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Growth Changes in Asian Dinosaurs and Some Problems of Their Taxonomy

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In order to determine the scope and boundaries of a species, it is essential to have information on individual variability; the wider the possible limits of variation, the more necessary is this information. It is particularly important for the systematics of such a group of fossil reptiles as the dinosaurs, in which growth changes are very clearly displayed not only in absolute body dimensions, but also in the form of considerable morphological differences.

In the case of dinosaurs, however, such information is fairly fragmentary and relates only to a few species. The most detailed data on growth changes are given by Brown and Schlaikjer (1940), for the primitive horned dinosaur *Protoceratops andrewsi*. There are isolated references to growth changes in hadrosaurs (Ornithopoda) in the works of Gilmore (1933), Sternberg (1955) and Rozhdestvensky (1957; 1964b). Colbert (1961) gives some examples of growth changes in other groups of dinosaurs, the Theropoda and Sauropoda.

Sexual dimorphism in dinosaurs has hardly been studied at all. Nopsca's attempts (1929) in this direction cannot be considered successful; comparing the different genera (*Prosaurolophus* and *Saurolophus*), he took one for female and the other for male, although they are separated by a considerable interval of geologic time and represented by *only one specimen each*. Brown and Schlaikjer (1940) attempted to determine sexual as well as age differences in *Protoceratops andrewsi*, but not very convincingly. Their views, however, have found support in Davitshavili's book (1961) on the theory of sexual selection as exemplified mainly in reptiles, including dinosaurs. Discussing the genus *Corythosaurus* of the family Hadrosauridae, comprising six species, remains of which were all collected in one locality (Alberta, Canada) and from one formation (the Belly River, although from different stratigraphic levels), Davitshavili suggests that the intraspecific (and possibly intrageneric) differences in the shape of the hood are primarily due to sexual dimorphism.

It must be said, however, that sexual differences in reptiles (not only fossil, but also modern) are on the whole weakly expressed and it is particularly difficult to identify them from osteological material. It is essential, of course, to remember that individual variations can be interpreted correctly only when there is bulk material for the species in question. As a rule, it is precisely the dearth of adequate serial dinosaur remains that precludes elucidation of their individual variability. Some authors nevertheless restrict themselves to diagnostic description of a holotype, even when bulk material is available, usually taking the "average specimen" of the series as the holotype. In most cases age and sex variation is not taken into account at all. This inevitably leads to artificial and, moreover, highly intensive "species formation", based not on specific differences but on individual variation.

The extent of growth variation in dinosaurs is sometimes so great that juvenile individuals outwardly look very similar to adults of the preceding species rather than to adult individuals of the species to which they in fact belong. Growth changes are therefore of the greatest importance in determining the scope and boundaries of a species in this group.

The present paper is based on examples of growth changes in dinosaurs from Central Asia and the northern part of South Asia, from which areas serial dinosaur remains have reached the author for direct study.

In 1933 Gilmore drew attention to the fact that adult individuals of *Bactrosaurus johnsoni* (family Hadrosauridae), described by him from the Upper Cretaceous (Iren Dabasu Formation) of Inner Mongolia, differed greatly from young specimens of the same species, in that their bones were more massive and there were more rows of teeth in the jaws. In adult bactrosaurs the number of vertical rows on the maxilla was 28 and the number on the dentary 23, compared with 17 - 18 and 16, respectively, in very young individuals. In late iguanodonts, which were the direct ancestors of hadrosaurs (including bactrosaurs), there were more than 23 dental rows on the maxilla and 22 on the dentary. The number of vertical tooth rows in later hadrosaurs increases to 40 - 50. At the same time the number of layers increases (5 - 6 per tooth row), whereas in adult bactrosaurs the tooth rows are in three layers, and in two layers in iguanodonts and young bactrosaurs. In other words, young bactrosaurs are even more primitive with regard to the structure of the dental system than their ancestors the iguanodonts. There are also differences in the structure of the postcranial skeleton: in young individuals of *Bactrosaurus johnsoni*, as also in the iguanodonts, the phalanges are acuminate and the bones less massive and of slightly different proportions and shape in comparison with the bones of adult *Bactrosaurus johnsoni* individuals.

Brown and Schlaikjer (1940) repeated Gilmore's observations of growth changes in another dinosaur species, *Protoceratops andrewsi*, for which there is bulk material (more than 40 specimens) from the Upper Cretaceous deposits of Mongolia (Bayn Dzak site).

The age differences revealed in *Protoceratops andrewsi* give a fair idea of the range of age variation within one species. In young individuals of this species, for example (Figs. 1 and 2), the antorbital part of the skull is short, there is a short and slightly dilated "frill" (formed as a result of growth of the parietals and squamosals); there are large and round orbits, a low median crest and large frontals; horizontally-oriented jugals and a slight widening of the skull in the jugal region; a straight ventral margin of the lower jaw; and a poorly developed crest on the surangular.

Adult individuals of the same species (Figs. 1 and 2) are differentiated by the elongate antorbital part of the skull, with a rudimentary horn on the nasals; the "frill" has lengthened and widened; the orbits and frontals have become perceptibly reduced and the jugals are vertically-oriented; the skull widens considerably in the jugal region and the lower jaw has an abruptly curved ventral margin; and a powerful crest on the surangular. In the structure of the dental system differences similar to those between young and adult individuals of *Bactrosaurus johnsoni* are also observed in *Protoceratops*. The postcranial skeleton in adult individuals of *Protoceratops andrewsi* is more massive than in the young; in the sacrum, for example, all eight sacral vertebrae fuse in the adults, while only four of them do so in the young.

No less impressive age differences are observed in the Late Cretaceous hadrosaurs from Nemegtu (Mongolian People's Republic), *Saurolophus angustirostris* (Rozhdestvensky, 1957). The young individuals of this species are much closer to the preceding species, *Saurolophus osborni* (Brown, 1912), than to adults of their own species with regard to the skull structure, with its short crest that does not overhang the occipital margin, and the ratio of the other skull bones, as well as the postcranial skeleton; in the adult *angustirostris* the crest protrudes well beyond the occipital margin and the rostral part of the skull is strongly elongate (Figs. 3 and 4).

In the example given the range of variation due to age is so great that at the extremes the differences can easily be mistaken for specific or even generic differences. This was just the kind of error made by Young (1941 - 1951), who had at his disposal a series of more than 70 specimens of Late Triassic prosauropods from Lufeng (Yunnan, China) and described 5 species: *Lufengosaurus huenei, L. magnus, Yunnanosaurus huangi, Y. robustus* and *Gyposaurus sinensis*, which in fact represented different growth stages of one species alone (Rozhdestvensky, 1964a), *Lufengosaurus huenei*. To judge from the holotype (V 15)*, this occupies a "central position" in the series of prosauropods from Yunnan. The giant individual (postcranial skeleton), referred to the carnivorous dinosaur *Sinosaurus triassicus* by Young, belongs to the same species.

The diagnosis which Young (1941a) gives for the genus and species *Lufengosaurus huenei* contains in the main general information applicable not only to other prosauropod genera, but also to this suborder as a whole. There are some inaccuracies of detail. The report that the *Lufengosaurus* skull is less elongate than that of *Plateosaurus*, for example, is note borne out by the facts: in *Lufengosaurus* the length-height ratio of the skull is roughly 2.3, versus roughly 2.0 in *Plateosaurus*. There is a reference to a very small antorbital foramen in the diagnosis, whereas the drawing contradicts this. In *Plateosaurus* this depression is not larger than in

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* Catalog number of specimen.

Lufengosaurus. The *Plateosaurus* orbits are no less round and large than those of *Lufengosaurus*.

The part of the diagnosis relating to the postcranial skeleton is obviously less reliable for determining generic or species affinity, particularly as these characters also occur in other Prosauropoda. Incidentally, Young shows three vertebrae in the sacrum, whereas in fact there are four of them, as can clearly be seen from the structure of the sacral ribs and the articulation surfaces on the ilia. The measurements of the *Lufengosaurus huenei* bones given by Young in the text do not correspond to the sizes of these bones in the drawings, while the figures on which the table is based (Young, 1951) correspond neither to the text nor to the drawings. The drawings, which have been kept to one scale, are evidently nearer the truth. If the proportions are corrected, the character of the bones becomes normal.

The absence of clear distinctions from *Plateosaurus* in the *Lufengosaurus* diagnosis and the inaccuracies mentioned make it difficult to form any opinion at all about *Lufengosaurus* and even make the independent existence of this genus somewhat dubious.

The nearest species to *Lufengosaurus huenei* is *L. magnus* (Young, 1947), described on the basis of a postcranial skeleton from the same horizon as the *L. huenei* holotype (the dull-purplish beds). According to Young's data, the new species is distinguished by larger dimensions (roughly one-third larger than *L. huenei*) and more massive bones. But this could easily be due to growth changes: in large adult individuals the bones will naturally coarsen and become more massive as the load on the skeleton increases. The ratio between the length of the posterior and anterior limbs is roughly the same in both species (slightly larger than 2.0). There are thus no serious grounds at all for distinguishing *L. magnus* as an independent species and it must be regarded as a synonym of *L. huenei* and as merely an individual of the same species, larger than the holotype.

Fragments of the upper and lower jaws (V 24) served as the holotype of *G. sinensis*, the smallest of the forms described by Young (1941b, 1948b). In the description of the species, bones from the postcranial skeletons of other specimens were used as well. All these (V 25-V 27), like the holotype, came from the same "dull-purplish beds" as contained the holotypes of *Lufengosaurus huenei* (V 15) and *L. magnus* (V 82). To judge from the diagnosis, *Gyposaurus sinensis* is hardly distinguishable from *G. capensis*, described by Broom (1911) from the Upper Triassic of South Africa, but without visual comparison or more detailed descriptions than are now available it is impossible to decide what the relationship is between these two species. Let us compare the diagnoses of *Gyposaurus sinensis* and *Lufengosaurus huenei*. The author himself mentions no fundamental differences in the structure of the vertebral column and of the teeth in these two species, except serrations on both the anterior and posterior dental margins in *G. sinensis*. This is a primitive character, proper to carnivorous archosaurs, whereas in the majority of other archosaurs only the serration of the anterior margin persists. Nor is there any great difference in the limbs and their girdles. The length ratio between the fore and hind limbs is about 2.0 in *Lufengosaurus huenei*, versus 2.2 in *Gyposaurus sinensis*. This can be attributed to growth changes, since the ancestors of the prosauropods were "more bipedal" and the disproportion between the fore and hind limbs in them was also greater. The same explanation could easily account for the non-massive pelvis. In *Gyposaurus sinensis* the scapula is on the whole less massive and shorter than that of *Lufengosaurus huenei*: in *Gyposaurus sinensis* it is almost equal to the humerus, whereas in *Lufengosaurus huenei* it is roughly one-quarter longer, and one-third longer in the larger form of *L. magnus* (in "*Sinosaurus triassicus*" this difference is still greater). The reason is that in *Gyposaurus sinensis*, which is a juvenile individual, the distal end of the scapula had not yet ossified and was still cartilaginous. All the "species differences" indicated by Young for *Gyposaurus sinensis* are thus either also found in other Prosauropoda, or are due to the age of the individual. *Gyposaurus sinensis* should therefore be regarded as a synonym of *Lufengosaurus huenei*.

The holotypes of both species of the genus *Yunnanosaurus* came from higher beds that the holotypes of *Lufengosaurus huenei, L. magnus* and *Gyposaurus sinensis*, namely the dark-red beds. Young's (1942) diagnosis of *Yunnanosaurus huangi*, based on holotype V 20, like his previous descriptions, is too vague. The postcranial skeleton does not, on the whole, display important differences as compared with *Lufengosaurus* and *Gyposaurus*; but, for example, the limb bone epiphyses in *Yunnanosaurus*, to judge from their crested surface, are evidence of the presence of cartilage during the animal's lifetime, and this in turn may mean that the remains belong to a young individual; so too does the fact that the scapula is not yet concrescent with the coracoid. The most important differences are in the skull. This, as Young notes, is indeed more elongate and constricted than that of *Lufengosaurus* (although the anterior part in the latter had been reconstructed), but the upper jaw, for example, hangs conspicuously over the lower jaw, thus producing a resemblance to Pseudosuchia, the ancestral group to the dinosaurs. The serration of the posterior tooth margin still persists, but is less pronounced than in *Gyposaurus sinensis*. The superior temporal fenestra in *Yunnanosaurus*, unlike that of *Lufengosaurus*, has not yet moved upwards and is visible laterally, as in the pseudosuchians, related to the prosauropods and primitive theropods, while the inferior temporal fenestra has a conspicuous posterior excavation, which is also a primitive character. These features, proper to the older ancestral forms, are combined in *Yunnanosaurus* with such characters as the large diameter of the orbits and the smaller number of teeth than in *Lufengosaurus*, a feature characteristic of young individuals in herbivorous dinosaurs, as can be seen in hadrosaurs and protoceratopsians. The above-mentioned differences between *Yunnanosaurus* and *Lufengosaurus* with regard to the skull and postcranial skeleton are thus quite understandable. *Yunnanosaurus*, and in particular *Y.*

huangi, in fact obviously corresponds only to a relatively young individual of *Lufengosaurus huenei*, and in structure occupies an intermediate position between *L. huenei* and *Gyposaurus sinensis*. Since the *Yunnanosaurus huangi* holotype, according to Young, was found in higher beds than the *Lufengosaurus huenei* holotype, we might expect the former species to be more progressive than the latter. In reality, *Yunnanosaurus huangi* is the more primitive, and the explanation is to be found in growth changes.

The last of the prosauropod species described by Young is *Yunnanosaurus robustus* (Young, 1951). The holotype of this species (V 93) is represented by an incomplete postcranial skeleton and skull fragments. *Yunnanosaurus robustus* was roughly twice as large as *Y. huangi* and characterized by more massive bones. The obvious reason for the shorter tooth crown, mentioned by Young, is that the teeth have been more worn down. No considerable morphological differences are mentioned, and indeed there are none. There can be no doubt that *Y. huangi* and *Y. robustus* are only difference growth stages of the same species - *Lufengosaurus huenei*.

The postcranial skeleton (specimen V 100), erroneously assigned by Young (1951) to the carnivorous dinosaur *Sinosaurus triassicus*, which he had previously described (1948a) from various scattered fragments, including some from the jaws, belongs to *Lufengosaurus huenei*. This specimen (V 100) is nothing more than a giant individual of that species, and Young himself, incidentally (though without much confidence), asserted that specimen V 100 belonged to a carnivorous dinosaur. Having examined this specimen, I am sure that morphologically, apart from its larger size and massive bones, it is in no way different from other Lufeng prosauropods.

Young provides graphic tables (1951) showing the changes in the vertebral bones and a diagram of changes in the limb bone proportions, so as to illustrate the species differences between the prosauropods. All that these show, however, is that every prosauropod described by him, including the postcranial skeletal material referred to *Sinosaurus triassicus*, belongs to the same species, *Lufengosaurus huenei*, at different growth stages; if individuals of the different species are placed in sequence according to increase or decrease of absolute dimensions, the gaps in the broken line will simply disappear and we shall observe a normal sequence of growth changes[*]. Moreover, it must not be forgotten that the discussion concerns only six specimens in all, and that there is a good deal more material to fill the size gaps between the holotypes.

In order to settle the problem of the Yunnan prosauropods it is essential to refer again to their stratigraphic location, given in Young's summary (1951) review of the Lufeng fauna. The holotypes of *Gyposaurus sinensis, Lufengosaurus huenei* and *L. magnus* come from the lower

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[*] The data on the *Lufengosaurus huenei* holotype in the diagram (Fig. 19) are evidently not quite accurate, since they do not coincide with the measurements given in Table 16 or with the redescription (Young, 1941a).

beds, whereas the holotypes of *Yunnanosaurus huangi, Y. robustus* and the specimen described as *Sinosaurus triassicus* come from the upper ones. The specimens mentioned correspond respectively to small, medium and large forms from each horizon. The striking point here is that all six of the prosauropod species enumerated here recur in both horizons, the dull-purplish beds and the dark-red beds above them. The interval between the two bone horizons is about 200 m. It is very difficult to see why six mutually similar species, displaying morphological differences that can all be accounted for in terms of growth changes, should occur together. It is even more difficult to believe that an assemblage of six similar species, not isolated geographically, could have persisted, unchanged, for so long a time as the interval corresponding to the 200 m between the two horizons. However, the colorations of the remains and their conditions are different. In the *Yunnanosaurus huangi* holotype, for example, the skull and the first three cervical vertebrae are lilac-colored and very deformed, whereas the bones of the postcranial skeleton are gray and not deformed. This unavoidably suggests that the holotype bones may not belong to a single specimen and may have come from different horizons. It is obviously no accident that in Young's 1951 work there are interrogation marks in several places where there is a question of attributing the specimens to a particular horizon.

Both the morphological and geological data thus allow the existence of only one species to be recognized as valid. The name of this species, under the rule of priority of first description, is *Lufengosaurus huenei*.

Returning to the question of whether the genus *Lufengosaurus* has the right to exist, we must compare it with the similar, fairly well-known and also Late Triassic genus *Plateosaurus*, with which Young compared his genus but, unfortunately, for which he did not determine the diagnostic differences, and on which the reconstruction of *Lufengosaurus* was based (Huene, 1926 and Young, 1941a)[*].

Differences between *Plateosaurus* and *Lufengosaurus*

Plateosaurus:	*Lufengosaurus*:
1. Superior temporal fenestra usually visible from the side.	1. Superior temporal fenestra barely visible from the side (except in young individuals).
2. Inferior temporal fenestra with inferior dilation only posteriorly.	2. Inferior temporal fenestra with inferior dilation both posteriorly and anteriorly.
3. Ventro-posterior angle of skull sharply descendent.	3. Ventral surface of skull almost horizontal, slightly descendent in posterior part.

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[*] In *Principles of Paleontology* (Rozhdestvenskiy, 1964a, Fig. 580) the reconstruction given is of *Lufengosaurus huenei*, not, as the caption indicated, of *Plateosaurus quenstedti*.

4. Lower jaw abruptly dilated in posterior third, so that its height is about 1/5 of its length.	4. Lower jaw slightly dilated in posterior third (height about 1/7 its length or even less), with almost parallel margins throughout.
5. Lateral foramen in lower jaw below posterior orbital margin or protruding beyond it.	5. Lateral foramen in lower jaw not reaching posterior orbital margin.
6. Teeth lanceolate.	6. Teeth conical.
7. Neck of moderate length, slightly more than three times the length of the skull and folding more than 1.5 times into the length of the body.	7. Neck elongate, almost 4 times longer than the skull and folding less than 1.5 times into the length of the body.
8. Proximal and distal ends of scapula widen to approximately the same extent.	8. Proximal end of scapula considerably wider than distal (except in young individuals).
9. Coracoid of moderate size.	9. Coracoid large.
10. Pubis wider than ischium.	10. Pubis and ischium of approximately equal width.

Plateosaurus is thus more theropoid and *Lufengosaurus* more sauropoid in shape. Morphologically these two genera are very different from each other and there are adequate grounds for distinguishing *Lufengosaurus* as an independent genus.

We now go on to consider examples of growth changes in carnivorous dinosaurs. Maleev (1955a, 1955b) describes four new species of carnivorous dinosaurs, assigned to three genera, on the basis of material collected by the Mongolian Paleontological Expedition of the USSR Academy of Sciences (1946 - 9) in the Nemegtu Basin (Nemegtu, Altan-Ula, and Tsagan-Ula) from beds coeval (Upper Cretaceous) with those that contained the *Saurolophus angustirostris* skeletons.

The first of the four new species, *Tyrannosaurus bataar* (Maleev, 1955a), is distinguished from the known species *T. rex* by its more elongate skull and larger number of teeth. There are further differences between the two species in the shape of the skull fenestrae. *T. rex* (Osborn, 1905) is one of the latest and largest of the carnivorous dinosaurs. Its remains were found in the Hell Creek Formation of Montana, which corresponds to the Danian stage in Europe (including, possibly, the top of the Maastrichtian), whereas the *T. bataar* remains come from layers that, translated to the European scale, can be referred only to the Maastrichtian and then not to its top layers.

Almost simultaneously with *Tyrannosaurus bataar*, Maleev (1955b) described a new genus and species, *Tarbosaurus efremovi*, that, according to his data, was distinguished from the preceding species and from *Tyrannosaurus rex* by its smaller dimensions[*], less massive and

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[*] The scale under the picture of the *Tarbosaurus efremovi* skull (the true length of which is about 1 m) in Maleyev's work (1955b) was obviously inaccurately calculated.

more elongate skull, more strongly laterally compressed teeth, and shorter fore limbs. To base species distinctions on such data as dimensions is, of course, risky. As for the author's reference to the less massive and more elongate skull in *Tarbosaurus efremovi* as compared with *Tyrannosaurus bataar*, this is highly relative, since the massiveness of the skull is roughly the same in both species and, probably, in both specimens, just as the length-height ratio of the skull is about 1.7 in both specimens. The greater or lesser degree of compression of the teeth is also a relative criterion and not reliable as a species distinction. The tooth row in the *Tarbosaurus efremovi* skull has not been cleaned of rock as it should be and that may be why Maleev at first (1955a) reported twelve teeth in the maxilla, but later thirteen (1964). As for the fore limbs, according to Maleev's data the humerus in *Tarbosaurus efremovi* accounts for one-third of the length of the scapula, compared with one-quarter in *Tyrannosaurus rex* (Osborn, 1905). Consequently the fore limbs in the former are not shorter, but longer than in the latter, and this is quite understandable since *Tarbosaurus efremovi* is the older of the two; but the *T. bataar* holotype consists only of a skull. The fact that the remains are fragmentary would account for Maleev's reference to didactyl fore limbs in *Tarbosaurus efremovi*, since in *Tyrannosaurus rex*, a later carnosaur, the fore limbs are tridactyl (*sic*).

On the whole it is quite obvious that *Tyrannosaurus bataar* hardly differs at all from *Tarbosaurus efremovi*, and in any case is much smaller than *Tyrannosaurus rex*; that is, the "generic" differences turn out to be smaller than the specific differences. From this we can draw only one conclusion: *Tyrannosaurus bataar* and *Tarbosaurus efremovi* are one and the same species.

The other two species of carnivorous dinosaurs, assigned by Maleev (1955b) to the genus *Gorgosaurus*[*] - *G. lancinator* and *G. novojilovi*, are morphologically almost indistinguishable from Tyrannosaurus bataar and represented only by specimens smaller than its holotype. Maleev, comparing *G. lancinator* with other species of this genus described previously, mentions only a few different absolute measurements, and such characters as the less massive skull and narrower snout than in *G. libratus*. The absence of a bony prominence on the lacrimal bone in *G. lancinator*, characteristic of other species of the genus *Gorgosaurus*, is merely additional proof that the form in question does not belong to *Gorgosaurus*. Apart from the differences in structure of the lacrimal bone, *G. lancinator* also differs from other species of this genus in the shape of the skull fenestrae. The general skull proportions in *G. lancinator* are roughly the same as in *Tyrannosaurus bataar*. The number of teeth in *Gorgosaurus lancinator*, according to Maleev, is 4 + 12 in the upper jaw and 15 in the lower jaw (although the skull has not been adequately prepared); that is, there is one fewer tooth than in *Tarbosaurus efremovi* and

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[*] Later, Maleyev (1964) treats the genus *Gorgosaurus* as a synonym of *Deinodon*.

Tyrannosaurus bataar. It must be noted that the latest of the carnosaurs, *Tyrannosaurus rex*, is distinguished by having the smallest number of teeth, whereas *Gorgosaurus*, which is older (dated as Campanian), has 4 + 14 teeth in the upper jaw and 14 - 15 (?) in the lower. Consequently, according to this character as well, *Gorgosaurus lancinator* is nearer to the species of the genus *Tyrannosaurus* than to *Gorgosaurus*. The specimen described as *Gorgosaurus lancinator* should therefore, like *Tarbosaurus efremovi*, be regarded as a synonym of *Tyrannosaurus bataar*.

The skeleton described by Maleev (1955b) as the holotype of *Gorgosaurus novojilovi* is much smaller than the specimens of the carnosaur species discussed above, and evidently belongs to a comparatively young individual (medium-sized), with slightly different proportions than in the large specimens, as we should expect if they are of different ages. The *G. novojilovi* skull has been well-preserved only in the anterior part, and therefore the reconstruction of the orbits and the first antorbital fenestra given by the author cannot be considered completely reliable. With regard to the lower jaw, or more correctly the dentary, this is actually narrower than in the large carnosaurs, and at its narrowest is only one-third of the height of the maxilla, whereas in *Tyrannosaurus bataar*, *Tarbosaurus efremovi* and *Gorgosaurus lancinator* the corresponding proportion is roughly one-half. Consequently, according to this character *G. novojilovi* occupies the same position relative to the other species of the same genus, *G. lancinator*, as it does relative to species of other genera - *Tarbosaurus* and *Tyrannosaurus*. A completely similar pattern is also observed in the proportions of the postcranial bones: for example, in the specimen described as *Tarbosaurus efremovi*, the femur is longer than the tibia and almost twice as long as the metatarsus, whereas in *Gorgosaurus novojilovi* the femur is almost the same length as the tibia and less than 1.5 times longer than the metatarsus. All these differences once again point to growth, not species variations, and compel us to regard *G. novojilovi* as only a relatively young individual of *Tyrannosaurus bataar*[*].

Even more conspicuous age differences can be seen in the specimen of a carnivorous dinosaur exhibited in the Paleontology Museum of the USSR Academy of Sciences. This specimen is about 1 m long and comes from the same Nemegtu fossil horizon as the specimens discussed above, but is obviously a juvenile individual, as is clear particularly from the weak formation of the limb joints, which are on the whole best developed in the carnivorous dinosaurs. The skull has not been preserved in this young individual, except for the anterior ends of the jaws, and therefore comparison with adult specimens of the same species - that is, *Tyrannosaurus bataar* - must be confined to the postcranial skeleton. In the large

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[*] Similar relationships are observed between *Tyrannosaurus rex* and *Gorgosaurus lancensis* (Gilmore, 1946), and it is therefore possible that the latter species is a young individual of the former. The remains of both species come from the Hell Creek (Lance) Formation of Montana.

Tyrannosaurus bataar individuals, the humerus is roughly one-quarter the length of the femur and one-half the length of the scapula; in the young specimen we are discussing it is shorter than the femur by a factor of roughly 1.5 and is of roughly the same length as the scapula. The median (III) metatarsal is not reduced proximally, as it is in medium-sized and large individuals of the Mongolian carnivorous dinosaur species we have been considering. The strongly developed fore limb and the primitive structure of the metatarsal in the young individual are distinctly primitive characters, proper to older carnivorous dinosaurs, at least those from the beginning of the Late Cretaceous period. Roughly the same bone ratios were found in a large, obviously adult specimen recovered by the 1960 Soviet-Chinese Paleontological Expedition from the bottom-most Upper Cretaceous horizons at the Tao-Suei-Gou locality near Maortu in the Alashan, and described by Hu Shou-yung under the name *Chilantaisaurus tashuikouensis*.

From the example of the carnivorous dinosaur species described by Maleev from Nemegtu, it can be seen that the large individuals are on the whole practically indistinguishable from one another, whereas in the medium-sized and small individuals the structural proportions of the skull and postcranial skeleton are different. These differences can be fully explained as growth changes, by analogy with other dinosaurs species. Moreover, ecological considerations make it highly unlikely that at least three morphologically very close giant predators - *Tyrannosaurus bataar, Tarbosaurus efremovi* and *Gorgosaurus lancinator* - could have coexisted. Lastly, the saurolophs accompanying the carnosaurs at several of the same sites in the Nemegtu Basin and belonging only to different growth stages of the same species - *Saurolophus angustirostris*, also confirm, if only indirectly, that in the Nemegtu carnosaurs we do not have different general and species but only different growth stages of a single species.

If we compare the adult individuals of the Mongolian carnosaurs described by Maleev with the later *Tyrannosaurus rex* and the older *Gorgosaurus libratus*[*], we can list certain basic differences (see table).

Description		Name of Species	
	Gorgosaurus libratus	*Tyrannosaurus bataar* (= *Tarbosaurus efremovi*; = *Gorgosaurus lancinator*)	*Tyrannosaurus rex*
1. Skull length-height ratio	1.8	1.7	1.5
2. Antorbital fenestrae	rounded pentagonal	rounded pentagonal	subquadrate

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[*] *Tyrannosaurus rex* and *Gorgosaurus libratus* are the species which have been most thoroughly studied, the former being the type species of the genus and the latter described by Lambe (1914).

3. Orbits	oval, wide	bean-shaped, wide	bean-shaped, narrow
width-height ratio	more than 1/2	about 1/2	about 1/3
4. Jugal	moderately large, with cuneate ascending branch; posterior branch reaches only the middle of the inferior temporal fenestra	moderately large, with cuneate ascending branch; posterior branch reaches only the middle of the inferior temporal fenestra	with strongly dilated ascending branch of tetragonal shape; posterior branch almost reaches posterior wall of inferior temporal fenestra
5. Dentary	long, about 3/4 total lower jaw length	long, about 3/4 total lower jaw length	short, slightly more than 1/2 total lower jaw length
6. Teeth	fairly strongly laterally compressed	not strongly laterally compressed	slightly laterally compressed
i. Number in upper jaw	4 + 14	4 + 13 (12)	4 + 12
ii. Number in lower jaw	15 (?) - 14	15 - 14 (?)	14
7. Pubic symphysis	relatively small, about 1/2 length of ilium	moderately large, about 1/2 length of ilium	very large, 2/3 length of ilium
8. Length of metatarsal III	more than 3/5 femur length	more than 1/2 femur length	less than 1/2 femur length
9. Maximum body length	up to 9 m	up to 12 m	up to 14 m

Analyzing the above data, we can see that *Tyrannosaurus bataar* and its synonyms occupy a position between *Tyrannosaurus rex* and *Gorgosaurus libratus*; the differences between it and each of these are considerable and of roughly the same importance. The descriptions given for *Tyrannosaurus rex* and *Gorgosaurus libratus* practically coincide with the generic diagnoses; the diagnosis of *Tyrannosaurus bataar* and its synonyms does not fit into either of them, so we have grounds for assigning them neither to *Tyrannosaurus* nor to *Gorgosaurus*, but to some other genus. Since the synonyms of *Tyrannosaurus bataar* include, as we have seen, *Tarbosaurus efremovi*, that is, a species with a different generic name, the rules of paleozoological nomenclature require that for all Mongolian species described by Maleev that are synonyms of one another (*Tyrannosaurus bataar* = *Tarbosaurus efremovi* = *Gorgosaurus lancinator* = *G. novojilovi*), the generic name *Tarbosaurus* should be retained. In this case, however, the type species of the genus *Tarbosaurus* will not be *Tarbosaurus efremovi* but *Tyrannosaurus bataar*, since the latter species is a senior synonym of the former. Consequently, the operative specific name for all Mongolian carnosaurs described by Maleev will be *Tarbosaurus bataar* (Maleev)[*].

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[*] Maleev = Maleyev.

Summarizing the examples of variability due to individual age considered in this paper, we must conclude that it is essential to take individual growth variations into account in establishing species criteria, since such variation is considerable in dinosaurs and therefore of great importance for the systematics of this group of vertebrates. Elucidation of growth changes (and of individual variations in general) is the only reliable guarantee for establishing the criteria for a given species, and consequently for getting a correct idea of its true boundaries and scope.

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Figure Captions

Fig. 1. *Protoceratops andrewsi* Granger et Gregory; skull, side view: a - very young individual, b - adult individual (Brown and Schlaikjer, 1940; simplified). Ej - epijugal, F - frontal, J - jugal, Mx - maxilla, N - nasal, P - parietal, Pmx - premaxilla, Po - postorbital, Prf - prefrontal, Q - quadrate, Qj - quadratojugal, r - rostral, Sq - squamosal.

Fig. 2. *Protoceratops andrewsi* Granger et Gregory; skull, seen from above: a - very young individual, b - adult individual (Brown and Schlaikjer, 1940; simplified). Symbols as for Fig. 1.

Fig. 3. *Saurolophus osborni* Brown; lateral view of adult skull (Brown, 1912; the reconstruction of the extremity of the skull crest has been altered). D - dentary, Pd - predentary, Sa - surangular; other symbols as for Fig. 1.

Fig. 4. *Saurolophus angustirostris* Rozhdestvensky; skull, lateral view: a - young individual, b - adult individual (Rozhdestvensky, 1957). Symbols as for Figs. 1 - 3.