

## ON THE EVOLUTION OF PREDATORY DINOSAURS\*

New data on the early and especially the later stages of predatory dinosaur development have recently become available. These data make it quite conceivable that the evolution of this group will draw increased attention. The development of the most ancient saurischians are among the most complex and fundamental questions. The discovery of previously unknown theropods in Mongolia have greatly expanded notions of predatory dinosaur evolution.

Most saurischian classifications are based on the notion of three evolutionary lineages—coelurosaurs, carnosaurs (in the broad sense) and prosauropods-sauropods—that appeared in the Triassic and continued into the Mesozoic.

The coelurosaur and carnosaur lineages and the “basal” part of the third lineage, prosauropods, are commonly thought to be kindred, and consequently grouped in the suborder Theropoda. Sauropods are separated into an independent suborder (Romer, 1956). This scheme is partly “vertical” and partly “horizontal” because it combines three lineages of Triassic dinosaurs and two post-Triassic dinosaurs within the suborder Theropoda. If we consider prosauropods-sauropods to be a single lineage, this scheme virtually disrupts the lineage.

A classification that unites carnosaurs (in the broad sense) and coelurosaurs as theropods (Marsh, 1881) is more logical. Prosauropods, which occupy an intermediate position between theropods and sauropods, are separated into the rank of an independent suborder (Rozhdestvenskiy, 1964).

In this scheme, Triassic and Late Mesozoic carnosaurs are considered to be a single lineage. The connection between Triassic “carnosaurs” and prosauropods is obviously acknowledged, but the vague term “intermediate position” merely emphasizes its uncertainty.

Huene (1914, 1920, 1932, 1956) proposed another scheme for classifying saurischians. His scheme combined carnosaurs with prosauropods and sauropods in the suborder Pachypodosauria. He also put coelurosaurs, which form a fairly isolated line in the Triassic, into an independent suborder.

The probable heterogeneity of carnosaurs, whose Triassic representatives are now prone to be combined with the prosauropods, are widely discussed in modern literature on saurischian evolution. Charig, Attridge and Crompton (1964) suggested a broad polyphyly of saurischians that originated, in their opinion, from quadrupedal thecodonts which formed several independent trunks. They admitted only coelurosaurs and post-Triassic carnosaurs into theropods; they put Triassic “carnosaurs” with prosauropods.

Colbert (1964, 1970) made a more useful classification, wherein he combined Triassic “carnosaurs” with prosauropods in the suborder Palaeopoda on the basis of their brachyiliac pelvic girdle. He put post-Triassic “true” carnosaurs (Megalosauridae, Tyrannosauridae) and coelurosaurs, which have a dolichoiliac pelvis, into the suborder of true theropods (Theropoda). Colbert emphasized that the brachyiliac pelvis was probably inimical to the bipedal saurischian ancestors which were part of the thecodonts. At the base of the trunk of theropods (and post-

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Triassic “true” carnosaur), Colbert mixed in Triassic coelurosaurs. This position reflects the notion of coelurosaurs as the most ancient and isolated group of saurischians whose ancestors were considered to be common for all of the other lines of saurischian dinosaurs—prosauropods, sauropods and carnosaur in the broad sense of the word (Huene, 1932, 1956).

Clearly, however, removing the lineages of post-Triassic “true” carnosaur from the coelurosaur trunk is met with a number of significant problems. Peculiarities in the development of these theropods most likely testify to the divergence of both lines at the earliest stage of saurischian radiation, although there are presently no hard data (with respect to true carnosaur). The specialization of the earliest known true carnosaur over a long time period shows that their evolutionary direction differed from that of early coelurosaurs, although there were several trends that were common in both groups.

The early stages of saurischian development are still insufficiently well known to speak of their polyphyletic origin. The data on their structural evolution allow us to make some judgments about the clear manifestation of some common trends. However, during the Late Triassic they occurred differently in palaeopods and theropods, which is most clearly seen in their pelvic structure (brachyilia and dolichoilia) (Fig. 1).

Along with this we must note that the similarity among palaeopods (brachyilia, forelimb proportions, autopodia) does not span the differences which, despite insufficient evidence, testifies for the divergence of these animals over a fairly long time during the Late Triassic. The high probability that palaeopods adapted to various foods (vegetation and flesh) and to means of locomotion (rudimentary bipedalism and possible quadrupedalism) provide a basis for seeing manifestations of their evolutionary differentiation.

The “theropod” evolutionary trends that took place in predatory palaeopods led researchers to perceive a direct kinship between both groups. However, the establishment of a number of similarities between theropods and predatory palaeopods—previously manifested—and the closely related trends toward reduction in the lateral digits of the pes and manus, bipedalism at varying degrees of perfection, and the resultant features (sigmoid flexure of the femur, high location of the fourth trochanter, relative length of the metapodia), adaptation to flesh-eating, all bear the nature of common adaptations to the initial demands of the environment. It is difficult to resolve unambiguously whether we are dealing with convergence that suggests a polyphyletic development of palaeopods and theropods or parallelism, albeit remote, that is based upon genetic kinship.

Specific structural features firmly established in coelurosaurs and carnosaur—the size of the body and skull, forelimb proportions, fundamental details of the dolichoiliac structure—are often contradictory in both groups. On this basis we may consider the theropod trunk to have diverged much earlier than the discovered carnosaur remains indicate, which must have been isolated at the end of the Triassic, but not afterward.

The establishment of new theropod groups that were previously unknown —Deinocheiridae and Therizinosauridae (Osmólska, Roniewicz, 1970; Maleyev, 1954; Rozhdestvenskiy, 1970; Barsbold, 1976) opens new pages in the evolution of predatory dinosaurs, showing the multi-layered scheme of their development. To begin, we must note that dividing theropods into only carnosaur and coelurosaurs is inadequate.

True theropods (suborder Theropoda) will be examined further within the framework of the following classification (Barsbold, 1976):

#### Small Theropods

Infraorder    Coelurosauria (Podokesauridae, Coeluridae)  
                  Deinonychosauria (Dromaeosauridae, Saurornithoididae)  
                  Oviraptorosauria (Oviraptoridae)

#### Large Theropods

Infraorder    Carnosauria (Megalosauridae, Tyrannosauridae)  
                  Ornithomimosauria (Ornithomimidae)  
                  Deinocheirosauria (Deinocheiridae, Therizinosauridae)

Naturally, the concept of large and small is conditional under the best of circumstances, a certain ecological sense. The development of unique “non-carnosaurian” large theropods presents a new and interesting problem in the evolution of predatory dinosaurs.

We will now examine common and specific features in the structural evolution of theropods. Common features have been established in large and small theropods, mainly in the structure of the dolichoiliac pelvis, which is proprietary to all of the presently known true theropods and is associated with mastering topography and strengthening certain muscle groups, mainly the thigh flexors (Colbert, 1964). Colbert believed that the dolichoiliac pelvis is more ideal and better suited to the bipedal locomotion of theropods, in comparison with the brachyiliac pelvis of palaeopods, which are less well-adapted to bipedalism. The dolichoiliac pelvis is characterized in particular by large sacral vertebrae that are connected as a unit. There are as many as five or six vertebrae in later theropods, but not fewer than four in earlier theropods. The brachyiliac pelvis of palaeopods has no more than three vertebrae in the sacrum (Colbert, 1964).

The dolichoiliac pelvis varies widely in fundamental details between large and small theropods (see Fig. 1). In small theropods, a short ischium and the development of a low obturator process were established, which is especially typical of Late Mesozoic coelurosaurs. The ischium of carnosaurs is not short, the obturator process is more proximal, and the pubis has undergone significant distal enlargement. From the earliest stages of their evolution, large theropods probably developed in the direction of increasing body size, whereas no similar phenomenon has been noted in small theropods.

The size of the skull in some large theropods (true carnosaurs) underwent enlargement and at the same time became taller (there is no known skull of Deinocheiridae and Therizinosauridae). The skull of small theropods is comparatively small and low, although in other Late Mesozoic groups (Dromaeosauridae) are representatives that had larger and higher skulls (Ostrom, 1969; Colbert, Russell, 1969). Along with increasing skull size the carnosaur neck became shorter, whereas the neck is relatively long in small theropods.

The relative sizes of the forelimbs and especially the structure of the autopodia are a number of fundamental evolutionary phenomena seen in theropods that bear the nature of a common directional development. The forelimbs of small theropods are typically well developed. The forelimbs of the carnosaurs, especially later groups (Tyrannosauridae), are reduced. Also, as has been noted, there were large theropods in the Late Cretaceous of Mongolia whose forelimbs were not reduced.

Already in the Triassic, the theropod pes was undergoing a reduction of the lateral digits, whereby it acquired an “avian” structure. The first pedal digit is significantly reduced in various theropod groups; in specialized groups the fifth digit is absent altogether (the first digit is absent in Ornithomimidae). The outside digits of the manus also underwent reduction, which in

Tyrannosauridae left only two digits. Three digits were preserved in other Late Mesozoic groups with different specialization in the various forms.

The increasing reduction of manual and pedal digits in different theropod groups is a common trend in their evolution, a trend that extended to palaeopods. We may assume that the reduction of digits in various saurischians (including palaeopods) was part of a general trend for perfecting locomotor functions. In theropods this trend would serve as a basis for acquiring parallel specializations, including the development of a modified second pedal digit having a predatory “claw” (Ostrom, 1969; Barsbold, 1974). Specialization might have taken other directions, sometimes leading to total loss of the first digit (Ornithomimidae).

The reduction in the number of theropod pedal digits accompanied the decrease in the number (and possible fusion) of the tarsal elements. As a rule, two tarsal elements, identified as the third and fourth, remained in Late Mesozoic groups. The metatarsal elements (first and fifth) underwent roughly the same reduction in the various theropod groups. The three middle elements, maintaining a single structural scheme, differ in a number of fundamental features in the various theropod groups. More typically, in true carnosaurs, Ornithomimidae, and Saurornithoididae the third metatarsal element is very compressed from the sides in the proximal region and plays almost no part in articulation with the epipodium. This element underwent slight compression in the small theropods Dromaeosauridae and Oviraptoridae. In carnosaurs and Ornithomimidae the second and fourth metatarsal elements form the basic component of articulation with the epipodium. In Saurornithoididae the second metatarsal element is more compressed from the sides; therefore, the epipodium articulated mainly with the very wide articular surface of the fourth metatarsal element. In Oviraptoridae the articular surface is created in almost equal measure by all three metatarsal elements, which is typical even in Triassic coelurosaurs.

Reduction of the outside manual digits apparently corresponded to the development and perfection of its primary “grasping” function. Further evolutionary transformations took place on this basis. A good illustration of this is the diverse structure of the tridactyl manus with an enhanced “grasping” ability of Dromaeosauridae, which was weak in Ornithomimidae, presumably webbed in Oviraptoridae, and adapted to swimming with huge (up 50-60 cm), flat ungual phalanges in Therizinosauridae and massive, thick ungual phalanges in Deinocheiridae.

The presentation of a single basis in the development of the manus in the aforementioned Late Mesozoic theropods is confirmed by the disc-like structure of the carpal bones that allowed the hand to move freely only in the plane of the metacarpals, and sharply limited the possibility of flexing and rotational movements. In Tyrannosauridae, which had only two manual digits, are four carpal elements that preserve the “non-disc-like” structure that is more or less comparable with what is observed in the primitive manus of earlier theropods. This shows that the reduction in the number of digits in true carnosaurs happened in different ways than in theropods (large and small) with unreduced limbs.

Aspects in the structural evolution of true theropods have been distinguished that reflect the common trends as well as the specific directions of development that took place on the background of these common trends.

To the more common trends must be assigned the adaptations that perfected bipedal locomotion which was associated with an active predatory lifestyle. In this sense earlier theropods had already surpassed palaeopods (even the predatory forms). Further coelurosaurian evolution was in the direction of perfecting bipedalism. The perfection of the grasping function of the manus was an essential event that led to the wide dissemination of “tridactyly”. The “grasping” basis of this

manus did not impede future extremely unique specializations that characterized the forelimbs of Late Mesozoic theropods.

The tridactyl manus proved promising for the non-reduced forelimbs. Reducing the number of digits in the structural basis in carnosaurs with reduced forelimbs (Megalosauridae and Tyrannosauridae) occurred differently. This shows that the reduction of outside manual digits is a phenomenon that was not unique in an evolutionary sense: it was a common trend that embraced various theropod groups, especially after the Triassic. Predatory palaeopods experienced this trend during the early radiation of saurischians.

Consequently, we must distinguish the common trends that developed on a different basis (convergence) from the common and specific trends that occurred on a more or less single basis (parallelism). From these positions the separation of palaeopods and theropods, on a par with the division of the various lines within theropods (Fig. 2), assumes greater significance. Theropods previously took a developmental path that was isolated from that of palaeopods.

The coelurosaur lineage (Podokesauridae-Coeluridae), spanning the boundary between the Triassic and Jurassic, continued to ascend, undergoing only a narrower specialization presumably within roughly the same adaptive zone as at the end of the Triassic. The evolutionary trends in Coeluridae, which continued the lineage of Triassic coelurosaurs, were even more explicit.

Presumably at the end of the Mesozoic the coelurosaur lineage radiated, forming new lines of more narrowly specialized forms. To these lines belong Deinonychosauria (Dromaeosauridae and Saurornithoididae) which developed in parallel in the direction of developing the “predatory” claw on the second pedal digit.

The “predatory” claw and digit, capable of powerful rearward flexure, was excluded from the locomotor function in deinonychosaur and became an effective organ for attack and capture (Ostrom, 1969), thereby becoming an example of expanded functionality in the pes and entire hind limb. Only two pedal digits (the third and fourth) functioned primarily during deinonychosaur locomotion. Thus, the deinonychosaur foot became didactyl in locomotor function. The acquisition of an additional function (equivalent to support on two digits) must have affected the hind limb musculature. The subparallel location of the pubis and ischium (in Dromaeosauridae) presumably reflect these changes.

Consequently, the entire structural system of deinonychosaur limbs was modified and thus explicitly connected with exiting into a new adaptive zone where the acquired adaptations gave them a massive evolutionary advantage over coelurosaurs. If we ignore the changes in the pes (development of the “predatory” claw) and pelvis, then Dromaeosauridae would differ from Coeluridae only by the extent of specialization that had already taken place in coelurosaurs, beginning in the Triassic.

In another deinonychosaur group—Saurornithoididae—the acquisition of teeth and development of a “predatory” claw was notably less intense, the pelvis was not modified as in Dromaeosauridae, and the third metatarsal element was very compressed in the proximal region, whereas this is not seen in Dromaeosauridae. Moreover, in the latest (Maastrichtian) Mongolian Dromaeosauridae a major reduction in the “predatory” claw occurred, whereas in earlier Central Asian and North American representatives (including Early Cretaceous forms) this structure was more highly developed.

Oviraptorosaurs—the next group of highly specialized small theropods that presumably diverged from coelurosaurs—developed in an extremely unique adaptive zone. Oviraptorosaurs became completely edentate and their skeletal structure retains many “coelurosaur” features that became more highly specialized. Interestingly, the structure of the tridactyl manus, in which the

second and third digits are very thick but did not lose the full number of phalanges, indicates the possible development of a swimming membrane. Also, the structure of the manual and carpal elements corresponds to late “theropod” evolutionary stages. The short ischium with a large obturator processes and the narrow pubis with a slight distal enlargement are completely characteristic for late branches associated with coelurosaurs.

It must be emphasized that deinonychosaur (especially dromaeosaurs) and oviraptorosaurs clearly illustrate the mosaic evolution phenomenon wherein many primitive features are retained along with progressive features.

The greatest changes occurred in the oviraptorosaur skull. The absence of teeth as in Ornithomimidae, combined with the development of a short, massive beak as in “horned” dinosaurs, and the adductor projection on the lower jaw that is analogous to the coronoid process in a number of herbivorous dinosaurs, show the transition of these unique predators into an adaptive zone that was atypical of theropods. Mediocranial mobility in oviraptorosaurs is very different from the metakinesis of predatory reptiles and suggests that oviraptorosaurs fed on solid food that required the jaws to develop a powerful crushing force (to break the hard shells of mollusks). The ecological niche occupied by oviraptorosaurs required additional adaptations that were expressed, in part, by the acquisition of a primarily “grasping” tridactyl manus along with the functions of a swim organ. This must be seen as an expansion of the function of the forelimbs because the structure of the manus shows that its “grasping” ability was retained. Oviraptorosaurs were apparently the first amphibian theropods and, consequently, they made a breakthrough into what was actually a new adaptive zone (Barsbold, 1976).

Both common “theropod” and specific trends occurred in carnosaur evolution. However, the common features that were linked with the perfection of bipedalism and flesh-eating say nothing about a direct phyletic link with small theropods. Reduction of the forelimbs and the decrease in the number of digits happened differently than in theropods without reduced forelimbs; the relationships between other structures (the large skull, short neck, etc.) suggest that carnosaurs diverged early from their common theropod ancestors.

From the position of evolutionary trends in the development of true carnosaurs, it is quite justifiable to examine Megalosauridae and Tyrannosauridae as a single lineage in which a more or less singular direction of specialization was maintained throughout the entire Late Mesozoic. In fact, the “carnosaurian” specializations in the families under discussion were acquired by later representatives (Tyrannosauridae) and in the main were only more highly expressed than in the earlier representatives (Megalosauridae). The strong reduction of the forelimbs and all of the presumably correlated changes probably reflect the development of carnosaurs in the direction of gigantism that was already manifested in the early stages of their evolution.

Ornithomimosaur are the second group of edentate theropods that were previously assigned to coelurosaurs in the broad sense. By their structure ornithomimosaur reflect the seeming connection between “coelurosaur” and “carnosaur” features: on one hand the small skull, long neck, non-reduced forelimbs, and tridactyl manus; on the other hand the “carnosaurian” pelvis and the primitive carpal structure. Specific ornithomimosaur features are rather distinct: the pes having a completely reduced first digit, the very weakened “capturing” function of the manus, and the toothless jaw. It is assumed that ornithomimosaur may have more links with large theropods than with small forms. These links must probably be assigned to the comparatively early stages in the development of true theropods. An extremely narrow and unique ornithomimosaur specialization greatly complicates efforts to investigate their historical development. Opinions vary as to the systematic position of Ornithomimidae—they have long been assigned to small theropods

(Matthew, 1915) and this view is widely held even today. Attempts have been made (Abel, 1919) to assign them to large theropods.

The body structure of Ornithomimidae is characterized on the whole by “carnosaurian” features, which is confirmed by the pubis having a massive distal enlargement, the narrow ischium having the proximally shifted obturator process, and the high ilium (in contrast with the low ilium of small theropods). Assigning Ornithomimidae to coelurosaurs is contradicted by the modification of their pelvis through the acquisition of “carnosaurian” features. Indeed, the “coelurosaurian” pelvis is such a fundamental structure as in carnosaurs and is associated with complete bipedalism of small theropods. The theropod pelvis underwent significant changes at times, as for example in Dromaeosauridae, but always retained either the initial “coelurosaurian” or “carnosaurian” structure. It is difficult to find any significant basis from the contemporary data for the possibility that the “coelurosaurian” pelvis changed to a “carnosaurian” pelvis in Ornithomimidae. Besides, the carpal elements of Ornithomimidae did not transform into the disc-like structure and their tridactyl manus retains its primitive structure, more like what is seen in carnosaurs. All of this suggests that ornithomimosaurians are an isolated lineage linked with the development of large theropods.

It must be noted that ornithomimid forelimbs are notably weak, which is in stark contrast with those of small theropods which show signs of having developed a powerful pectoral girdle. With their weakening, ornithomimosaur forelimbs are perhaps closer to carnosaurs than to coelurosaurs in the broad sense of the word.

The absence of teeth, the comparatively small skull, the long neck and forelimbs in ornithomimosaurians clearly testify for their development in a “non-carnosaurian” direction. It is quite conceivable that ornithomimosaurians acquired the aforementioned structural features in parallel with other groups of small theropods.

Examination of deinocheirosaurs, including Deinocheiridae and Therizinosauridae, is difficult because of the lack of more complete data regarding their morphology (at present all that is known of them is their forelimbs and girdle). We can say with certainty that these large predatory dinosaurs developed without reduction of the forelimbs after tridactyly had been established in the theropod specimen. The significant difference between them and known theropods is the development of large ungual phalanges, especially in Therizinosauridae. The absence of forelimb reduction allows us to propose that deinocheirosaurs were an independent lineage of large theropods far removed from true carnosaurs. It is possible that deinocheirosaurs are closer to ornithomimosaurians than to true carnosaurs. In fact, the structures of the forelimb and manus (excluding the ungual phalanges) in Deinocheiridae are similar to those of Ornithomimidae (Rozhdestvenskiy, 1970).

It remains to propose that at a comparatively early stage of their evolution, large theropods diverged into several lineages that developed with reduced forelimbs as well as without them (true carnosaurs and ornithomimosaurians, deinocheirosaurs). We may assume that theropod lineages (large and small) with non-reduced forelimbs and some other structures corresponded in development in roughly the same manner to the demands of the environment. The parallel evolution of theropod branches having non-reduced forelimbs apparently happened in other ways than the development of true carnosaurs.

It is difficult at the present time to simply divide theropods into two groups (carnosaurs and coelurosaurs). The notions of large and small theropods are broader. Within a single trunk of theropods are no fewer than six lines that developed in parallel in some features and specifically in others.

In the initial stage of saurischian radiation, theropod development went in the direction of perfecting bipedal locomotion, which corresponded in large degree to the common evolutionary trends of Triassic saurischians. In this direction predatory palaeopods were less successful because of the inadaptable nature of fundamentally important structures such as the pelvis and other correlated elements.

Theropod radiation, which occurred on a more adaptive basis than in Palaeopoda, led to splitting of a number of lineages (see Fig. 2) that developed in the direction of parallel specializations that is illustrated by the theropod lineages without reduced forelimbs. Not the size of the bodies (large and small), but the degree of forelimb development and all of the associated correlative changes may be laid at the foundation for further development of notions regarding theropod evolution.

The late stages of theropod development were characterized by more rapid evolution in a number of lineages, which is confirmed by their development of more fundamental adaptive transformations such as pelvis modification and the "predatory" claw on the pes of the Deinonychosauria, the lack of teeth in ornithomimosaurs and oviraptorosaurs, the acquisition of a special kinesis in oviraptorosaurs, the large ungual phalanges of the manus and the hypertrophic development of the forelimbs in deinocheirosaurs. All of this provides a foundation to examine these comparatively rapidly evolving lines at the level of a high taxonomic rank (infraorder).

In later stages of theropod evolution specialization took on a more profound character corresponding to new adaptive zones by which the theropod lineages disseminated. The development of small theropods (deinonychosaurians and oviraptorosaurs) is an example of the evolution of highly specialized branches toward the end of the Mesozoic.

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#### FIGURE CAPTIONS

Figure 1. Pelves of different theropod groups (schematically). For comparison the brachyiliac pelvis of *Palaeosaurus*, Palaeopoda (1) is shown. (2) *Coelophysis*, Coelurosauria; (3) *Antrodemus*, Carnosauria; (4) *Tarbosaurus*, Carnosauria; (5) *Gallimimus*, Ornithomimosauria; (6) *Oviraptor*, Oviraptorosauria (7) *Saurornithoides*, Deinonychosauria; (8) *Adasaurus*, Deinonychosauria. Images 1-3 from Colbert, 1964; image 4 from Maleyev, 1974.

Figure 2. Development of theropod evolutionary lines. Key: (a) Triassic; (b) Jurassic; (c) Cretaceous; (d) thecodonts.