zones, of which segnosaurids may serve as an example. However, thanks to this variety, the unity of all lineages of theropods is clearly illustrated.

The information accumulated until now testifies clearly enough against theropod "diphyly" – only carnosaurs and coelurosaurs – and their position in this representation of theropod evolution supports the conception of multi-lineage, parallel evolution in carnivorous dinosaurs.

The possible family types of theropods are examined, both [in size] among dinosaurs and archosaurs in general, as well as *Archaeopteryx*. The possibility of a repeated structural reformation in the theropod pelvis is allowed, illustrating its high plasticity and the possible path of origination of the ornithischian pelvis from the saurischian, and thus supporting the monophyly of dinosaurs.

A whole complex of avian or proto-avian [structures] are diffusely distributed in parallel lineages of carnivorous dinosaurs, marking a clear "ornithization" that leads ultimately to birds. Archaeopteryx could not have avoided the theropod stage of evolution, and it represents one of the parallel lineages evolving on the general [saurischian] base, reflecting its kinship with birds.

8. A high degree of indigenous evolution is substantiated for the Central Asiatic group of carnivorous saurischians during the later stages of their evolution. Similarly, the intensive faunal exchange with North America at the end of the Mesozoic did not lead to major deviations in their composition and evolution.

9. The complex of narrowly specialized morphological features is analyzed in a series of theropods, allowing their functional interpretation and basing the identification of the major ecological types of carnivorous dinosaurs.

10. Regional and intercontinental (with North America) correlations are shown among the stratigraphic horizons of the Cretaceous of the MPR, on the basis of complexes of theropods and other faunal groups during the Aptian/Albian-Lower Maastrichtian interval, inclusive (all five basic consequential horizons).

11. A systematic description of the factual material, which lies at the base of this work, is constructed based on a monographic collection of Mongolian theropods that most completely represents the wide variety of later lineages of carnivorous dinosaurs. Compact and, at the present time, exhaustive information about the taxonomy of different ranks is included in the summary. The definition of the suborder Theropoda, as well as the characteristics of the seven infraorder, 10 families, four subfamilies, 14 genera, and 16 species are examined among their number.

BIBLIOGRAPHY

Abel, O. 1909. Neuere Anschauungen über den Bau und die Lebensweiseder Dinosaurier. *Verh. Zoologische Bot. Geschichte Vienna* 59: 117-123.

Abel, O. 1919. *Die Stämme der Wirbeltiere.* Berlin & Leipzig: 914 pp.

Andrews, R. C. 1927. Explorations in Mongolia. *Geographic Journal* 69(1): 1-23.

Bakker, R. T. 1971a. Dinosaur physiology and the origin of mammals. *Evolution* 25(4): 626-658.

Bakker, R. T. 1971b. The ecology of brontosaurs. *Nature* 229(5281): 172-174.

Bakker, R. T. 1972. Anatomical and ecological evidence of endothermy in dinosaurs. *Nature* 238: 81-85.

Bakker, R. T. 1974. Endothermy, dinosaurs, and *Archaeopteryx*. *Evolution* 28(3): 502-503.

Bakker, R. T. 1975a. Dinosaur renaissance. *Scientific American* 232(4): 58-78.

Bakker, R. T. 1975b. Experimental and fossil evidence for the evolution of tetrapod bioenergetics. In D. M. Gates and R. B. Schmerl (eds.), *Perspectives of Biophysical Ecology.* Springer Verlag, New York: 365-399.

Bakker, R. T. and P. M. Galton. 1974. Dinosaur monophyly and a new class of vertebrates. *Nature* 248: 168-172.

Barsbold, R. 1970.

Barsbold, R. 1972a.

Barsbold, R. 1972b.

Barsbold, R. 1974. Saurornithoididae, a new family of small theropod dinosaurs from Central Asia and North America. *Palaeontologica Polonica* 30: 5-22.

Barsbold, R. 1976. A new Late Cretaceous family of small theropods (Oviraptoridae n. fam.) in Mongolia. *Doklady Akademii Nauk SSSR* 226(3): 685-688.

Barsbold, R. 1977. Kinetism i osobennosti stroenia chelustnogo apparata u oviraptorov (Theropoda, Saurischia). *Trudy Sovm. Sov. Mong. Pal. Exped.* 4: 34-47.

Barsbold, R. 1977. O evolutsiy chishcheich dinosavrov. *Trudy Sovm. Sov. Mong. Pal. Exped.* 4: 48-56.

Barsbold, R. 1979. Opisthopubic pelvis in the carnivorous dinosaurs. *Nature* 279: 792-793.

Barsbold, R. 1981. [Predatory toothless dinosaurs from Mongolia.] *Trudy Sovm. Sov. Mong. Pal. Exped.* 15: 28-39.

Barsbold, R. and A. Perle. 1979. Modiphikatsiy tasa sayrisziy i parallelinoe rasvitie zishchnich dinosavrov. *Trudy Sovm. Sov. Mong. Pal. Exped.* 8: 39-44.

Barsbold, R. and A. Perle. 1980. Segnosauria, a new infraorder of carnivorous dinosaurs. *Acta Palaeontologica Polonica* 25(2): 187-195.

Barsbold, R., Voronin, and Shegallo. 1971.

Beliaeba, Trofimov, and Reshetov. 1974.

Bennett, A. F. 1974. A final word. *Evolution* 28(3): 503.

Bennett, A. F. and B. Dalzell. 1973. Dinosaur physiology: a critique. *Evolution* 27: 170-174.

Berkey, C. P. and F. K. Morris. 1922. Important results of the Central Asiatic Expeditions. *Natural History* 26(5): 527-534.

Bock, W. J. 1960.

Bock, W. J. 1964. Kinetics of the avian skull. *Journal of Morphology* 114: 1-42.

Bock, W. J. 1969.

Bohlin, B. 1953. Fossil reptiles from Mongolia and Kansu. *Report of the Scientific Expedition to the Northwest Provinces of China, Publication 37(6), Vertebrate Paleontology* 6: 1-113.

Bonaparte, J. F. 1969.

Borsuk-Bialynicka, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologica Polonica* 37: 5-64.

Brown, B. and E. M. Schlaikjer. 1940. The origin of ceratopsian horn-cores. *American Museum Novitates* 1065: 1-7.

Brett-Surman, M. K. 1979. Phylogeny and palaeobiogeography of hadrosaurian dinosaurs. *Nature* 277: 560-562.

Budiko, M. I. 1978. [The thermal regime of dinosaurs.] *Zhurnal Obs. Biol*. 39: 179-188.

Budiko, M. I. 1979.

Camp, C. L. 1936. A new type of small bipedal dinosaur from the Navajo Sandstone of Arizona. *University of California Publications Bulletin of the Department of Geological Sciences* 24(2): 39-56.

Camp, C. L. and S. P. Welles. 1956.

Casamiquela, R. M. 1967. Un nuevo dinosaurio ornitisquio (*Pisanosaurus mertii*; Ornithopoda) de la formacion Ischigualasto, Argentina. *Ameghiniana* 5(2): 47-64.

Casier, E.. 1960. *Les Iguanodons de Bernissart*. Institute Royale des Sciences Naturelles de Belgique, Bruxelles: 134 pp.

Chao, S. 1962. On a new species of psittacosaur from Laiyang, Shantung. *Vertebrata PalAsiatica* 6(4): 349-360.

Charig, A. 1970.

Charig, A. 1972. The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. In K. A. Joysey and T. S. Kemp (eds.), *Studies in Vertebrate Evolution*. Oliver & Boyd, Edinbugh: 121-155.

Charig, A. 1973. Jurassic and Cretaceous dinosaurs. In A. Hallam (ed.), *Atlas of Palaeobiogeography*. Elsevier: 339-352.

Charig, A. J., J. Attridge and A. W. Crompton. 1964. On the origin of the sauropods and the classification of the Saurischia. *Proceedings of the Linnean Society of London* 176(2): 197-221.

Cobban and Reeside. 1952.

Colbert, E. H. 1964. The Triassic dinosaur genera *Podokesaurus* and *Coelophysis*. *American Museum Novitates* 2168: 1-12.

Colbert, E. H. 1970. A saurischian dinosaur from the Triassic of Brazil. *American Museum Novitates* 2405: 1-39.

Colbert, E. H. and D. A. Russell. 1969. The small Cretaceous dinosaur *Dromaeosaurus.* *AMerican Museum Novitates* 2380: 1-49.

Cracraft, J. 1971. Caenagnathiformes, Cretaceous birds convergent in jaw mechanism of dicynodont reptiles. *Journal of Paleontology* 45(5): 805-809.

Crompton, A. W. and A. Charig. 1962. A new ornithischian from the Upper Triassic of South Africa. *Nature* 196: 1074-1077.

Dashzeveg, D. 1975.

de Beer, G. R. 1954. *Archaeopteryx* and evolution. *Advancements in Science* 11: 160-170.

de Beer, G. R. 1956. The evolution of ratites. *Bulletin of the British Museum of Natural History, Zoology* 4: 57-70.

de Beer, G. R. 1964. *Archaeopteryx.* In L. Thomson (ed.), A New Dictionary of Birds. London: 58-62.

Elements of Paleontology. 1964.

Efremov, I. A. 1949. [The preliminary results of the first Mongolian paleontological expedition of the USSR Academy of Sciences in 1946.] *Trudy Mongol. Comissii Akademiy Nauk SSSR* 38: 5-28.

Efremov, I. A. 1954a. Nekotorye eamechaniya po voprosam istoricheskogo raevitiya dinosavrov. *Trudy Paleontologicheskogo Instituta Akademiy Nauk SSSR* 48:125-141.

Efremov, I. A. 1954b.

Farlow, J. O. 1976a. A consideration of the trophic dynamics of a Late Cretaceous large-dinosaur community (Oldman Formation). *Ecology* 57:841-857.

Farlow, J. O. 1976b. Speculations about the diet and foraging behavior of large carnivorous dinosaurs. *American Midland Naturalist* 95(1): 186-191.

Feduccia, A. 1973. Dinosaurs as reptiles. *Evolution* 27: 166-169.

Feduccia, A. 1974. Endothermy, dinosaurs, and *Archaeopteryx.* *Evolution* 28: 503-504.

Fox, R. C. 1970. A bibliography of Cretaceous and Tertiary vertebrates from western Canada. *Bulletin of Canadian Petrology and Geology* 18(2): 263-281.

Fox, R. C. 1971a.

Fox, R. C. 1971b.

Frazzetta, T. H. 1962. A functional consideration of cranial kinesis in lizards. *Journal of Morphology* 111(3): 287-319.

Galton, P. M. 1970a. Ornithischian dinosaurs and the origin of birds. *Evolution* 24(2): 448-462.

Galton, P. M. 1970b. The posture of hadrosaurian dinosaurs. *Journal of Paleontology* 44(3): 464-473.

Galton, P. M. 1971. The mode of life of *Hypsilophodon*, the supposedly arboreal ornithopod dinosaur. *Lethaia* 4(4): 453-465.

Galton, P. M. 1972. Classification and evolution of ornithischian dinosaurs. *Nature* 239: 464-466.

Gilmore, C. W. 1909. Osteology of the Jurassic reptile *Camptosaurus*, with a revision of the species of the genus, and descriptions of two new species. *Proceedings of the United States National Museum* 36: 197-332.

Gilmore, C. W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum* 110: 1-154.

Gilmore, C. W. 1933. On the dinosaurian fauna of the Iren Dabasu Formation. *American Museum Novitates* 671(2): 23-78.

Grabau. 1923.

Gradzinsky, R. 1970. Sedimentation of dinosaur-bearing Upper Cretaceous deposits of the Nemegt Basin, Gobi Desert. *Paleontologica Polonica* 21: 147-229.

Gradzinsky, R, J. Kazmierczak, and J. Lefeld. 1969. Geographical and geological data from the Polish-Mongolian palaeontological expeditions. *Paleontologica Polonica* 19: 33-82.

Gradzinsky, R, Z. Kielan-Jaworowska, and T. Maryanska. 1977.

Granger, W. and W. K. Gregory. 1923. *Protoceratops andrewsi*, a pre-ceratopsian dinosaur from Mongolia. *American Museum Novitates* 72: 1-9.

Gregory, W. K. 1927. The Mongolian life record. *Science Monthly* 24: 169-181.

Hay, O. P. 1908. On certain genera and species of carnivorous dinosaurs, with special reference to *Ceratosaurus nasicornis* Marsh. *Proceedings of the United States National Museum* 35: 351-366.

Hu, S.-y. 1964. Carnosaurian remains from Alashan, Inner Mongolia. *Vertebrata PalAsiatica* 8(1): 42-63.

Huene, F. v. 1909. Skizze zu einer Systematik und Stammesgeschichte der Dinosaurier. *Centralblatt für Mineralogie, Geologie und Paläontologie* 1909: 12-22.

Huene, F. v. 1914. Saurischia and Ornithischia. *Geological Magazine* 9(1): 444-445.

Huene, F. v. 1914. Das natürliche System der Saurischia. *Centralblatt für Mineralogie, Geologie und Palätontologie* 1914: 154-158.

Huene, F. v. 1915. Beiträge zur Kenntnis einiger Saurischier der schwäbischen Trias. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 1915(1): 1-27.

Huene, F. v. 1920. Stammesgeschichtliche Ergebnisse einiger Untersuchungen an Trias-Reptilien. *Zeitschrifte Undukt. Amstamm. Vererbungsl*. 24: 159-163.

Huene, F. v. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monogr. Geol. Pal*. I, 4 (pts. 1 & 2): 1-361.

Huene, F. v. 1942.

Huene, F. v. 1956.

Hughes. 1963.

Janensch, W. 1935.

Kalandadze, N. N. and S. M. Kurzanov. 1974. [Lower Cretaceous localities of terrestrial vertebrates in Mongolia.] *Trudy Sovm. Sov. Mong. Pal. Exped.* 1: 288-295.

Kielan-Jaworowska, Z. 1974a.

Kielan-Jaworowska, Z. 1974b.

Kielan-Jaworowska, Z. and R. Barsbold. 1972. Narrative of the Polish-Mongolian paleontological expeditions, 1967-1971. *Paleontologica Polonica* 27: 5-13.

Krebs, V. B. 1963. Bau und Funktion des Tarsus eines Pseudosuchiens aus der Trias des Monte San Giorgio. *Palaontologische Zeitschrifte* 37: 88-95.

Krebs, V. B. 1965.

Krebs, V. B. 1973. Die Archosaurier. *Naturwissenschaften* 61(1): 17-24.

Kuhn, O. 1965. Saurischia (Supplementum I). *Fossilum Catalogus I Animalia* Pars 109: 94 pp.

Kuhn, O. 1966. *Die Reptilien. System und Stammesgeschichte.* Krailling b. Munchen, Oeben: 154 pp.

Kurzanov, S. M. 1976. Brain-case structure in the carnosaur *Itemirus* n. gen. and some aspects of the cranial anatomy of dinosaurs. *Paleontological Journal* 1976(3): 361-369.

Lefeld. 1965.

Lefeld. 1971.

Lull, R. S. 1933. A revision of the Ceratopsia or horned dinosaurs. *Memoirs of the Peabody Museum of Natural History* 3(3): 1-175.

Madsen, J. H., Jr. 1974. A new theropod dinosaur from the Upper Jurassic of Utah. *Journal of Paleontology* 48(1): 27-31.

Madsen, J. H., Jr. 1976a. *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineral Survey Bulletin* 109: 1-163.

Madsen, J. H., Jr. 1976b. A second new theropod dinosaur from the Late Jurassic of east central Utah. *Utah Geology* 3(1): 51-60.

Maleev, E. A. 1954. Noviy cherepachoobrazhniy yashcher v Mongolii. *Priroda* 1954(3): 106-108.

Maleev, A. E. 1955a. Chishchnie dinosavri Mongolii. *Priroda* 1955(6): 112-115.

Maleev, A. E. 1955b. [The gigantic carnivorous dinosaurs of Mongolia.] *Doklady Akademii Nauk SSSR* 104(4): 634-637.

Maleev, A. E. 1955c. [New carnivorous dinosaurs from the Upper Cretaceous of Mongolia.] *Doklady Akademii Nauk SSSR* 104(5): 779-782.

Maleev, E. A. 1974. Gigantskie carnosavri semeystva Tyrannosauridae. *Trudy Sovm. Sov. Mong. Pal. Exped.* 1: 132-193.

Marinov. 1957.

Marsh, O. C. 1881. A new order of extinct Jurassic reptiles (Coeluria). *The American Journal of Science* 21: 339-343.

Marsh, O. C. 1884. Principal characters of American Jurassic dinosaurs. Part VIII. The order Theropoda. *The American Journal of Science* 27: 329-340.

Martinson. 1973.

Martinson. 1975.

Martinson and Shuvalov. 1973.

Martinson, Sochava, and R. Barsbold. 1969

Maryanska, T. 1977. Ankylosauridae (Dinosauria) from Mongolia. *Paleontologica Polonica* 37: 85-151.

Maryanska, T. and H. Omsólska. 1974. Pachycephalosauria, a new suborder of ornithischian dinosaurs. *Paleontologica Polonica* 30: 45-102.

Maryanska, T. and H. Omsólska. 1975. Protoceratopsidae (Dinosauria) of Asia. *Paleontologica Polonica* 33: 135-181.

Matthew, W. D. 1915.

Matthew, W. D. and B. Brown. 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Bulletin of the American Museum of Natural History* 46(6): 367-385.

Miller. 1969.

Moberly. 1960.

Morris, F. K. 1936. Central Asia in Cretaceous time. *Bulletin of the Geographic Society of America* 47: 1477-1534.

Novozhilov. 1954.

Nowinski, A. 1971. *Nemegtosaurus mongoliensis* n. gen., n. sp. (Sauropoda) from the uppermost Cretaceous of Mongolia. *Palaeontologica Polonica* 25(Results of the Polish-Mongolian Palaeontological Expeditions - Part III.): 57-81.

Olshevsky, G. 1978. The archosaurian taxa (excluding the Crocodilia). *Mesozoic Meanderings* 1: 1-50.

Osborn, H. F. 1906. *Tyrannosaurus*, an Upper Cretaceous carnivorous dinosaur. *Bulletin of the American Museum of Natural History* 21: 259-265.

Osborn, H. F. 1912. Crania of *Tyrannosaurus* and *Allosaurus*. *Memoirs of the American Museum of Natural History. New Series* 1(1): 1-30.

Osborn, H. F. 1917. Skeletal adaptations of *Ornitholestes, Struthiomimus, Tyrannosaurus*. *Bulletin of the American Museum of Natural History* 35(43): 733-771.

Osborn, H. F. 1924a. Three new Theropoda, *Protoceratops* zone, central Mongolia. *American Museum Novitates* 144: 1-12.

Osborn, H. F. 1924b. Sauropoda and Theropoda from the Lower Cretaceous of Mongolia. *American Museum Novitates* 128: 1-7.

Osmólska, H. 1976. New light on the skull anatomy and systematic position of *Oviraptor*. *Nature* 262A: 683-684.

Osmólska, H. 1981. Coossified tarsometatarsi in theropod dinosaurs and their bearing on the problem of bird origins. *Palaeontologica Polonica* 42: 79-95.

Osmólska, H. and E. Roniewicz. 1970. Deinocheiridae, a new family of theropod dinosaurs. *Palaeontologica Polonica* 21: 5-19.

Osmólska, H., E. Roniewicz and R. Barsbold. 1972. A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. *Palaeontologica Polonica* 27: 103-143.

Ostrom, J. H. 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. *Bulletin of the American Museum of Natural History* 122(2): 33-186.

Ostrom, J. H. 1964.

Ostrom, J. H. 1969a. A new theropod dinosaur from the Lower Cretaceous of Montana. *Postilla* 128: 1-17.

Ostrom, J. H. 1969b. Osteology of *Deinonychus antirrhopus,* an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum Bulletin* 30: 1-165.
Ostrom, J. H. 1970b. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming. *Peabody Museum Bulletin* 35: 1-234.
Ostrom, J. H. 1972. Were some dinosaurs gregarious? *Palaeogeography, Palaeoclimatology, Palaeoecology* 11: 287-301.
Ostrom, J. H. 1973. The ancestry of birds. *Nature* 242: 136.
Ostrom, J. H. 1974a. *Archaeopteryx* and the origin of flight. *Quarterly Review of Biology* 49(1): 27-47.
Ostrom, J. H. 1976a. Some hypothetical anatomical stages in the evolution of avian flight. *Smithsonian Contributions to Paleobiology* 27:1-21.
Ostrom, J. H. 1976b. *Archaeopteryx* and the origin of birds. *Biological Journal of the Linnean Society* 8(2): 91-182.
Ostrom, J. H. 1976c. On a new specimen of the Lower Cretaceous dinosaur *Deinonychus antirrhopus*. *Breviora* 439: 1-21.
Ostrom, J. H. 1978. The osteology of *Compsognathus longipes* Wagner. *Zitteliana* 4: 73-118.
Parks, W. A. 1933. New species of dinosaur and turtles from the Upper Cretaceous formations of Alberta. *University of Toronto Studies in Geology Series* 34: 3-33.
Perle, A. 1979. Segnosauridae - novoe semeistvo teropod is posdnego mela Mongolii. *Trudy Sovm. Sov. Mong. Pal. Exped.* 8: 45-55.
Piveteau, J. (ed.) 1955. *Traite de Paléontologie, Volume 5*. Masson et Cie, Paris: 1113 pp.
Raath, M. A. 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. *Arnoldia* 4(28): 1-25.
Reig, O. A. 1970. The Proterosuchia and the early evolution of the archosaurs: an essay about the origin of a major taxon. *Bulletin of the Museum of Comparative Zoology* 139(5): 229-292.
Ricqlès, A. de. 1967. L'origine des dinosaures. *Atomes* 242: 258-260.
Romer, A. S. 1923. The pelvic musculature of saurischian dinosaurs. *Bulletin of the American Museum of Natural History* 48(19): 605-617.
Romer, A. S. 1927. The pelvic musculature of ornithischian dinosaurs. *Acta Zoologica* 8: 225-275.
Romer, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago: 771 pp.
Romer, A. S. 1966. *Vertebrate Paleontology.* University of Chicago Press, Chicago: 468 pp.
Romer, A. S. 1971. The Chañares (Argentina) Triassic reptile fauna. X. Two new but incompletely known long-limbed pseudosuchians. *Breviora* 378:1-10.
Romer, A. S. 1972. The Chañares (Argentina) Triassic reptile fauna. XV. Further remains of the thecodonts *Lagerpeton* and *Lagosuchus*. *Breviora* 394: 1-7.
Rozhdestvensky, A. K. 1952a. [A new representative of duck-billed dinosaurs from the Upper Cretaceous deposits of Mongolia. *Doklady Akademii Nauk SSSR* 86(2): 405-408.
Rozhdestvensky, A. K. 1952b. [The discovery of iguanodonts in Mongolia.] *Doklady Akademii Nauk SSSR* 84(6): 1243-1246.
Rozhdestvensky, A. K. 1955. [New data on psittacosaurs, Cretaceous ornithopods.] *Voprosy Geol. Asii* 2: 783-788.
Rozhdestvensky, A. K. 1957a. Duck-billed dinosaur - *Saurolophus* from Upper Cretaceous of Mongolia. *Vertebrata PalAsiatica* 1(2): 148-149.
Rozhdestvensky, A. K. 1957b. Dinosaur localities of the Upper Cretaceous on the Amur River. *Vertebrata PalAsiatica* 1(4): 285-291.
Rozhdestvensky, A. K. 1957c.
Rozhdestvensky, A. K. 1960.
Rozhdestvensky, A. K. 1961.
Rozhdestvensky, A. K. 1964. New data on the localities of dinosaurs in Kazakhstan and middle Asia. *Nauchnye Trudy Tashkent Univ. Geol. Series* 234(20): 227-241.
Rozhdestvensky, A. K. 1965. Vosractnay ismenchivosty i nekotorie voprosi sistematiki dinosavrov Asii. *Paleontologicheskiy Zhurnal* 1965(3): 95-109.
Rozhdestvensky, A. K. 1966. Novye igyanodonti ie tsentrallinoy Asii. phillogeneticheskye y taksonomicheskye veaimoothoshenia poednich Iguanodontidae y rannich Hadrosauridae. *Paleontologicheskiy Zhurnal* 1966(3): 103-116.
Rozhdestvensky, A. K. 1968.
Rozhdestvensky, A. K. 1970. Giant claws of enigmatic Mesozoic reptiles. *Paleontological Journal* 1970(1): 117-125.

Rozhdestvensky, A. K. 1971. Esuchenie dinosavrov Mongolii i ich rolb v raschleneniy kontinentaljnogo Mesosoa. *Trudy Sovm. Sov. Mong. Nauk Issled. Geol. Exped.* 3: 21-32.

Rozhdestvensky, A. K. 1974.

Russell, D. A. 1967. A census of dinosaur specimens collected in western Canada. *Natural History Papers of the National Museum of Canada* 36: 1-13.

Russell, D. A. 1970. Tyrannosaurs from the Late Cretaceous of western Canada. *National Museum of Natural Sciences Publications in Paleontology* 1: 1-32.

Russell, D. A. 1972. Ostrich dinosaurs from the late Cretaceous of western Canada. *Canadian Journal of Earth Sciences* 9: 375-402.

Russell, L. S. 1930.

Russell, L. S.. 1964. Cretaceous non-marine faunas of northwestern North America. *Royal Ontario Museum Contributions to the Life Sciences* 61: 1-24.

Seeley, H. G. 1887. The classification of the Dinosauria. *Report of the British Association for the Advancement of Science* 57: 698-699.

Shuvalov, V. F. 1970a.

Shuvalov, V. F. 1970b.

Shuvalov, V. F. 1974.

Shuvalov, V. F. 1975. [Buylyasutiun-Khuduk, a new locality of early Cretaceous dinosaurs.] Trudy: *Vypusk 2 Iskopayemaya fauna i flora Mongolii*: 210-213.

Simpson, G. G. 1946.

Sloan, R. E. 1970.

Sochava, A. V. 1969. [Dinosaur eggs from the Upper Cretaceous of the Gobi Desert.] *Palaeontological Zhurnal* 1969(4): 76-88.

Sochava, A. V. 1975.

Soderbergh. 1947.

Spock. 1930.

Steel, R. 1969. *Handbuch der Paläoherpetology: v. 15: Ornithischia*. Gustav Fischer Verlag, Jena: 1-87.

Steel, R. 1970. *Handbuch der Paläoherpetology: v. 16: Saurischia*. Gustav Fischer Verlag, Jena: 1-84.

Sternberg, C. M. 1940.

Suzuki. 1943.

Tatarinov, L. P. 1965.

Tatarinov, L. P. 1966.

Tatarinov, L. P. 1967.

Tatarinov, L. P. 1977.

Thulborn, R. A. 1970a. The skull of *Fabrosaurus australis*, a Triassic ornithischian dinosaur. *Palaeontology* 13(3): 414-432.

Thulborn, R. A. 1970b. The systematic position of the Triassic ornithischian dinosaur *Lycorhinus angustidens*. *Zoological Journal of the Linnean Society* 49(3): 235-235.

Thulborn, R. A. 1971. Origins and evolution of ornithischian dinosaurs. *Nature* 234: 75-78.

Thulborn, R. A. 1973. Thermoregulation in dinosaurs. *Nature* 245: 51-52.

Thulborn, R. A. 1975. Dinosaur polyphyly and the classification of archosaurs. *Australian Journal of Zoology* 23(2): 249-270.

Turischev. 1954.

Turischev. 1955.

Turischev. 1956.

Vasiliev et al. 1959a.

Vasiliev et al. 1959b.

Versluys. 1910. Streptostylie bei Dinosauriern, nebst Bemerkungen uber die Verwandtschaft der Vögel und Dinosaurier. *Zoologische Jahrbuch Anatomische* 30: 175-260.

Versluys. 1912. Das Streptostylie-Problem und die Bewegungen im Schädel bei Suaropsiden. *Zoologische Jahrbuch Anatomische Supp.* 15(2): 545-714.

Versluys. 1936.

Walker, A. D. 1961.

Walker, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society of London Series B* 248: 53-134.

Walker, A. D. 1972.

Walker, A. D. 1977. Evolution of the pelvis in birds and dinosaurs. In S. M. Andrews, R. S. Miles and A. D. Walker (eds.), *Problems in Vertebrate Evolution*. Linnean Society Symposium Series: 319-358.

Welles, S. P. 1970. *Dilophosaurus* (Reptilia: Saurischia), a new name for a dinosaur. *Journal of Paleontology* 44(5): 989.

Wellnhofer, P. 1974. Das funfte Skelettexemplar von *Archaeopteryx*. *Palaeontographica A* 147(4-6): 169-216.

Wetmore, A. 1956.

Wetmore, A. 1960.

White, T. E. 1973. Catalogue of the genera of dinosaurs. *Annals of the Carnegie Museum* 44(9): 117-155.

Wyeth, F. J. 1924. The development of the auditory apparatus in *Sphenodon punctatum*. *Philosophical Transacations of the Royal Society of London* 212: 259-368.

Young, C.-C. 1958. The dinosaurian remains of Laiyang, China. VI. Psittacosauridae from the Chinshan Beds. *Palaeontologia Sinica* Whole Number 143: 116-138.

Yakushina. 1964.

Yordansky. 1966.

Yordansky. 1968.