

RECONSTRUCTIONS OF THE SMALL CRETACEOUS THEROPOD

Stenonychosaurus inequalis AND A HYPOTHETICAL DINOSAUROID

D.A. Russell and R. Séguin

National Museum of Natural Sciences

Ottawa K1A 0M8

Syllogeus No. 37

National Museums of Canada

National Museum of Natural Sciences

Les Musées nationaux du Canada

Musée national des Sciences naturelles

ABSTRACT

Deinonychosaurs are small, carnivorous dinosaurs that are currently divided into two lineages: dromaeosaurs and the more gracile saurornithoids. The most complete saurornithoid specimen known from North America is *Stenonychosaurus inequalis* from late Cretaceous deposits near Dinosaur Provincial Park, Alberta. It is used as the basis for constructing a life-size, coloured model of the species. Speculations are made on how descendants of *S. inequalis* with its large brain, stereoscopic vision, opposable fingers and bipedal stature might have changed had they survived the terminal Mesozoic extinctions, and achieved an encephalization quotient similar to that of *Homo sapiens*. A model of this hypothetical creature, the dinosauroid, was "restored" and cast in the same manner as *Stenonychosaurus*, and the rationale behind the physical features of the dinosauroid model is given.

RÉSUMÉ

Les dinonychosaures sont de petits dinosaures carnivores actuellement répartis en deux lignées: les droméosaures, et les saurornithoïdes plus frêles. Le spécimen le plus complet de saurornithoïde connu en Amérique du Nord est un *Stenonychosaurus inequalis* trouvé dans un gisement du Crétacé supérieur près du Parc provincial des Dinosaures en Alberta. Il a servi de modèle à la réalisation d'une maquette en couleurs grandeur nature de l'espèce. Étant donné les caractéristiques de *S. inequalis* - cerveau volumineux, vision stéréoscopique, doigts opposables et station bipède - l'auteur formule des conjectures sur l'évolution qu'auraient pu connaître les descendants de l'espèce s'ils avaient survécu à l'extermination survenue à la fin du Mésozoïque et atteint un quotient d'encéphalisation semblable à celui d'*Homo sapiens*. Une maquette de cet être hypothétique, baptisé dinosauroïde, a été "reconstituée" et réalisée de la même manière que celle de *Stenonychosaurus*, et l'auteur justifie les caractéristiques physiques qu'il attribue à son modèle.

INTRODUCTION

During the past decade a group of small, raptorial dinosaurs that lived near the end of the age of reptiles has received much paleontological attention. Reconstructions of one variety (*Deinonychus*) have been widely circulated in technical and popular publications (e.g. Ostrom 1969B, frontispiece; 1978A, pp. 160-161), and the presence of an enlarged brain in another (*Stenonychosaurus*) has stimulated discussion on the evolution of intelligence in reptiles (e.g. Hopson 1980, Russell 1981). Few reconstructions of the latter form are available, and a new one is presented here to partly meet this need. In addition to its typically dinosaurian attributes, *Stenonychosaurus* may also have possessed overlapping visual fields and an opposable digit in the manus. This cluster of characteristics has prompted many informal questions on what the subsequent history of these animals might have been had the dinosaurs not become extinct. A tentative, three-dimensional model responding to these questions is presented here. It is hoped that this model will promote consideration of the effects of encephalization on vertebrate morphology.

Although our professional formation has been in different areas (D.A.R., paleontology; R.S., taxidermy), the two models discussed below are the result of a collaboration in which it is difficult to separate the individual contributions.

ACKNOWLEDGEMENTS

We are grateful to Drs. Francis Cook and Henri Ouellet, of the Vertebrate Zoology Division, National Museum of Natural Sciences, for information on viviparity in reptiles and the morphology of the claws in raptorial birds; to Dr. Philip Currie, of the Provincial Museum of Alberta, for the cast of a *Stenonychosaurus* specimen in the collections of his institution; to Dr. Arnold Wiegert, of the Hydraulics Laboratory, National Research Council of Canada, for measuring the displacement of the completed *Stenonychosaurus* model; and to our colleagues in the Paleobiology Division for many hours of stimulating discussion during the period when the models were being fabricated.

We wish to thank Mrs. Gail Rice and Dr. C.R. Harington for help in preparation of the final draft of this publication. Ms. Nancy Archambault (Systemhouse Ltd.) typed the manuscript.

ABBREVIATIONS

Abbreviations of institutional names which precede specimen numbers referred to in the text are as follows:

AMNH - American Museum of Natural History

NMC - National Museums of Canada

PMA - Provincial Museum of Alberta

YPM - Yale Peabody Museum

DEINONYCHOSAURS

About fifty years ago, the remains of several small, related carnivorous dinosaurs were identified in late Cretaceous strata in North America and central Asia (Table 1). The anatomical peculiarities of these creatures were inadequately appreciated by the paleontological community until the morphology of *Deinonychus*, an early Cretaceous member of the group, was described in detail by Ostrom (1969A, 1969B, 1976). They were then recognized as a special infraorder of theropod dinosaurs which possessed raptorial claws on the inside of an otherwise didactylate cursorial foot, and were termed deinonychosaurs (Colbert and Russell 1969, Ostrom 1969B). The function of these claws as disemboweling devices was graphically demonstrated by the discovery of a fossilized *Velociraptor* skeleton clinging to the body of a small plant-eating dinosaur (*Protoceratops*, see Barsbold 1974A; Ostrom 1978A, photograph on p. ii). Raptorial claws have also been reported on the inner side of the foot in *Naosaurus*, a small theropod from the terminal Cretaceous of Argentina (Bonaparte and Powell 1980). If these structures were not independently evolved, they can be cited as evidence that deinonychosaurs arose and spread throughout the world before the separation of the continents during early Cretaceous time (cf. Galton 1980). Resemblances between the skeleton of *Archaeopteryx*, widely considered to represent that of an ancestral late Jurassic bird, and deinonychosaurs have also been noted (Ostrom 1974, Barsbold and Perle 1979). However, the foot in *Archaeopteryx* lacks the specializations seen in deinonychosaurs (cf. Wellnhofer 1974) and the relationship may not be close.

Two lineages are currently recognized within the Deinonychosauria: the Dromaeosauridae including *Deinonychus*, *Velociraptor* and *Dromaeosaurus*, and the Saurornithoididae including *Saurornithoides* and *Stenonychosaurus* (Ostrom 1969B, Fig. 83; Colbert and

Russell 1969, p. 39; Russell 1969; Barsbold 1974B, 1976; Sues 1978). The general morphology of dromaeosaurs is now relatively well understood, and considered to be typical for the infraorder. However, saurornithoids differ from dromaeosaurs in many skeletal characteristics. The animals were more gracile than were dromaeosaurs. The skull and teeth were relatively small. The eyes and brain were larger than in dromaeosaurs, and the former were anteromedially inclined suggesting the existence of broadly overlapping visual fields. The centra of the presacral vertebrae lack the excavations (pleurocoels) seen in dromaeosaurs, and the zygapophyses of the distal caudal vertebrae are shorter. Saurornithoids were thus a distinct group of late Cretaceous theropods.

MODELLING *Stenonychosaurus inequalis*

The most complete saurornithoid specimen so far known from North America is NMC 12340 belonging to *Stenonychosaurus inequalis* (Russell 1969), which is about as complete as the famous australopithecine skeleton "Lucy" from the Afar region of Ethiopia (Johanson and Edey 1981). It was collected from 76 million-year-old fluviodeltaic deposits (Judith River = Oldman Formation) near Dinosaur Provincial Park, Alberta, the paleoecology of which has been reviewed by Béland and Russell (1978). The dimensions of skeletal elements preserved in NMC 12340 provided the scale for a three-dimensional plastic skeletal reconstruction (Figs. 1-5) into which the morphology of known skeletal fragments of *S. inequalis* was incorporated, in general conformity with more complete material of closely related forms.

The skull (Fig. 6) is modelled after cranial fragments preserved in NMC 12340, NMC 12392 an isolated maxilla, NMC 8540 a dentary (cf. Russell 1969), and a fronto-parietal in which the crests along the posterior border of the temporal fossae are exceptionally well preserved (PMA P79.8.1), supplemented by morphology preserved in crania of *Saurornithoides mongoliensis* and *S. junior* (Barsbold 1974B). If it has been properly reconstructed, the skull is broader and shorter than in the Asian species (cf. Russell 1969, p. 600).

The vertebral column is represented only by a fragment of one presacral (dorsal) centrum in NMC 12340, together with a distal caudal vertebra in this specimen and another in NMC 8539. Its reconstruction thus presented substantial difficulties, as well as opportunities for error. The reconstructed length of the central fragment, by comparison with the vertebral form as preserved in *Saurornithoides mongoliensis* (Russell 1969), *Deinonychus antirrhopus* (Ostrom 1969B, Fig. 34) and *Saurornitholestes langstoni* (Sues 1978), is

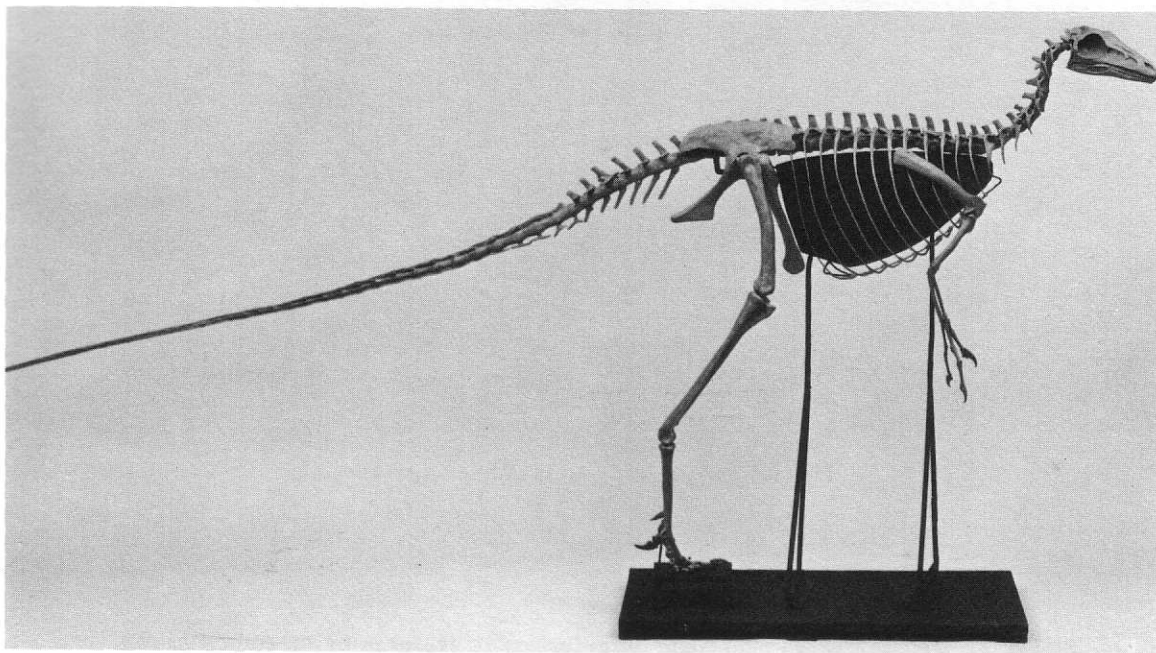


FIGURE 1. *Reconstructed skeleton of STENONYCHOSAURUS INEQUALIS,*
lateral aspect (NMC neg. 81-1668).



FIGURE 2. *Reconstructed skull and anterior axial skeleton of STENONYCHOSAURUS INEQUALIS* (NMC neg. 81-1671).

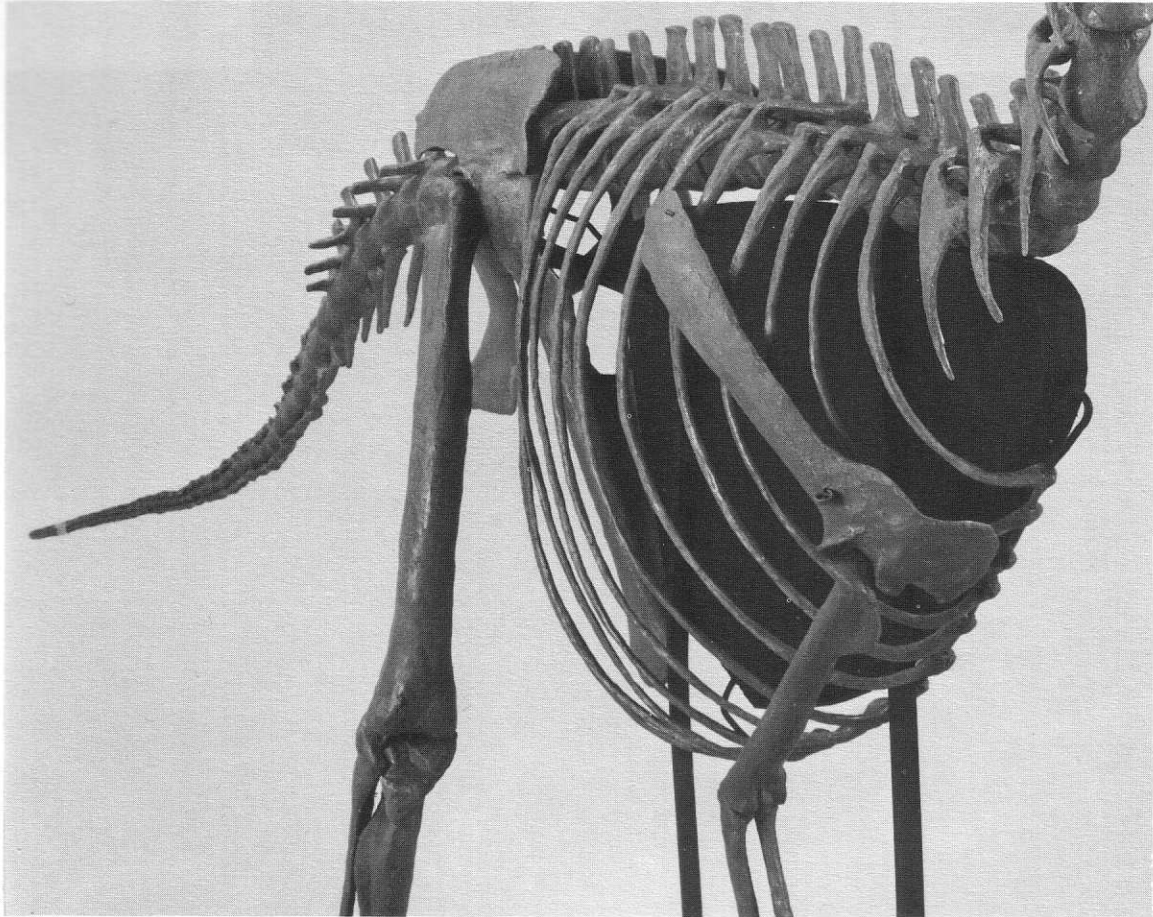


FIGURE 3. *Reconstructed appendicular girdles and axial skeleton of STENONYCHOSAURUS INEQUALIS, anterolateral aspect (NMC neg. 81-1667).*



FIGURE 4. *Reconstructed manus of STENONYCHOSAURUS INEQUALIS, dorsal aspect*
(NMC neg. 81-1670).

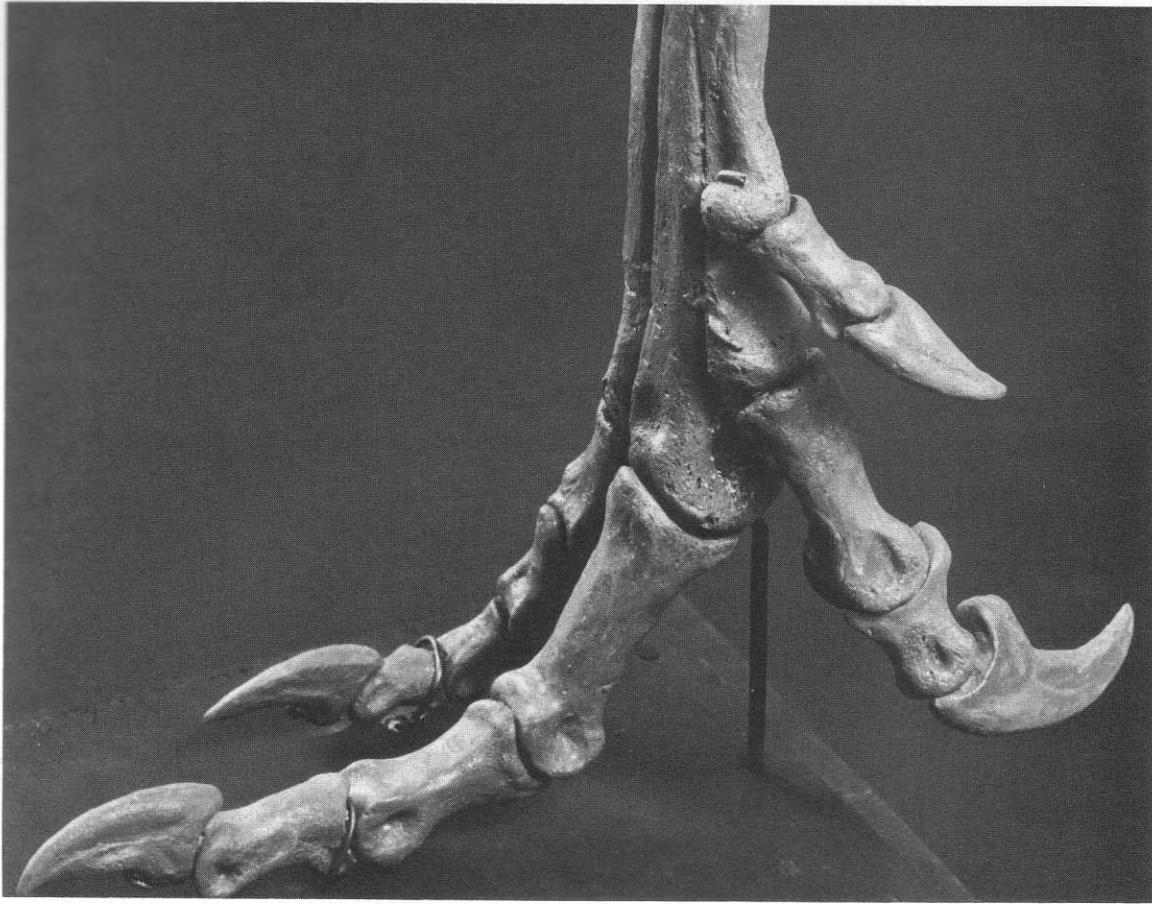
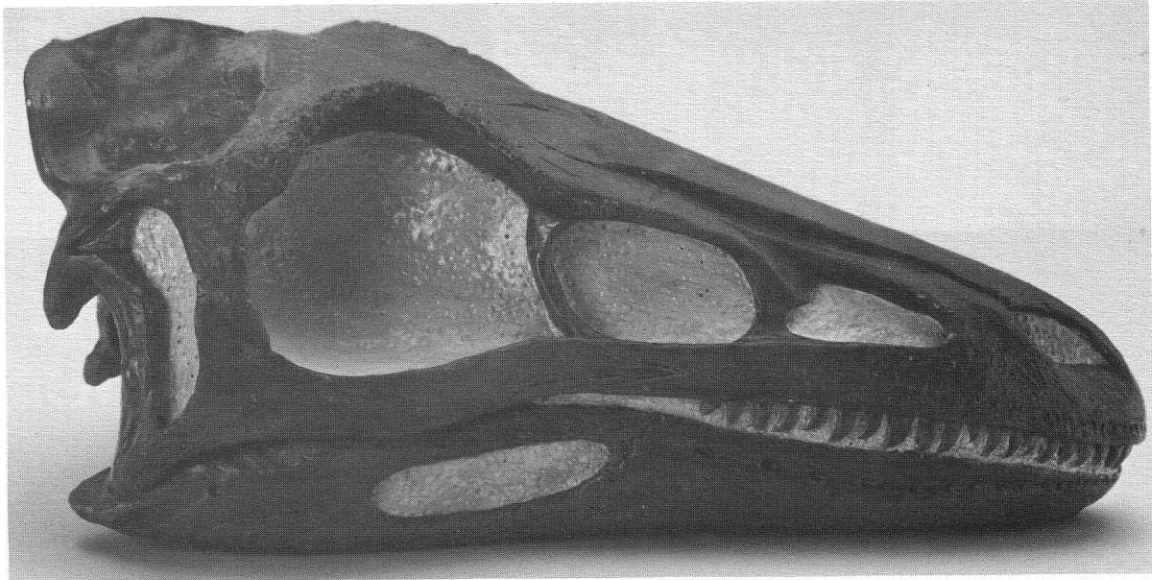
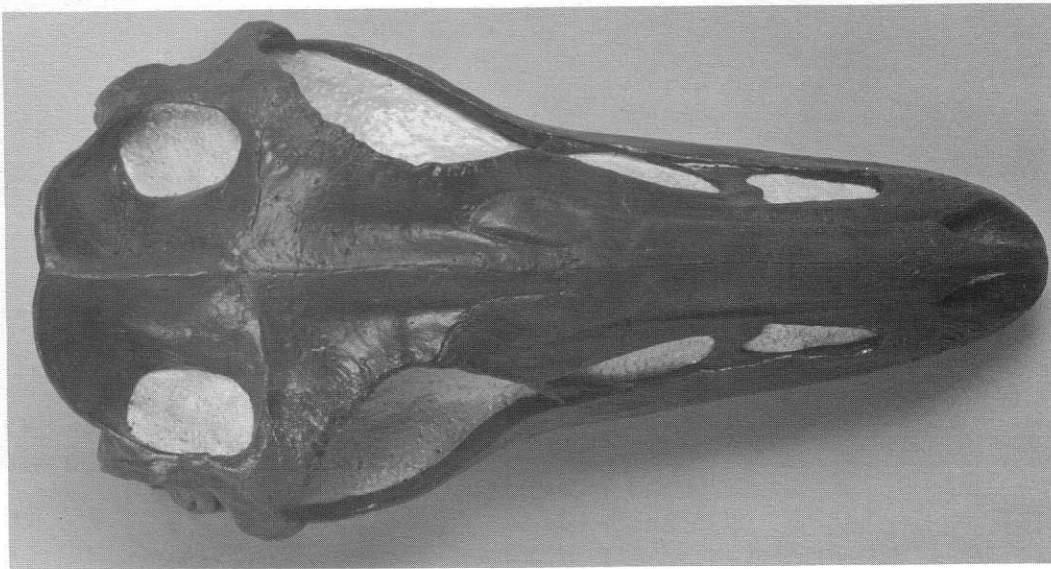


FIGURE 5. *Reconstructed pes of STENONYCHOSAURUS INEQUALIS, medial aspect*
(NMC neg. 81-1674).



A



B

FIGURE 6. *Reconstructed skull of STENONYCHOSAURUS INEQUALIS (A - NMC neg. 81-7494, lateral aspect; B - 81-7493, dorsal aspect).*

estimated to be 36 mm. The length of the presacral column is calculated according to vertebral proportions in AMNH 3015 (*D. antirrhopus*, Ostrom 1969B, Table 4), allowing 3 mm for each inter-vertebral disc. The combined length of six sacral centra is estimated according to central proportions in the sacrum of *S. mongoliensis* (Russell 1969, Table 7). The proximal caudals have been restored after those in *S. junior* (Barsbold 1974B, Pl.4, Figs. 2-3), again scaled to central lengths expected at the base of the tail in NMC 12340. In all cases extrapolations are approximately linear, as insufficient materials are available to serve as a basis for the identification of allometric trends. The similarity between the lengths of posterior dorsal, sacral and basal caudal centra in AMNH 6516 (*S. mongoliensis*) is here interpreted as evidence that the caudal series in the specimen of *S. junior* cited above includes the base of the tail.

Of the elements of the forelimb, only the ulna is completely preserved in NMC 12340. The length of the humerus is restored according to humeral-ulnar proportions in *D. antirrhopus* (Ostrom 1969B, Table 10). Fragments of phalangeal elements and unguals suggest that manual proportions in NMC 12340 were about three-quarters of those in YPM 5206 (*D. antirrhopus*, Ostrom 1969B, Fig. 62).

The pelvis was restored after that of *Saurornithoides* (Barsbold 1977, Figs. 1-7). The diameters of the femora in NMC 12340 and AMNH 6516 (*S. mongoliensis*) were employed to scale up the lengths of the femur and tibia-astragalus as estimated for the latter specimen (Russell 1969, Table 8) to the proportions of the skeletal reconstruction. The pes is restored after NMC 8539 and NMC 12340. Measurements of the reconstructed skeletal components are given in Table 2.

The soft parts of *Stenonychosaurus inequalis* were modelled directly onto the skeletal reconstruction, permitting a dimensional control that would otherwise not have been possible. The effects of this control can be seen by comparing a model on a scale of 1:7 (Fig. 7), which was prepared as the skeletal parts were being cast, with the completed full-scale model (Fig. 8). The presence of a skeletal framework also facilitated the speed, accuracy and confidence with which a reconstruction of the body form was completed. The preliminary scale-model was primarily designed to identify a balanced, life-like pose for the skeletal reconstruction.

The muscular system is basically as described by Romer (1956) for reptiles, modified to fit a theropod frame, and the myology of the pelvic region is adapted from that in ornithomimids as restored by Russell (1972). The shapes of the muscle masses were

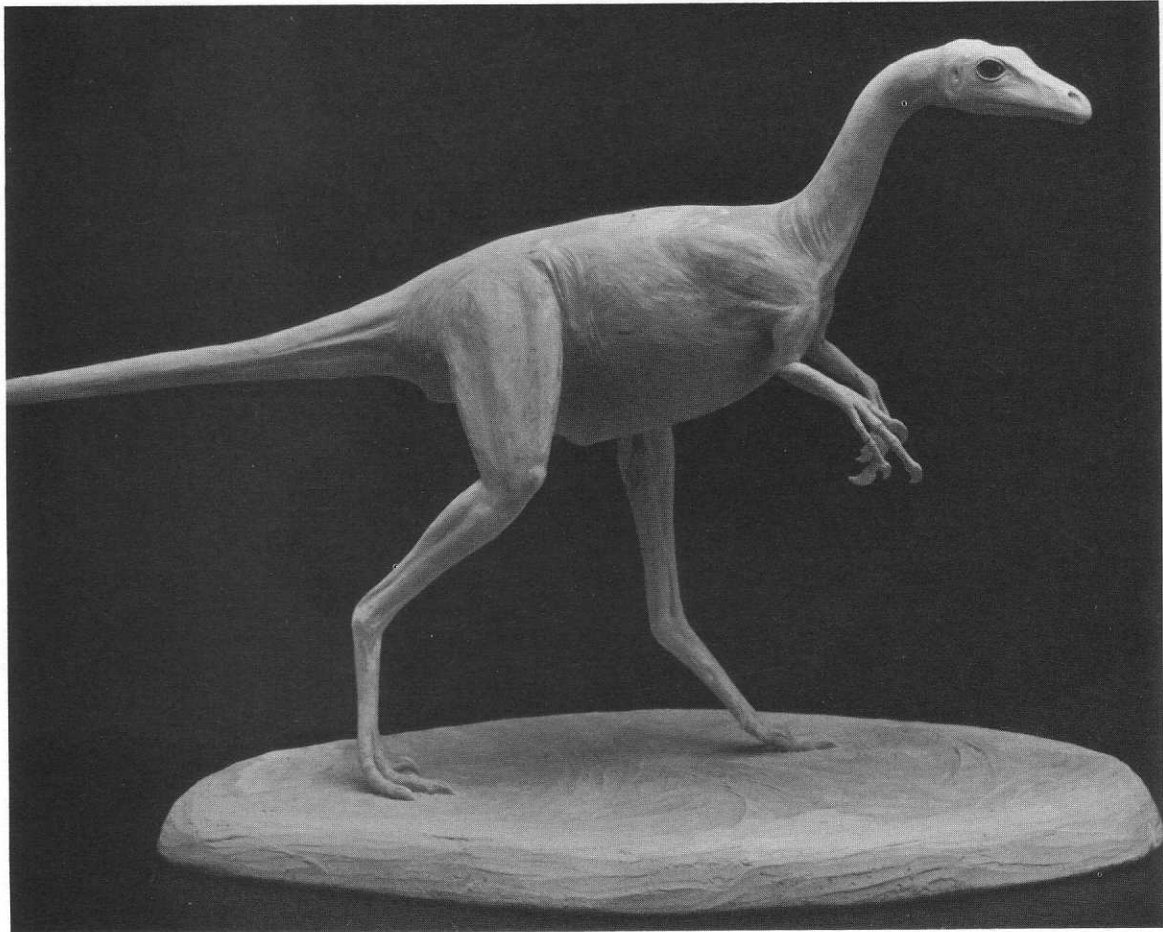


FIGURE 7. *Preliminary scale model (1:7) of body form of STENONYCHOSAURUS INEQUALIS, lateral aspect (NMC neg. 81-1665).*

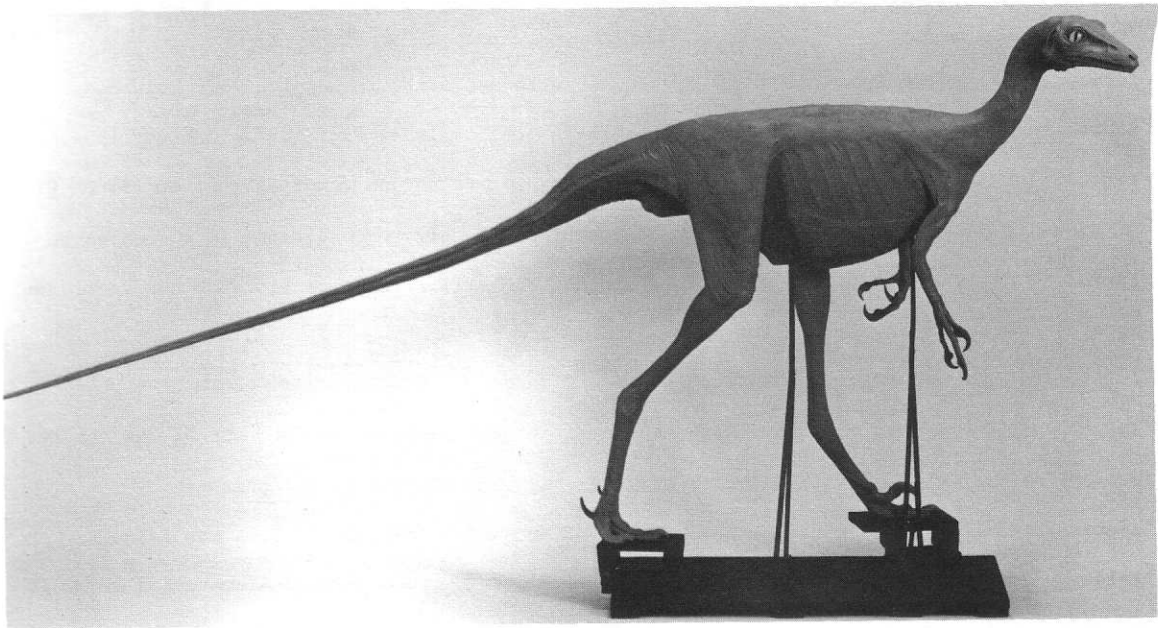


FIGURE 8. Completed scale model (1:1) of body form of *STENONYCHOSAURUS INEQUALIS*, lateral aspect (NMC neg. 81-1244).

approximated by excelsior bundles, which were coated with papier mâché and completed with a thin layer of plasticene. Ribs associated with NMC 12340 defined the cross-sectional shape of the body, and the distal elements of the pelvis defined its ventral contour. It may be noted that the pelvic canal in saurornithoids is relatively as large as in ornithomimids (cf. Russell 1969, p. 608). A flexible plastic tube was used to approximate the possible course of the trachea. Photographs of large lizards (Schmidt and Inger 1957, Pls. 33, 34, 52; Figures on pp. 171, 172) provided details which were incorporated into skin texture, skin folds, eyelids and lips. Articulations between foot bones in *Stenonychosaurus*, as well as those in many other theropods, are strongly reminiscent of those in large ground birds, and the external morphology of the ratite and particularly the cassowary foot has been closely followed (cf. Gilliard 1958, Pl. 6, Fig. on p. 21; Stanek 1962, Figs. on pp. 338-341). The forms of the claws of the hands and feet were patterned after impressions of keratinous sheaths preserved in *Archaeopteryx lithographica* (Ostrom 1974, Fig. 10; Wellnhofer 1974, Fig. 13) and in its tiny theropodous contemporary *Compsognathus longipes* (Ostrom 1978B, Pl. 9, Fig. 5), but lengthened somewhat to conform more closely to conditions in modern large raptorial birds (H. Ouellet, personal communication 1981). The appearance of the completed model is depicted in Figs. 8-12.

The restoration of the eye deserves special comment. A diameter of 52 mm given by Russell (1969, p. 597) presumes that the eye was closely applied to the roof of the orbital cavity. A more conservative diameter of 44 mm has been adopted in the present reconstruction. It is apparent, however, that the eye in *Stenonychosaurus* was large relative to those of modern land-dwelling vertebrates, where a maximum diameter of 50 mm is attained in the ostrich (Walls 1942, p. 642). The average diameter of sclerotic rings reported in various dinosaurian taxa exceeds that of the ostrich eye, and only in *Psittacosaurus* are the dimensions of the human eye approximated (Table 3). Why did dinosaurs possess such large eyes? Were they essentially nocturnal creatures, thereby avoiding the heat loads that would otherwise have been acquired through diurnal activity? Were the light-transmitting properties of the atmosphere different then? In the case of *Stenonychosaurus*, with its highly developed raptorial claws, the following observations (Walls 1942, p. 209) may be relevant:

"The superior visual acuity of the diurnal vertebrate often enables him to maintain an enormous disparity between his armament and the defenses of his prey - as when a hawk seizes a gartersnake or a kingbird catches

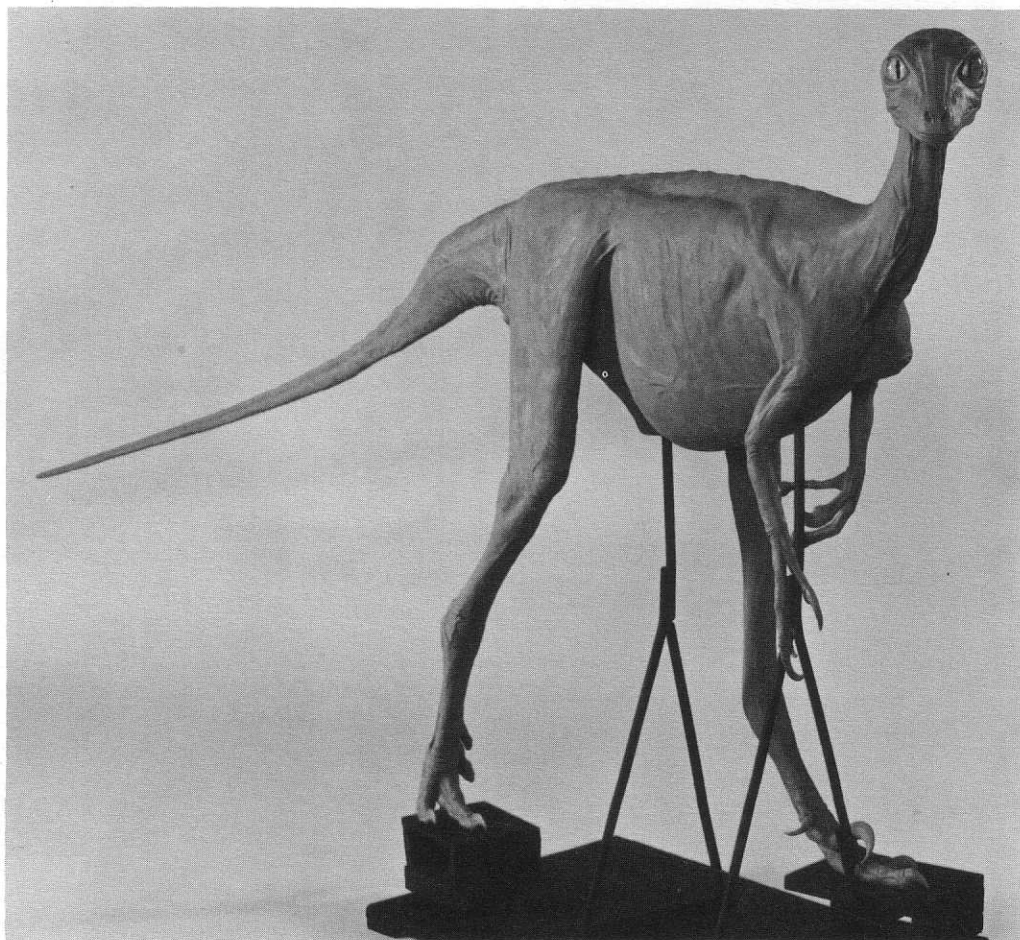


FIGURE 9. *Completed scale model of body form of STENONYCHOSAURUS INEQUALIS, anterolateral aspect (NMC neg. 81-1243).*



FIGURE 10. *Model of head in STENONYCHOSAURUS INEQUALIS, lateral aspect*
(NMC neg. 81-1242).

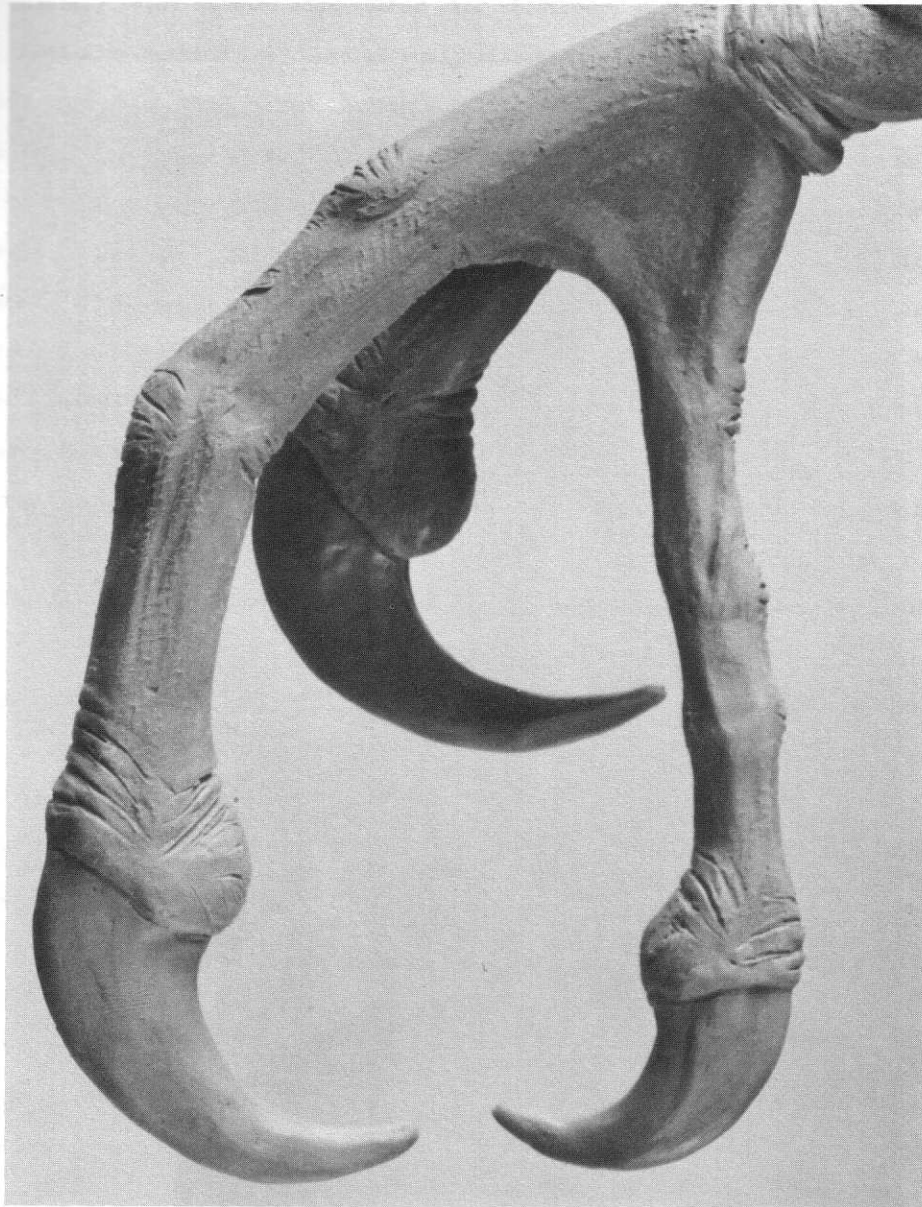


FIGURE 11. *Model of hand in STENONYCHOSAURUS INEQUALIS, lateral aspect*
(NMC neg. 81-1246).

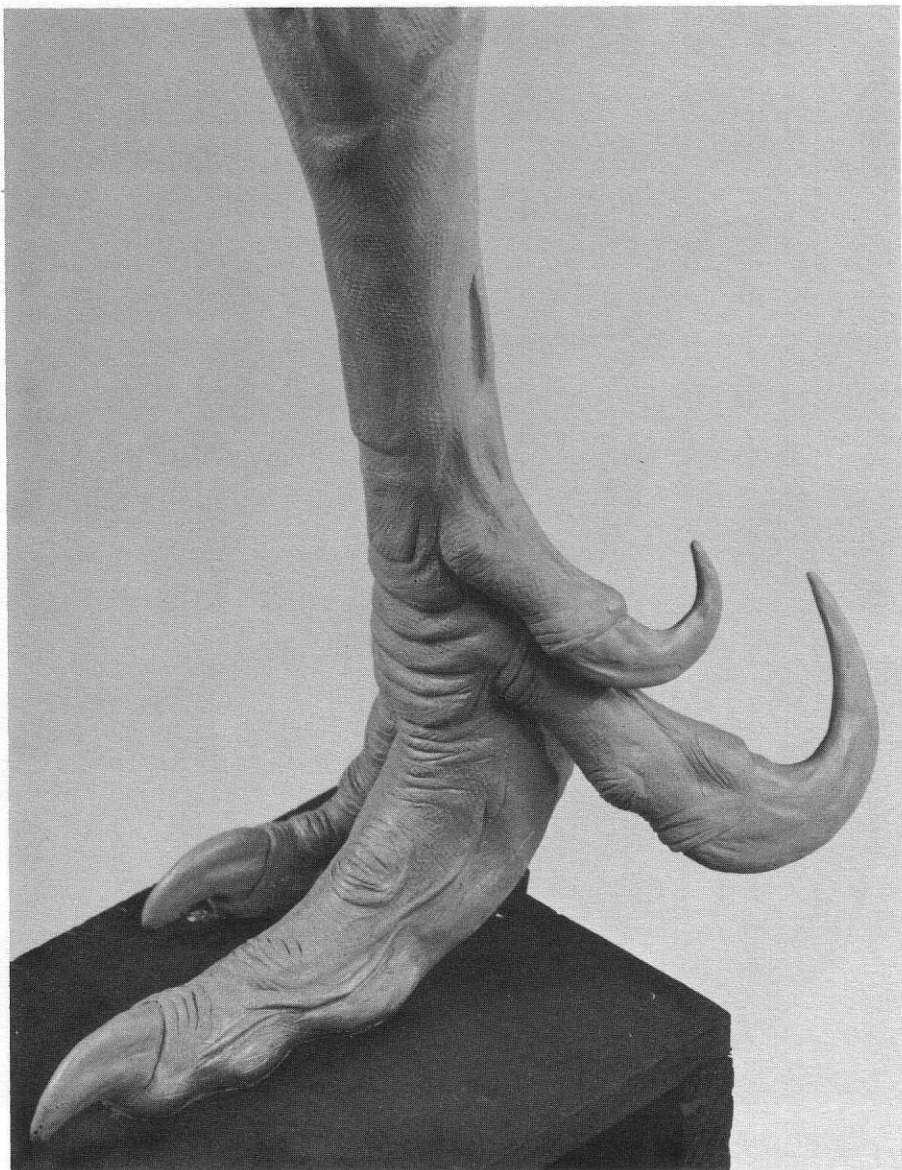


FIGURE 12. *Model of foot in STENONYCHOSAURUS INEQUALIS, medial aspect*
(NMC neg. 81-1249).

a fly. The nocturnal carnivore must have superior weapons, for he must usually fight on more equal terms with relatively much larger prey."

The similarity between the range of encephalization of carnivorous mammals and the herbivores upon which they preyed (Radinsky 1978) would suggest that the small raptorial dinosaur fed on similarly encephalized mammals, which were in turn presumably more active at night. It may thus be postulated that *Stenonychosaurus* was a crepuscular or nocturnal carnivore with unusually acute visual capabilities relative to those of modern terrestrial vertebrates. Geckoes are known for their visual acuity (Bellairs 1970, p. 350), and the eye in the reconstruction is accordingly patterned after that of *Gekko gekko* (Schmidt and Inger 1957, Pls. 22-23). It was cast in bioplastic in the shape of a hemisphere, and the iris and pupil were painted onto the flat internal surface.

A rubber latex mould was made from the model, and reinforced with multipieced fibreglass backing arranged so that only a single, narrow seam would remain on the cast. The internal surfaces of the mould were coated with a glass-fibre reinforced epoxy resin in which a metal framework was imbedded to add rigidity. A different mix of epoxy resin was used in the feet, reinforcing the otherwise weak contact between the feet and the base. The solidified material remained sufficiently flexible to permit removal of the latex mould from the hands and feet, but strong enough to enable the cast to withstand handling. The cast was mounted on a base simulating ripplemarked surfaces occurring in the late Cretaceous Horseshoe Canyon Formation of Alberta. It was coated by hand and with a spraying device with oil paints to resemble colour patterns typical of large reptiles inhabiting forested environments (cf. Schmidt and Inger 1957), analogous to those presumed to have been preferred by *Stenonychosaurus* (Béland and Russell 1978). It must be stressed that no attempt was made to make the painted cast (Fig. 13) appear alert or intelligent. Measurements of the finished reconstruction are given in Table 4. Seven months were required to complete the project.

ENCEPHALIZATION AND SUGGESTED HABITS OF *Stenonychosaurus*

Because *Stenonychosaurus* has figured in discussions of the parallel acquisition of intelligence in reptiles, its brain-body proportions were reassessed with the aid of the completed reconstruction. The model was found to displace 46.6 kg of water. Assuming the living animal had a specific gravity of 0.8 or 0.9 (Colbert 1962, p. 5), weights of 37.3 or 41.9 kg are indicated, which are less than the 45.3 kg estimated by Russell (1969, p. 599) on the basis of femoral proportions. The weight of the brain has been estimated at 37 (Hopson

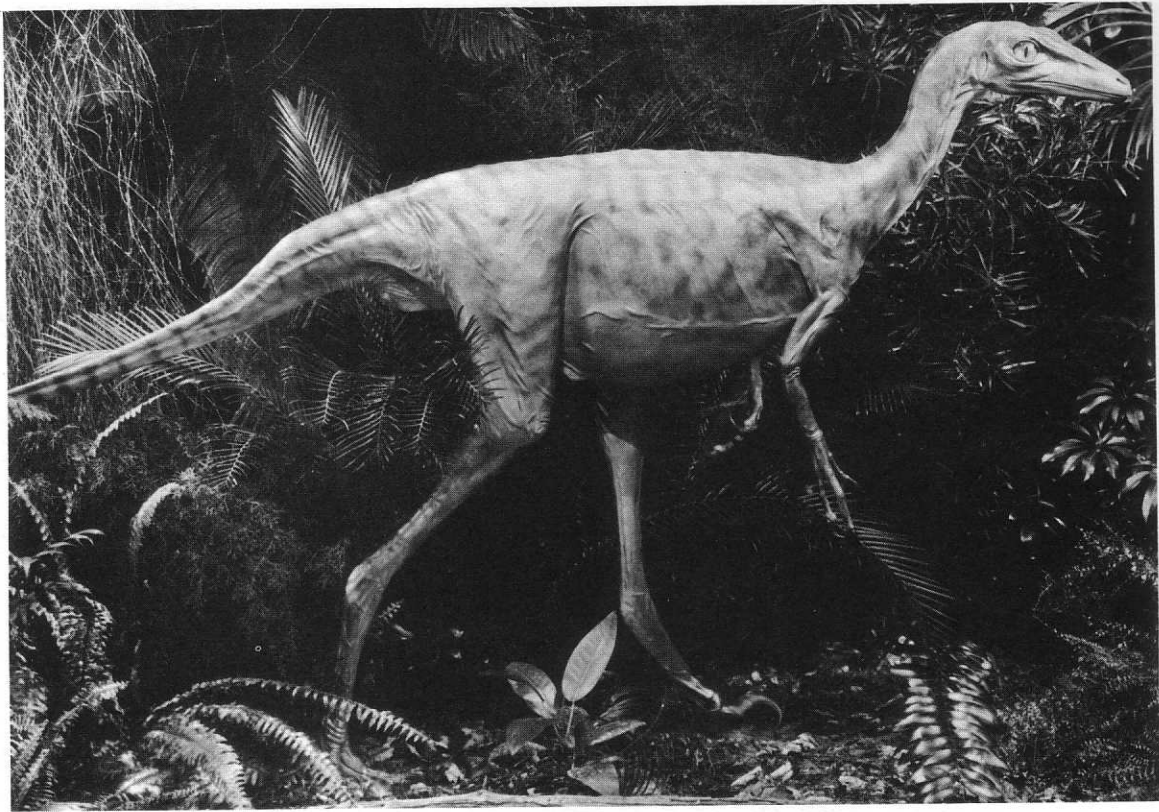


FIGURE 13. *Painted cast of reconstructed body form of STENONYCHOSAURUS INEQUALIS, lateral aspect (NMC neg. 81-3251).*

1980, Table 1, p. 297) and 45 gm (Russell 1969, p. 599). Using Jerison's (1973) general relationship between brain weight (E, gms) and body weight (P, gms) in mammals:

$$E \text{ expected} = 0.12 P^{2/3} \quad (\text{equation 1})$$

and definition of Encephalization Quotient (EQ)

$$EQ = E \text{ observed} / E \text{ expected} \quad (\text{equation 2})$$

encephalization (EQ) values were obtained for *Stenonychosaurus* which vary between 0.24 and 0.34 (Table 5). This approximates the range of encephalization observed between guinea fowl and bustards, between armadillos and opossums (Crile and Quiring 1940) or among the basal insectivores (Jerison 1973, Table 10.3).

Although the brain was relatively much larger in *Stenonychosaurus* than in most dinosaurs (Hopson 1980), other small theropods had also attained comparable levels of encephalization (cf. Russell 1972, Hopson 1977, Sues 1978). Because these creatures, and small dinosaurs in general, are so poorly known, it is probable that forms which remain to be described will displace *Stenonychosaurus* at the recorded apogee of dinosaurian encephalization. If the reconstruction presented here (Fig. 12) is approximately correct, it was nevertheless surely an interesting animal. With a weight of about 40 kg, it is one of the smallest dinosaurs known from western Canada. Its large eyes suggest agility (Walls 1942, p. 173), as do its stereoscopic vision, long legs and a lightly-constructed frame. The tail was most flexible at its base, implying that it controlled the angular momentum of the body through elevation or extension in rapid turns. The shape of the ulna indicates that the forearm could be rotated, and the structure of the carpal block suggests that the third finger could possibly have been opposed to the other two (Russell 1969). Flesh-eating habits are clearly reflected in the structure of the limbs, where the hands were adapted to grasp a victim while it was being eviscerated by the talons on the inside of the feet. *Stenonychosaurus* was a highly progressive animal for its day, and, perhaps, would not seem too out of place among today's Australian fauna.

THE DINOSAUROID - A HYPOTHETICAL DESCENDENT OF *Stenonychosaurus*

A curve representing the maximum level of encephalization known in organisms living on our planet can be drawn across the last 600 million years of Phanerozoic time (Russell 1981, Fig. 1). Man and his immediate antecedents lie on this curve, and *Stenonychosaurus* closely approached it during late Mesozoic time. *S. inequalis* (NMC 12340) lived approximately 12 million years before the end of the age of reptiles. Although isolated saurornithoid bones

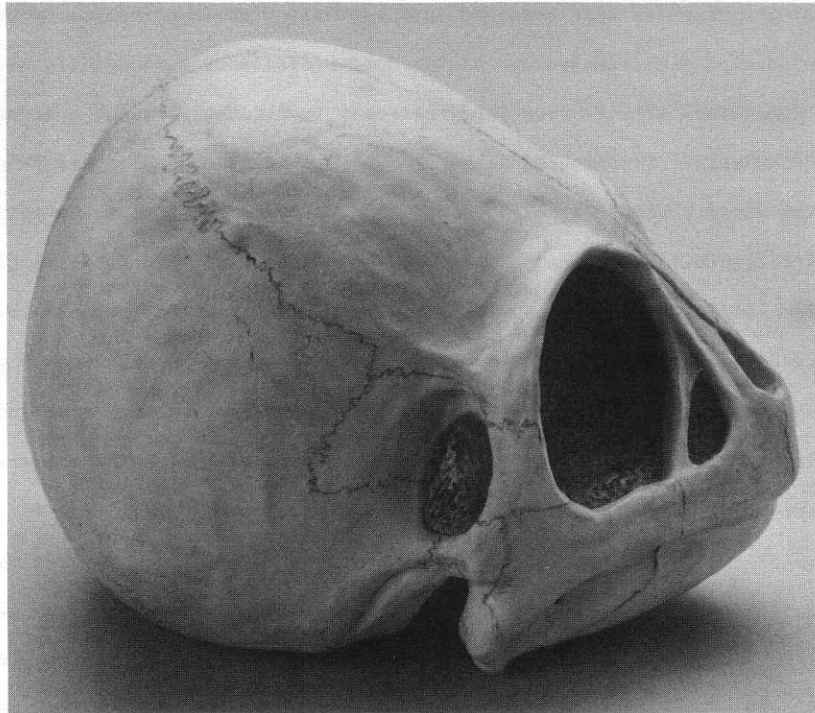
are known in the youngest Mesozoic deposits (K. Carpenter, personal communication 1981), no skeletal fragments have been collected which are sufficiently complete to yield brain-body weight estimates. Sixty-four million years ago the dinosaurs, including the saurornithoid lineage, vanished from the surface of our planet in a catastrophe the dimensions of which are only currently beginning to be explored. It would be fascinating to learn how the saurornithoid attributes of large brain size, stereoscopic vision, opposable fingers and bipedal stature changed, if at all, during the remainder of Mesozoic time. It might also be entertaining to speculate in a qualitative manner on how the descendants of *S. inequalis* might have appeared had they survived the terminal Mesozoic extinctions, and achieved an encephalization quotient similar to that of *Homo sapiens* (about 7.5, cf. Jerison 1973, Table 16.3), 76 million years along the curve of maximum encephalization into their future.

The cerebral hemispheres of *S. inequalis* were approximately triangular in dorsal aspect, more closely resembling those of birds than the more elliptical form seen in anthropoids (cf. Russell 1969, Fig. 3; Romer 1962, Fig. 388; Gregory 1951, Fig. 23.64). This general shape was retained as the endocranial volume was increased to 1,100 ml to equal that of the skull of a small human female skeleton in the collections of the Paleobiology Division. As the endocranial volume is increased the facial region diminishes in relative size, and the craniofacial proportions of a chick embryo (Goodrich 1958, Fig. 622) were selected as a guide for constructing a model of the hypothetical skull. The teeth in saurornithoids are reduced relative to those of dromaeosaurs, and it was decided to eliminate them altogether in favour of keratinous occlusal surfaces similar to those of turtles and, to a lesser degree, of ornithomimids. The paedomorphic features of a relatively large brain and reduced dentition are also characteristic of the higher anthropoids (Gould 1977). The elevated metabolic requirements of a large brain (Sokoloff 1976) are consistent with the attainment of endothermy and the need for energy-rich food. A potential hazard of tooth decay, given frugivorous as well as carnivorous habits, is avoided through the suppression of teeth. The external nares were elevated in the model to accommodate a secondary palate, as is known to occur in ornithomimids (Russell 1972, p. 399). By definition, a high level of encephalization implies that the head will be heavy relative to the total weight of the body, and will present special support problems. In *Pachycephalosaurus* the comparably massive, although bony cranium is balanced over an occipital condyle and foramen magnum which have been displaced toward the centre of the undersurface of the skull (Brown and Schlaikjer 1943, Pl. 39, Fig. 1).

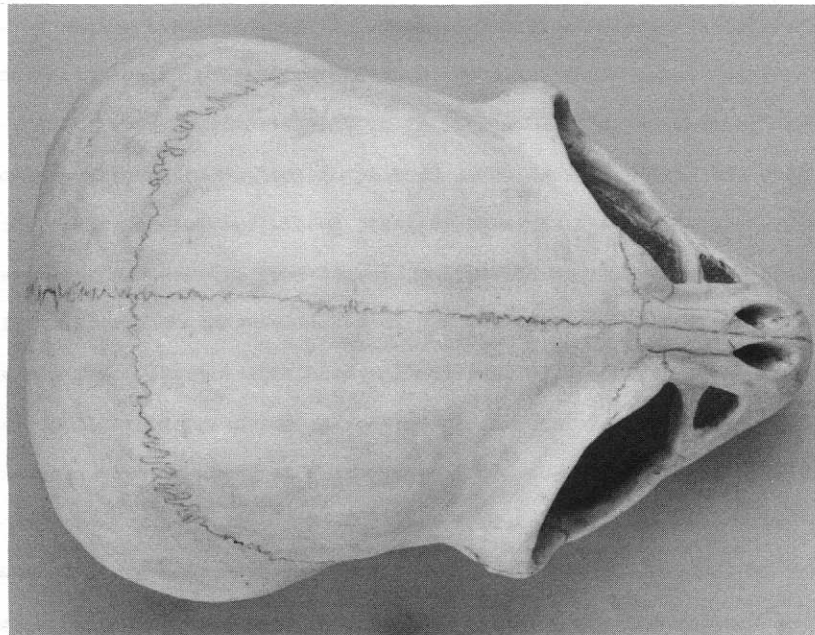
The foregoing attributes were combined into a model of the hypothetical skull (Fig. 14), upon which the sutural patterns between the cranial elements of *S. inequalis* have been imposed. The dimensions of the orbit were retained, in deference to the generally large size of the eye in dinosaurs. The lateral temporal fenestra of *S. inequalis* has been closed by alae from the squamosal, postorbital and jugal, and the quadratojugal was eliminated. Only a single antorbital fenestra has been retained in the maxilla, and the external mandibular fenestra has been suppressed. Osteological simplifications similar to these are often evident in vertebrate phyla which have persisted over many tens of millions of years. In conformity with the typical reptilian condition, the craniomandibular articulation is placed below the occlusal surface rather than above it as in most mammals. The architecture of the jaws is at least as powerfully developed as in our own species.

The posture of the vertebral column in a hypothetical highly encephalized derivative of *S. inequalis* is more problematic. Perhaps an enlarged head could effectively be supported through a redistribution of body weight to a position behind the legs, and the formation of a ligamentous suspensor above the chest and neck (visualizing these adaptations in ratites and in sauropods). However, it is the experience of many people throughout the world that large loads can more easily be carried balanced on the head than attached to the back or held in the arms. Using this example as an analogy to define a limiting condition in cranial support, it seems reasonable to suppose that it is energetically more efficient to balance an enlarged head on a vertical neck than to suspend it on the end of a horizontal neck with muscles and ligaments. Brown and Schlaikjer (1943, p. 138) postulated that *Pachycephalosaurus* was habitually bipedal, and by inference possessed a more upright posture than other bipedal ornithischians. Unfortunately, the postcranial skeleton of this dinosaur is unknown. The tendency to position the head more directly over the vertebral column is seen in anthropoids of increasing brain size (Adams and Moore 1975). A shortened neck would diminish accelerations sustained by the fragile brain as a consequence of neck and body movements (cf. Oldendorf and Zabielski 1981).

With respect to the post-cervical portion of the vertebral column, it is known that the acquisition of an upright posture preceded the phylogenetic expansion of the brain in hominids (White 1980). Perhaps at about or slightly above the level of encephalization of the great apes, the ability to use tools becomes a factor of major importance in selection (Washburn 1978, Lewin 1981). An energetically efficient mode of locomotion (Rodman and McHenry 1980; per unit weight transportation costs are low in man relative to those in many

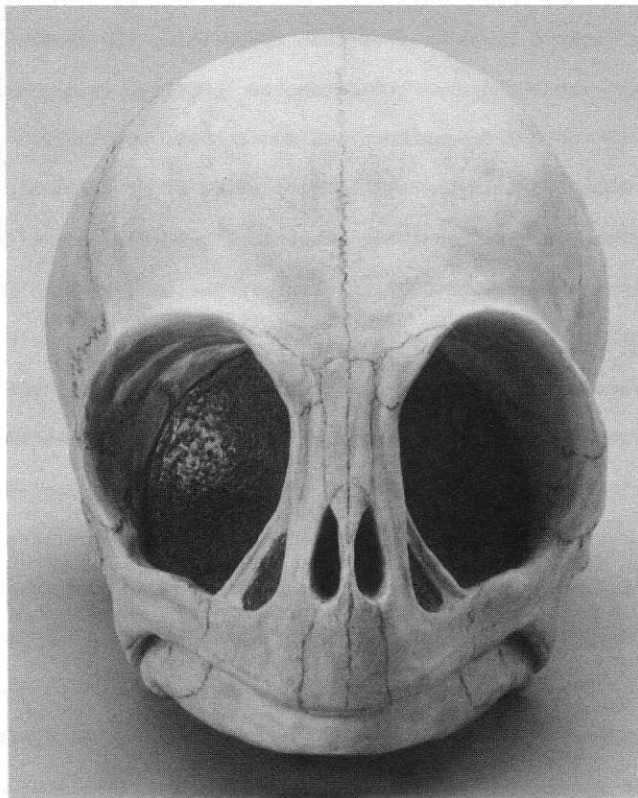


A



B

FIGURE 14. *Model of dinosauroid skull (A - NMC neg. 81-7491, lateral aspect; B - 81-7490, dorsal aspect).*



C

FIGURE 14. (*C - 81-7489, anterior aspect*).

land-dwelling vertebrates) may also be advantageous in searching for packets of energy-rich food (hunting-gathering) distributed unevenly through complex ecosystems. If these suppositions are valid, the energy required to support a somewhat enlarged head and forelimbs within a *Stenonychosaurus* skeletal framework would become greater, and an anteroposteriorly oriented vertebral column would increase the angular inertia of a rotating body, thereby damping an ability to hurl projectiles. These difficulties might better be resolved by rotating the vertebral column upward rather than by shifting the centre of gravity posteriorly. The legs, trunk and arms could then be mobilized into a system of levers in the application of force to tools (cf. Washburn and Moore 1980, pp. 69-79).

A crude skeletal model for a hypothetical derivative of *S. inequalis* or "dinosauroid", was fabricated around the cranial model and a vertical vertebral bar with an abbreviated neck region. In saurornithoids (Barsbold 1977, Figs. 1-7) the long axis of the ilium lies at right angles to those of the ventral pelvic elements, and its anterior blade is not expanded beyond conditions typical of contemporaneous theropods. In humans the anterior iliac blade is broadly expanded, and the pubic and ischiadic rami are rotated posteriorly (in a morphologic sense) relative to the position of the homologous structures in saurornithoids. In a peculiar theropod from the Cretaceous of Mongolia, *Segnosaurus*, the structure of the pelvis is approximately intermediate between these two extremes (cf. Perle 1979, Fig. 5), possibly as a result of a quasi-vertical orientation of the vertebral column in this genus. The pelvic canal of the hypothetical dinosauroid would be enlarged to facilitate the birth of highly encephalized young. It would appear to be not impossible to derive a hominid-like pelvis from the pelvic morphology of saurornithoids, and such a pelvis was accordingly attached to the posterior end of the presacral vertebral column of the model skeleton. The axial skeleton is completed by an externally visible caudal rudiment.

Stenonychosaurus was a highly cursorial animal, and the changes in leg structure required by a vertical spine would probably have impaired its ability to run (cf. Lovejoy 1981). Perhaps, this disability would be compensated by the selective advantages resulting from a more highly developed central nervous system. Instabilities caused by the position of both the knee and crurometatarsal articulations above the substrate may be energetically expensive in slow moving creatures because of the need for excessive muscular "fine-tuning". The metatarsus was therefore shortened in the model and placed in a horizontal position, and the tarsal region was lengthened (cf. Lessertisseur and Jouffroy 1975). Only two tarsal elements are present in saurornithoids (Barsbold 1974B, Fig. 5); perhaps the fifth metatarsal

(Russell 1969, Fig. 13) would be available for modification into a calcaneal ossification. The crurometatarsal articulation is concave in the model, as it is in both saurornithoids and ratites. Leg proportions are as in *H. sapiens*, assuming that the leg is well suited for upright walking in our species. A cnemial crest on the anteroproximal surface of the tibia, similar to the structure in theropods, replaces the platella as the point of insertion of the abductors of the lower leg. The non-raptorial toes in the model are patterned after those in the tree kangaroo (*Dendrolagus*, cf. Gregory 1951, Fig. 18.37Z), which in other respects generally resemble those of *S. inaequalis*. A sophisticated use of tools would obviate the need for bodily armament, just as enlarged canines were lost in our own ancestry.

The shoulders are as broad or broader in hominids than in brachiating anthropoids (cf. Gregory 1951, Figs. 24.1, 24.2), perhaps as a result of highly co-ordinated projectile hurling (Brues 1959). Prominent shoulders were placed on the model skeleton, which are braced against the sternum anteromedially through broad but elongate coracoids rather than clavicles. The rib cage is narrow and deep as it is in *S. inaequalis*. The proportions of the humerus and radius-ulna are similar to those in ornithomimids (Osborn 1917, Fig. 8), as well as hominids. The hand is tridactylate as in *S. inaequalis*, with the third digit in the position of a thumb. The digits end in flattened ungual phalanges.

The dinosauroid skeletal framework was then "restored" and cast in the same manner as was that of *Stenonychosaurus* (Figs. 15-19). As posed, the model stands 1350 mm high. It was determined that the mould could be completely filled by 31.7 l of sand. Assuming that the brain filled 80% of the endocranial cavity and that the specific gravity of the body was 0.9, a live weight of 28.5 kg and an encephalization quotient of 7.1 are indicated (equations 1 and 2). The level of encephalization of the dinosauroid thus falls within the human range (Jerison 1973, Table 16.3). Although the body weights indicated by the two models do not differ greatly (28 versus 40 kg), they do indicate that a high level of encephalization was attained through a loss of body tissue as well as an increase in brain weight. Three and one-half months were required to complete the second model. The presence or absence of several structures in its soft anatomy require further comment.

The texture of the skin and general colouration were adapted from the reconstruction of *Stenonychosaurus*. In the head, the eyes were rotated anteromedially as a consequence of the expansion of the braincase, producing a broader overlap of visual fields. A vertical lenticular pupil was retained from the earlier model, but the scalloped margins typical of some geckoes were deleted. The wattle or dewlap beneath the mandibles is a secondary sexual

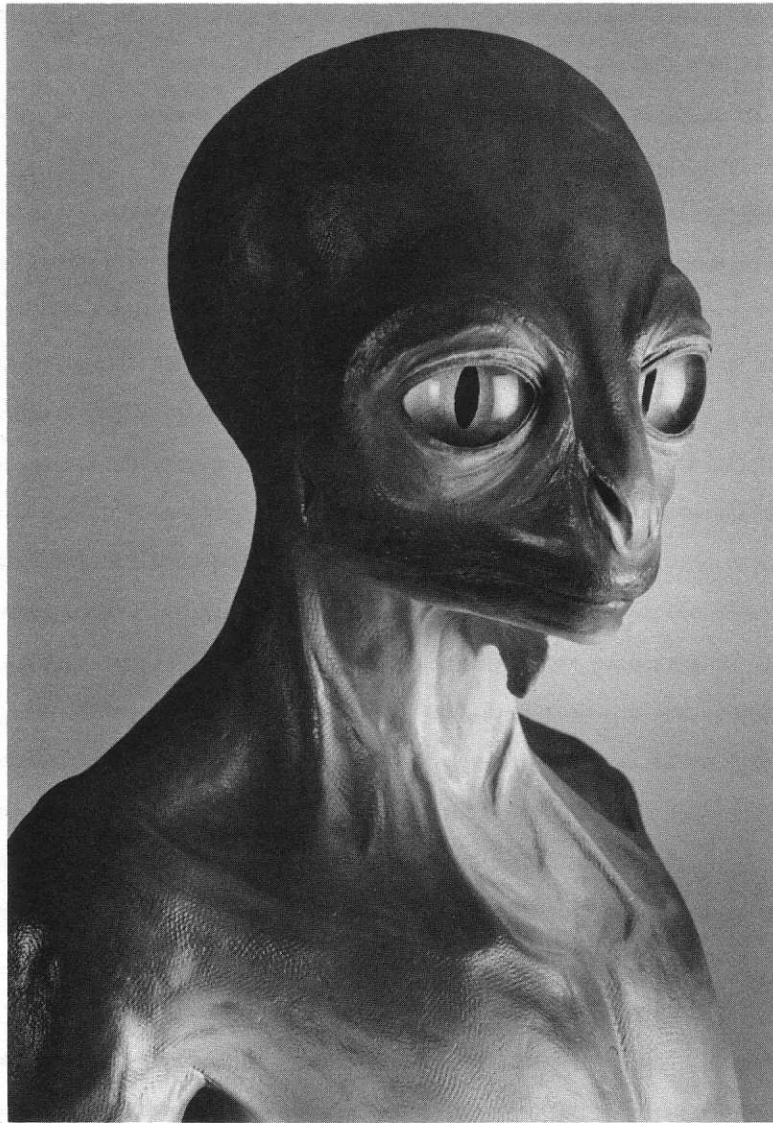


FIGURE 15. *Model of dinosauroid head, anterolateral aspect (NMC neg. 81-7485).*



FIGURE 16. *Model of dinosauroid hand, medial aspect (NMC neg. 81-7488).*

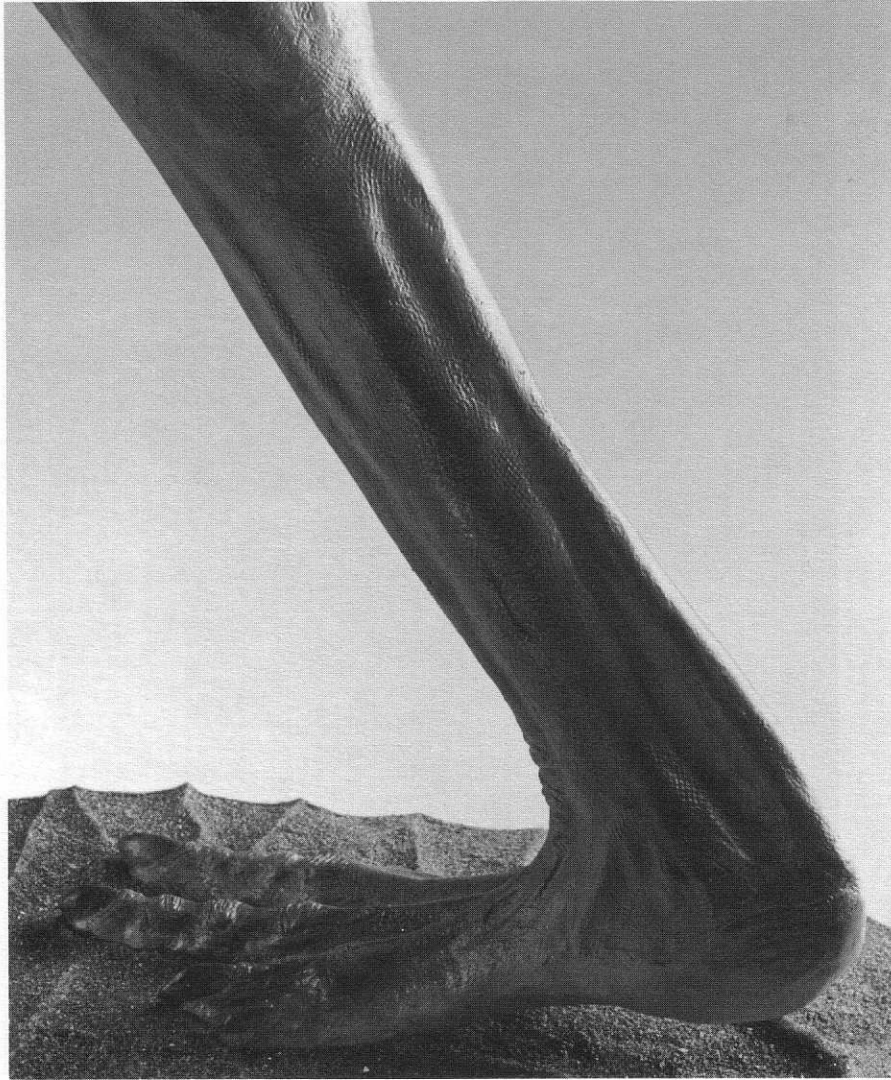


FIGURE 17. *Model of dinosauroid foot, medial aspect (NMC neg. 81-7487).*

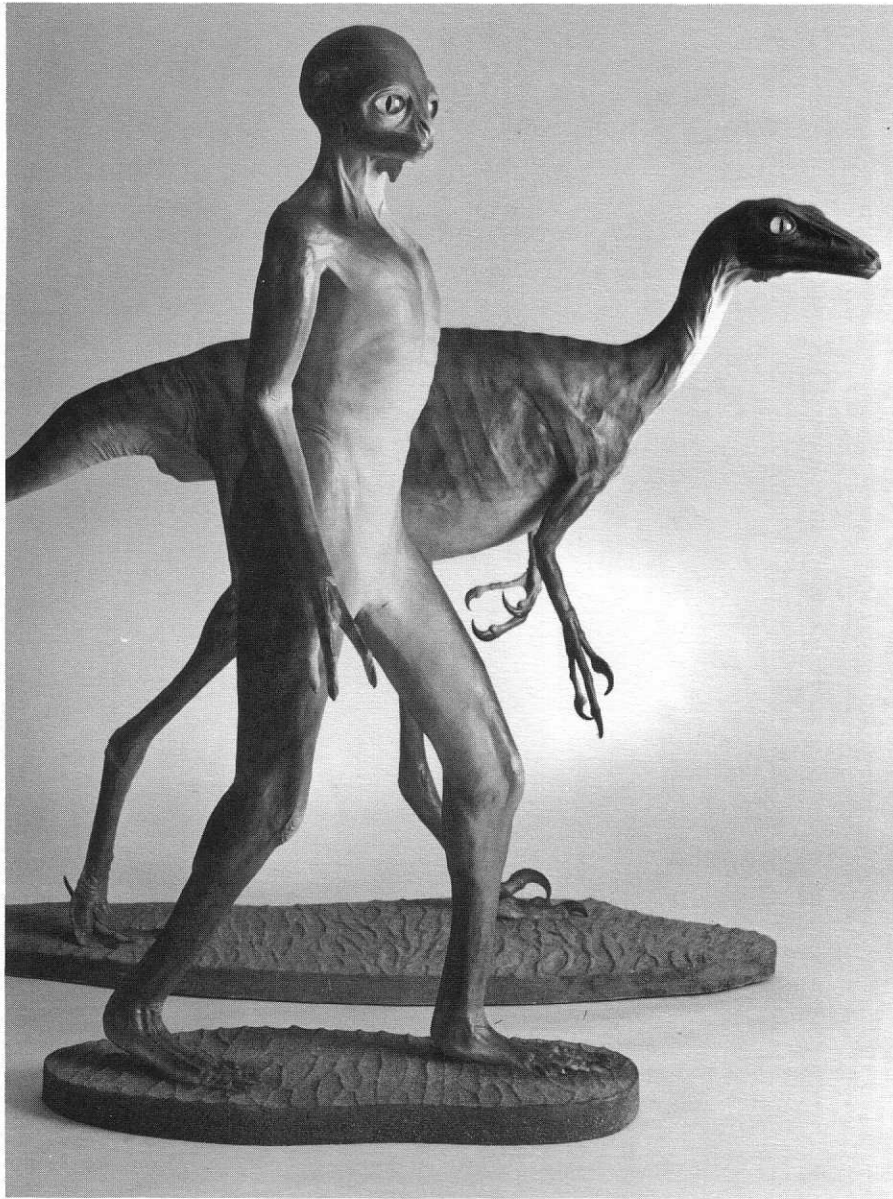


FIGURE 18. *Completed models of STENONYCHOSAURUS INEQUALIS and dinosaurid*
(A - NMC neg. 81-7483, right lateral aspect).

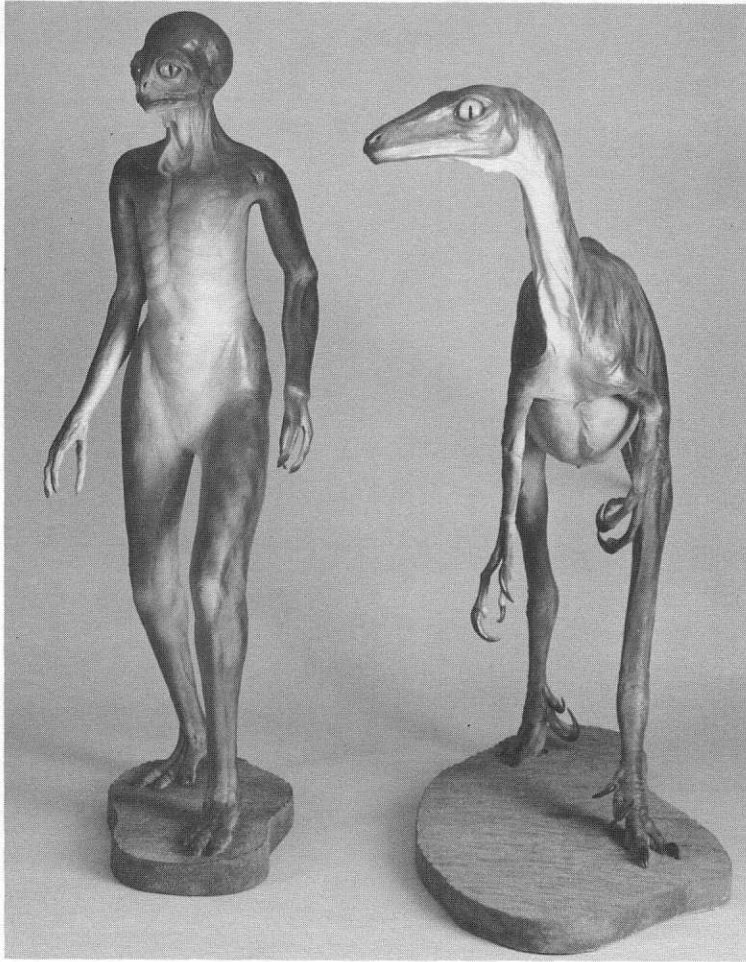


FIGURE 18. (B - 81-7481, *anterior aspect*).

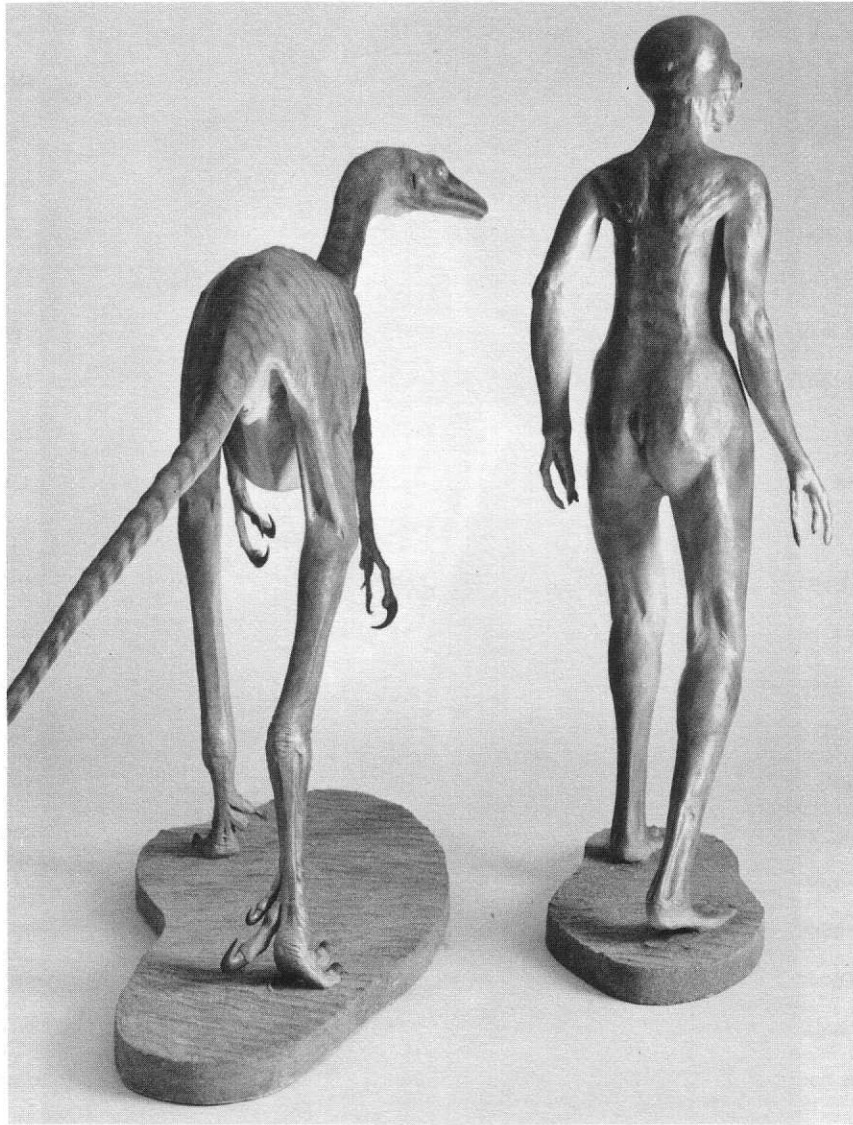


FIGURE 18. (C - 81-7482, *posterior aspect*).

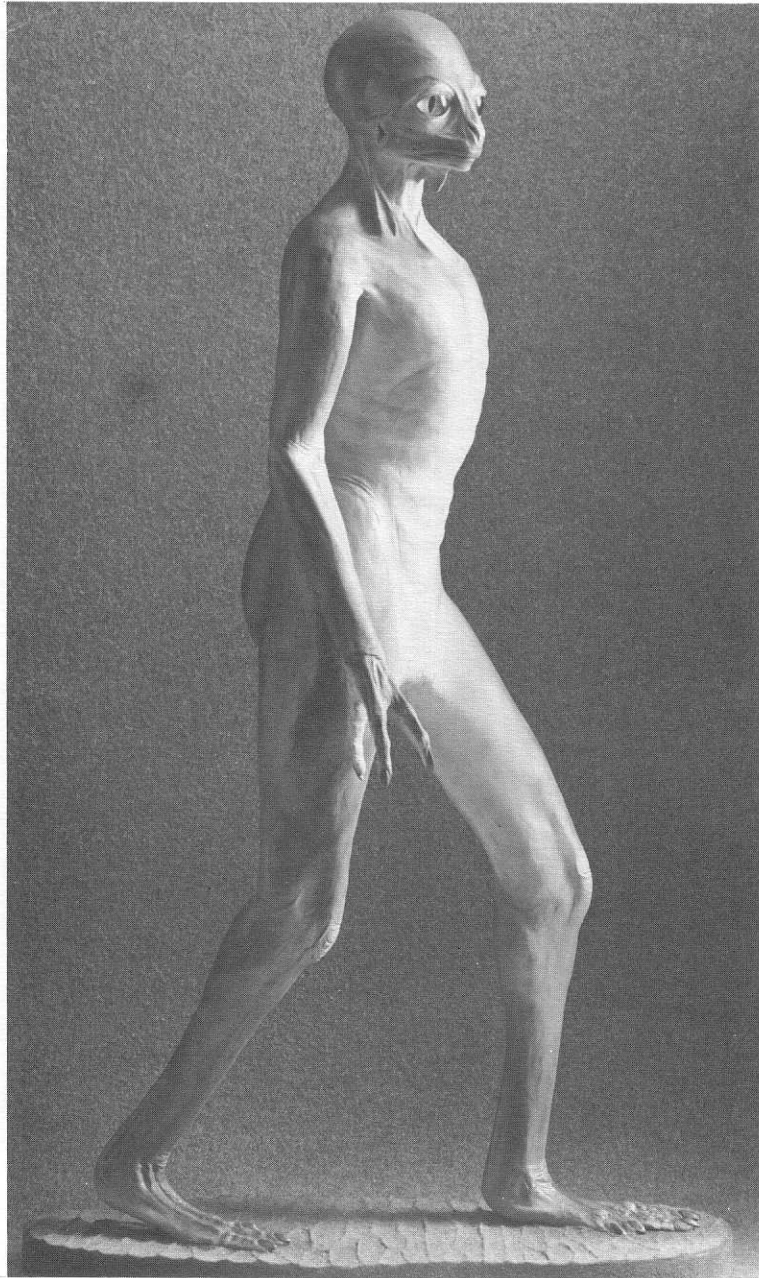


FIGURE 19. *Completed model of dinosauroid, right lateral aspect (NMC neg. 81-8401).*

character. As is usual in reptiles and birds there is no external auditory pinna. Similarly, there are no nipples on the ventral surface of the body; one may presume that the young were fed on food regurgitated by the parents. A broad pelvic canal is an impediment to efficient bipedal walking (Lovejoy 1975), and its diameter is minimized in man by bearing the young in a relatively immature condition when the head is smaller (Passingham 1975, p. 81). The presence of egg tissues would only exacerbate this problem. Because a well-developed placenta does occur in some reptiles (particularly in some skinks, cf. Bellairs 1970, pp. 449-452), a navel has been placed on the belly of the dinosauroid. A gluteal-like muscle mass covering the base of the pelvis is a consequence of the suppression of the tail and replacement of deep caudifemoral abductors by iliofemoralis muscles originating from the expanded anterior blade of the ilium (cf. Russell 1972, Figs. 7-8; Sigmon 1975, Figs. 3-4). There are no visible external genitalia, which normally lie within a cloaca in most reptiles and birds.

The reconstruction of *Stenonychosaurus* can be subject to verification through the discovery of more complete material. This is probably not even partly true in the case of the dinosauroid, as rates of change of maximum encephalization may not have been high enough during late Cretaceous time (cf. Russell 1981) to reveal detectable increases in the descendants of *S. inequalis* before the close of the period. The body form of *Homo sapiens* is possible because it exists. To the extent that it is approached by that of the dinosauroid, the latter also becomes a plausible biophysical configuration. But can this resemblance better be explained as the result of an "orthogenetic" bias? Perhaps. If so, however, it must also be admitted that existing within the spectrum of morphologies represented by terminal Cretaceous dinosaurs was a mosaic of characters which paralleled many seen in mammals and in the phylogenetic precursors of man. These circumstances should be evaluated in cognizance of the ubiquity of the phenomenon of parallel evolution in the history of life on Earth. On the other hand, could the dinosauroid indeed be too "reptilian" to be a reasonable configuration? Should not the eyes be smaller and the pupils more rounded? Would external ears not be useful in focusing sound toward the tympanum? Are the jaws too strong and the muzzle too elongate? Is the deep, narrow chest compatible with the presence of shoulders?

The dinosauroid may represent a solution to the physical and physiological stresses imposed on the vertebrate organism by a greatly hypertrophied brain in a terrestrial environment. If this is true, its general form may have a biological significance analogous

to, for example, the aviform shape of birds, bats and pterosaurs, the pisciform shape of bony fishes, sharks and porpoises, or the "equiform" shape of horses and certain extinct South American ungulates (litopterns). The presence of this body form in *Homo sapiens* demonstrates that the solution exists. It may, however, not be unique. We invite our colleagues to identify alternate solutions.

TABLE 1: EARLIEST DESCRIBED GENERA OF DEINONYCHOSAURS

GENUS	PROVENANCE	TYPE MATERIAL	AUTHOR(S)
<i>Dromaeosaurus</i>	Alberta	Skull, elements of feet	Matthew and Brown 1922
<i>Velociraptor</i>	Mongolia	Skull, elements of hands and feet	Osborn 1924B
<i>Sauornithoides</i>	Mongolia	Skull, elements of pelvic region and feet	Osborn 1924B
<i>Stenonychosaurus</i>	Alberta	Foot, elements of hand and tail	Sternberg 1932

TABLE 2: MEASUREMENTS OF SKELETAL ELEMENTS IN *Stenonychosaurus* RECONSTRUCTION*

Length of skull (premaxilla to occipital condyle)	242 mm
Maximum width of skull	145
Length of cervical series (10 vertebrae)	405
Length of dorsal series (12 vertebrae)	465
Length of sacral series (6 vertebrae)	222
Length of caudal series	1680
Length of humerus	157
Length of ulna	130
Length of digit II (manus)	192
Length of ilium	268
Depth of pelvis and sacrum	370
Length of femur	330
Length of tibia-astragalus	405

* In addition to providing a basis for the current skeletal reconstruction, these measurements may facilitate the identification of errors when more complete material is available.

TABLE 3: DIAMETER OF SCLEROTIC RING IN DINOSAURS

TAXON	APPROXIMATE DIAMETER	REFERENCE
Theropoda		
<i>Dromaeosaurus</i>	36 mm	Colbert and Russell 1969, Fig. 2
<i>Dromiceiomimus</i>	59	Parks 1928, Pl. 2
Sauropoda		
<i>Brachiosaurus</i>	70	Janensch 1935, p. 182
<i>Diplodocus</i>	55	Holland 1924, Pl. 40
<i>Nemegtosaurus</i>	73	Nowinski 1971, Fig. 8
Ornithopoda		
<i>Hypsilophodon</i>	31	Galton 1973, Fig. 6
<i>Parksosaurus</i>	37	Galton 1973, Fig. 3
<i>Anatosaurus</i>	80	Versluys 1923, Fig. 2
<i>Saurolophus</i>	88	Ostrom 1961, p. 146
<i>Lambeosaurus</i>	60	Ostrom 1961, p. 146
<i>Corythosaurus</i>	70	Ostrom 1961, p. 146
Ceratopsia		
<i>Psittacosaurus</i>	24	Osborn 1924A, Fig. 2
<i>Protoceratops</i>	50	Brown and Schlaikjer 1940, Fig. 17
<i>Centrosaurus</i>	50	Brown 1917, Pl. 12
AVERAGE	55.9	

TABLE 4: MEASUREMENTS OF *Stenonychosaurus* RECONSTRUCTION

Length (snout to vent)	1460 mm
Length (vent to tip of tail)	1620
Overall length (as posed)	2805
Depth of chest	384
Width of chest	240
Height at hips	980
Height at head	1190

TABLE 5: ENCEPHALIZATION INDICES CALCULATED FOR *Stenonychosaurus inequalis**

BRAIN WEIGHT (gm)	BODY WEIGHT (gm)	ENCEPHALIZATION QUOTIENT
37	45,000	0.2439
37	41,940	0.2556
37	37,280	0.2767
45	45,300	0.2953
45	41,940	0.3109
45	37,280	0.3363

*For further explanation see text p. 21.

REFERENCES

- Adams, L.M., and W.J. Moore. 1975. Biomechanical appraisal of some skeletal features associated with head balance and posture in the Hominoidea. *Acta Anatomica* 92: 580-594.
- Barsbold, R. 1974A. Duel of the dinosaurs (in Russian). *Priroda* 1974(2): 81-83.
- _____. 1974B. Saurornithoididae, a new family of small theropod dinosaurs from Central Asia and North America. *Palaeontologia Polonica* 30: 5-22.
- _____. 1976. On the evolution and systematics of late Mesozoic carnivorous dinosaurs (in Russian). *Transactions of the Soviet-Mongolian Paleontological Expedition* 3: 68-75.
- _____. 1977. On the evolution of carnivorous dinosaurs (in Russian). *Transactions of the Soviet-Mongolian Paleontological Expedition* 4: 48-56.
- Barsbold, R., and A. Perle. 1979. Modification of the pelvis in the Saurischia and parallel evolution in carnivorous dinosaurs (in Russian). *Transactions of the Soviet-Mongolian Paleontological Expedition* 8: 39-44.
- Béland, P., and D.A. Russell. 1978. Paleocology of Dinosaur Provincial Park (Cretaceous), Alberta, interpreted from the distribution of articulated vertebrate remains. *Canadian Journal of Earth Sciences* 15: 1012-1024.
- Bellairs, A. 1970. The life of reptiles. Universe Books, New York. 589 pp.
- Bonaparte, J.F., and J.E. Powell. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda - Coelurosauria - Carnosauria - Aves). *Mémoires de la Société géologique de France (n.s.)* 139: 19-28.
- Brown, B. 1917. A complete skeleton of the horned dinosaur *Monoclonius* and description of a second skeleton showing skin impressions. *American Museum of Natural History Bulletin* 37: 281-306.
- Brown, B., and E.M. Schlaikjer. 1940. The structure and relationships of *Protoceratops*. *Annals of the New York Academy of Science* 40: 133-266.
- _____. 1943. A study of the troödont dinosaurs with the description of a new genus and four new species. *American Museum of Natural History Bulletin* 82: 115-150.
- Brues, A. 1959. The spearman and the archer - an essay on selection in body build. *American Anthropologist* 61: 457-469.
- Colbert, E.H. 1962. The weights of dinosaurs. *American Museum of Natural History Novitates* 2076: 1-16.
- Colbert, E.H., and D.A. Russell. 1969. The small Cretaceous dinosaur *Dromaeosaurus*. *American Museum of Natural History Novitates* 10024: 1-49.
- Crile, G., and D.P. Quiring. 1940. A record of the body weight and certain organ and gland weights of 3690 animals. *Ohio Journal of Science* 40: 219-259.
- Galton, P.M. 1973. Redescription of the skull and mandible of *Parksosaurus* from the late Cretaceous with comments on the family Hypsilophodontidae. *Royal Ontario Museum Life Science Contribution* 89: 1-21.
- _____. 1980. *Dryosaurus* and *Camptosaurus*, intercontinental genera of upper Jurassic ornithopod dinosaurs. *Mémoires de la Société géologique de France (n.s.)* 139: 103-108.
- Gilliard, E.T. 1958. Living birds of the world. Doubleday, Garden City. 400 pp.
- Goodrich, E.S. 1958. Studies on the structure and development of vertebrates. Dover Publications, New York. 837 pp.
- Gould, S.J. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge. 501 pp.

- Gregory, W.K. 1951. Evolution emerging. MacMillan, New York. 1749 pp.
- Hanzak, J. 1965. The pictorial encyclopedia of birds. Hamlyn, London. 582 pp.
- Holland, W.J. 1924. The skull of *Diplodocus*. Memoirs of the Carnegie Museum 9: 379-403.
- Hopson, J. 1977. Relative brain size and behavior in archosaurian reptiles. Annual Review of Ecology and Systematics 8: 429-448.
- _____. 1980. Relative brain size in dinosaurs. American Association for the Advancement of Science Selected Symposium 28: 287-310.
- Janensch, W. 1935. Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus* aus den Tendaguru-Schichten Deutsch-Ostafrikas. Palaeontographica Supplement 7, Reihe 1, Teil 2: 145-298.
- Jerison, H.J. 1973. Evolution of the brain and intelligence. Academic Press, New York. 482 pp.
- Johanson, D.C., and M.A. Edey. 1981. Lucy, the beginnings of humankind. Simon and Schuster, New York. 409 pp.
- Lessertisseur, J., and F.K. Jouffroy. 1975. Comparative osteometry of the foot of man and facultatively bipedal primates. In: Primate Functional Morphology and Evolution. Edited by: R.H. Tuttle. Mouton Publishers, The Hague. pp. 327-340.
- Lewin, R. 1981. Ethiopian stone tools are world's oldest. Science 211: 806-807.
- Lovejoy, C. 1975. Biomechanical perspectives on the lower limb of early hominids. In: Primate Functional Morphology and Evolution. Edited by: R.H. Tuttle. Mouton Publishers, The Hague. pp. 291-326.
- _____. 1981. The origin of man. Science 211: 341-350.
- Matthew, W.D., and B. Brown. 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. American Museum of Natural History Bulletin 46: 367-385.
- Nowinski, A. 1971. *Nemegtosaurus mongoliensis* (Sauropoda) from the uppermost Cretaceous of Mongolia. Palaeontologia Polonica 25: 57-81.
- Oldendorf, W., and W. Zabielski. 1981. The buoyant brain. Science Digest 89: 94-96, 117.
- Osborn, H.F. 1917. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. American Museum of Natural History Bulletin 35: 733-771.
- _____. 1924A. *Psittacosaurus* and *Protiguanodon*: two lower Cretaceous iguanodonts from Mongolia. American Museum of Natural History Novitates 127: 1-16.
- _____. 1924B. Three new Theropoda, *Protoceratops* zone, central Mongolia. American Museum of Natural History Novitates 144: 1-12.
- Ostrom, J.H. 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. American Museum of Natural History Bulletin 122: 33-186.
- _____. 1969A. A new theropod dinosaur from the lower Cretaceous of Montana. Yale Peabody Museum Postilla 128: 1-17.
- _____. 1969B. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the lower Cretaceous of Montana. Peabody Museum of Natural History Yale University Bulletin 30: 1-165.
- _____. 1974. *Archaeopteryx* and the origin of flight. Quarterly Review of Biology 49: 27-47.

- _____. 1976. On a new specimen of the lower Cretaceous theropod dinosaur *Deinonychus antirrhopus*. Museum of Comparative Zoology Breviora 439: 1-21.
- _____. 1978A. A new look at dinosaurs. National Geographic Magazine 154: 152-185.
- _____. 1978B. The osteology of *Compsognathus longiceps* Wagner. Zitteliana 4: 73-118.
- Parks, W.A. 1928. *Struthiomimus samueli* a new species of Ornithomimidae from the Belly River Formation of Alberta. University of Toronto Studies, Geological Series 26: 1-24.
- Passingham, R.E. 1975. Changes in the size and organization of the brain in man and his ancestors. Brain, Behaviour and Evolution 11: 73-90.
- Perle, A. 1979. Segnosauridae - a new family of theropods from the late Cretaceous of Mongolia (in Russian). Transactions of the Soviet-Mongolian Paleontological Expedition 8: 45-55.
- Radinsky, L. 1978. Evolution of brain size in carnivores and ungulates. American Naturalist 112: 815-831.
- Rodman, P.S., and H.M. McHenry. 1980. Bioenergetics and the origin of hominid bipedalism. American Journal of Physical Anthropology 52: 103-106.
- Romer, A.S. 1956. Osteology of the reptiles. University of Chicago Press, Chicago. 772 pp.
- _____. 1962. The vertebrate body. Saunders, Philadelphia. 627 pp.
- Russell, D.A. 1969. A new specimen of *Stenonychosaurus* from the Oldman Formation (Cretaceous) of Alberta. Canadian Journal of Earth Sciences 6: 595-612.
- _____. 1972. Ostrich dinosaurs from the late Cretaceous of western Canada. Canadian Journal of Earth Sciences 9: 375-402.
- _____. 1981. Speculations on the evolution of intelligence in multicellular organisms. In: Life in the Universe. Edited by: J. Billingham. National Aeronautics and Space Administration Special Publication, in press.
- Schmidt, K.P., and R.F. Inger. 1957. Living reptiles of the world. Doubleday, Garden City. 287 pp.
- Sigmon, B.A. 1975. Functions and evolution of hominid hip and thigh musculature. In: Primate Functional Morphology and Evolution. Edited by: R.H. Tuttle. Mouton Publishers, The Hague. pp. 235-252.
- Sokoloff, L. 1976. Circulation and energy metabolism of the brain. In: Basic Neurochemistry, Second Edition. Edited by: G.J. Siegel, R.W. Alberts, R. Katzman, and B.W. Arganoff. Little, Brown and Company, Boston. pp. 388-413.
- Staneek, V.J. 1962. The pictorial encyclopedia of the animal kingdom. Hamlyn Publishing Group, London. 614 pp.
- Sternberg, C.M. 1932. Two new theropod dinosaurs from the Belly River Formation of Alberta. Canadian Field-Naturalist 46: 99-105.
- Sues, H.D. 1978. A new small theropod dinosaur from the Judith River Formation (Campanian) of Alberta, Canada. Zoological Journal of the Linnean Society 62: 381-400.
- Versluys, J. 1923. Der Schädel des Skelettes von *Trachodon annectens* im Senckenberg-Museum. Abhandlungen von der Senckenbergischen naturforschenden Gesellschaft 38: 1-19.
- Walls, G.L. 1942. The vertebrate eye and its adaptive radiation. Cranbrook Institute of Science Bulletin 19: 1-785.

- Washburn, S.L. 1978. The evolution of man. *Scientific American* 239: 194-208.
- Washburn, S.L., and R. Moore. 1980. Ape into human. Second Edition. Little, Brown and Company, Boston. 194 pp.
- Wellnhofer, P. 1974. Das fünfte Skelettexemplar von *Archaeopteryx*. *Palaeontographica Abteilung A* 147: 169-216.
- White, T.D. 1980. Evolutionary implications of Pliocene hominid footprints. *Science* 208: 175-176.