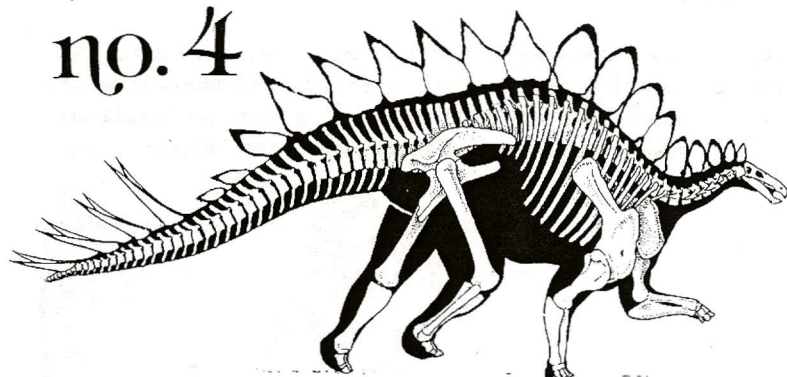


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THE SMALL PREDATORY DINOSAURS OF THE MID-MESOZOIC: THE HORNED THEROPODS OF THE MORRISON AND GREAT OOLITE – ORNITHOLESTES AND PROCERATOSAURUS – AND THE SICKLE-CLAW THEROPODS OF THE CLOVERLY, DJADOKHTA AND JUDITH RIVER – DEINONYCHUS, VELOCIRAPTOR AND SAURORNITHOLESTES

*Proceedings of the North American Paleontological Conference IV:
The Golden Age of Dinosaurs — The Mid-Mesozoic Terrestrial Ecosystem of North America
Field Trip and Colloquium.*

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and University Museum, University of Colorado, Boulder.*

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ABSTRACT

The small Jurassic theropods *Ornitholestes hermanni* and *Proceratosaurus bradleyi* share many characteristics, including the development of nasal horns, and can be allocated to the same subfamily within the Allosauridae. The Cretaceous theropods *Velociraptor mongoliensis*, *Deinonychus antirrhopus* and *Saurornitholestes langstoni* are more similar to each other than previously realized, and can be grouped within a single genus. The distribution of *Velociraptor* and other predatory dinosaurs indicates that there was a free interchange of tetrapods over the Late Cretaceous Bering land bridge. The similarity between *Proceratosaurus* and *Ornitholestes* suggests that the Late Jurassic continental disposition allowed frequent faunal interchange between North America and Europe.

INTRODUCTION

Ornitholestes hermanni was discovered by Hermann in the Morrison Formation in 1900 (Osborn, 1903) and remains the best known small predatory theropod from this rock unit. At about the same time *Proceratosaurus bradleyi* was recovered from the Great Oolite of the Middle Jurassic, and this specimen is still the only good small theropod skull from

England (Woodward, 1910). Reexamination of the skulls in these two genera shows them to be much more similar than previously realized — they seem to share nasal horns — and it can be argued that they belong together in a new family or subfamily. In 1923 Kaisen found a new theropod with a sickle claw on the second hindfoot digit, *Velociraptor mongoliensis* (Osborn, 1924), in the Late Cretaceous

Djadokhta Formation of Mongolia. The year 1931 saw the discovery of a similar sickle-claw theropod, *Deinonychus antirrhopus*, excavated by Brown in the late Early Cretaceous Cloverly Formation of Montana. The Cloverly sickle

claw was not appreciated until the Yale expeditions into the Cloverly during the 1960's, when much additional material was obtained (Ostrom, 1969a). An American Late Cretaceous sickle claw theropod, *Saurornitholestes langstoni*, was

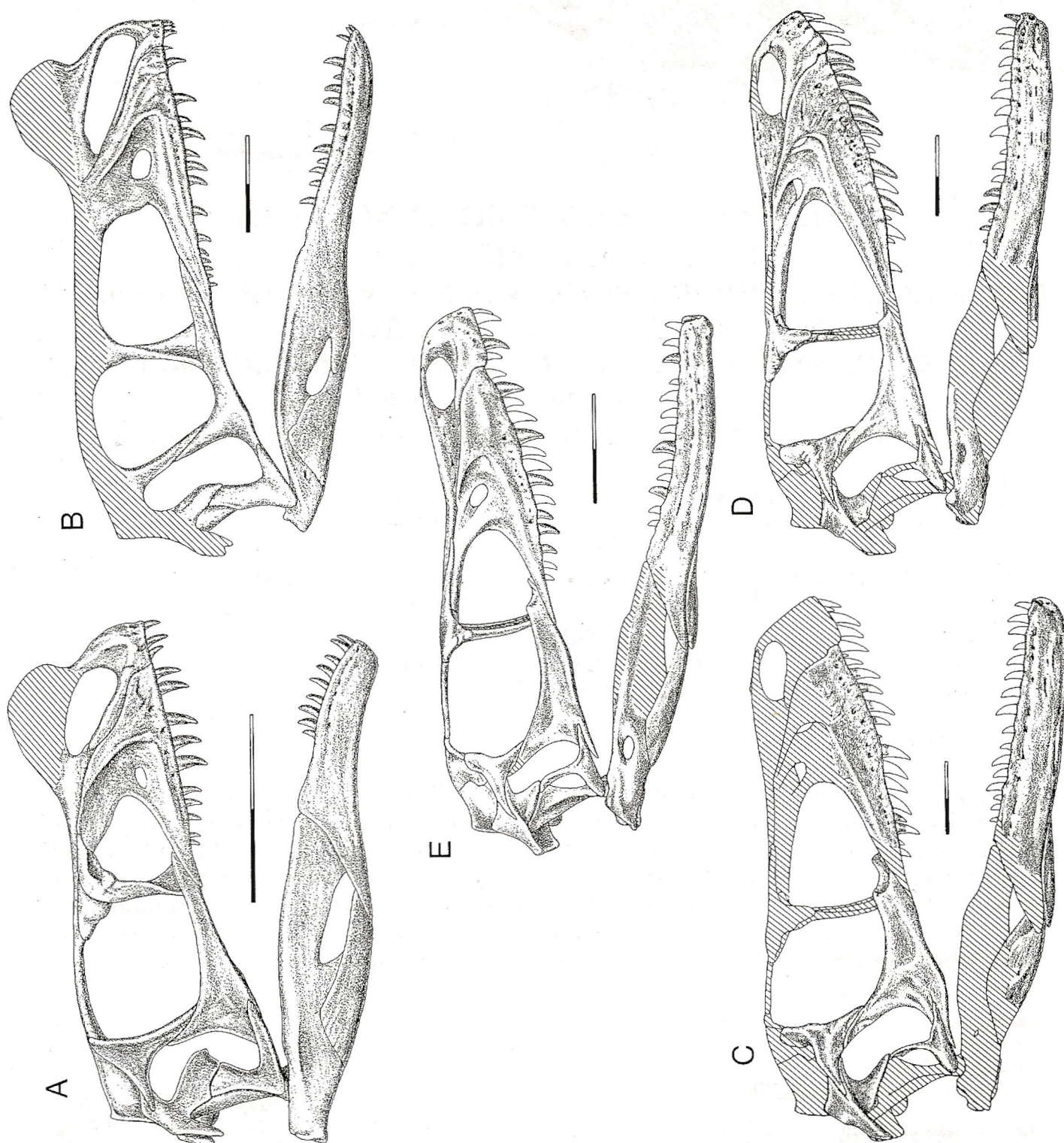


Figure 1—Skull restorations of ornitholestines: A) *Ornitholestes hermanni*, holotype AMNH 619, B) *Proceratosaurus bradleyi*, holotype BMNH R 4860. Dromaeosaurs: C) *Velociraptor antirrhopus*, YPM 5232; D) *V. cf. antirrhopus*, YPM 5210 with the maxilla of MCZ 4371 downscaled. Note: there is considerable variation in the Cloverly sample assigned to *V. antirrhopus*. "Robust" MCZ 4371 and YPM 5210 may represent a different species from that recorded by "gracile" AMNH 3015 and most of the YPM material including 5232, or they may be different sexes. E) *V. mongoliensis*, GI 100/25. Note that *V. mongoliensis* is especially like gracile *V. antirrhopus* YPM 5232 with its slender, curved dentary. Drawn to same upper jaw length, scale bars equal 50 mm.

collected by Vanderloh in 1974 in the Judith River Formation of Alberta (Sues, 1978). A reconsideration of all three sickle-claw taxa shows that they too are much more similar than realized, and should be placed in one genus. The temporal and biogeographical implications of these taxa are explored below.

A study of theropods as a whole is in preparation elsewhere (Paul, in prep.). Museum abbreviations — AMNH American Museum of Natural History, New York; BMNH British Museum of Natural History, London; GI Geological Institute, Ulan Bataar; MCZ Museum of Comparative Zoology, Cambridge; SANS Soviet Academy of Natural Sciences, Moscow; TM Tyrell Museum, Drumheller; YPM Yale Peabody Museum, New Haven.

THE LATE JURASSIC ORNITHOLESTINES

COMPARISON OF ORNITHOLESTES HERMANNI AND PROCERATOSAURUS BRADLEYI:

A study of the osteology of the *Ornitholestes hermanni* Osborn 1903 is in preparation by Ostrom, so only its general aspects are discussed here. It is important to note that Ostrom (1980) has shown that *Ornitholestes* is not a junior synonym of *Coelurus fragilis*. Indeed these two theropods are quite profoundly different. Only two *Ornitholestes* specimens are available, both from Bone Cabin Quarry: the holotype AMNH 619, which includes the skull, most of the vertebrae and limb elements, and the hand bones, AMNH 587 (Osborn, 1903, 1916). Since most of the hand is missing in the type, the reference of 587 to *Ornitholestes* must be tentative.

The skull of AMNH 619, though complete, is difficult to restore because one side is much more elongated than the other due to post mortem deformation. The restored skull shown here has a length closer to that of the shorter side as preserved. This side appears to be less distorted relative to the skull roof and mandible (Fig. 1A). A new skeletal restoration of *O. hermanni* is presented in Fig. 2A. It differs substantially from Knight's famous restoration of this "bird robber" grabbing *Archaeopteryx* (Massey-Czerkas and Glut, 1982) — mainly because Knight had followed Osborn's (1903) initial skeletal restoration, which is much too long in the neck and trunk.

The holotype and only specimen of *Proceratosaurus bradleyi* Woodward 1910, BMNH 4860, consists of a skull, minus the roof, mandible, and a possible hyoid element (Fig. 1B, p. 67 in Norman, 1985). It was first considered to be a species of *Megalosaurus* by Woodward. However Huene (1926) recognized that it shares little in common with *Megalosaurus bucklandi* Meyer 1832 proper, a much bigger theropod of which little of the skull is known. Because of its nasal horn Huene considered Woodward's species to be a relative of *Ceratosaurus nasicornis* Marsh 1884, which also has a nasal horn, a view that has been widely followed since. However, these two predators have skulls and teeth that are very different in design, and even the horns show striking

dissimilarities. In *C. nasicornis* the horn is made entirely of the nasals, and the horn base is set just above the posterior edge of the external nares. The *P. bradleyi* nasal horn is set much more forwards, well over the external nares, with perhaps a bit of the premaxilla participating in the front base of the horn. Another important difference is in the suspensorium. In *C. nasicornis* the descending process of the squamosal and the ascending process of the quadratojugal are long and very slender, and at their articulation with each other their tips barely overlap. *P. bradleyi* has shorter, much stouter processes that articulate via a fairly long suture. Finally, *Ceratosaurus* has unusually large, long, flattened blade teeth with full serrations along front and back keels. In *Proceratosaurus* the teeth are relatively small, more conical, and have serrations that are reduced or absent on the front keel. *Megalosaurus bucklandi* differs in its teeth from *P. bradleyi* in much the same way as *C. nasicornis*. Walker (1964) also recognizes that *P. bradleyi* is not closely related to ceratosaurs.

While differing from *C. nasicornis* in these regards, *P. bradleyi* has many similarities to *O. hermanni*, including the peculiar horns and teeth. Most of the premaxillary-nasal bar of AMNH 619 is missing, but what is preserved flares upwards in exactly the same place where the horn of *P. bradleyi* begins (Fig. 1A,B, see Fig. 1 in Osborn, 1916). Thus *O. hermanni* probably had some sort of nasal horn incorporating the nasals and perhaps the premaxillae. In neither species is the full size and form of the nasal horn known.

O. hermanni also shares with *P. bradleyi* small, rather conical teeth with reduced anterior serrations. They are heterodont in that the premaxillary teeth are more conical than the maxillary teeth. The tooth rows, especially the dentary sets, do not extend as far posteriorly as is the case for most other theropods. The two species share short, stout processes of the squamosal and quadratojugal that meet via long articulations. The premaxillae of the two species are short fore-to-aft; the external nares are elongated, and the maxilla, two preorbital openings, preorbital depression, jugal, and lacrimal are similar in shape, as is the overall configuration of their skulls. The orbit is larger and the snout shorter in the Morrison form, a difference that may be a simple function of its smaller size.

SYSTEMATIC PALEONTOLOGY

Family Allosauridae Marsh 1878

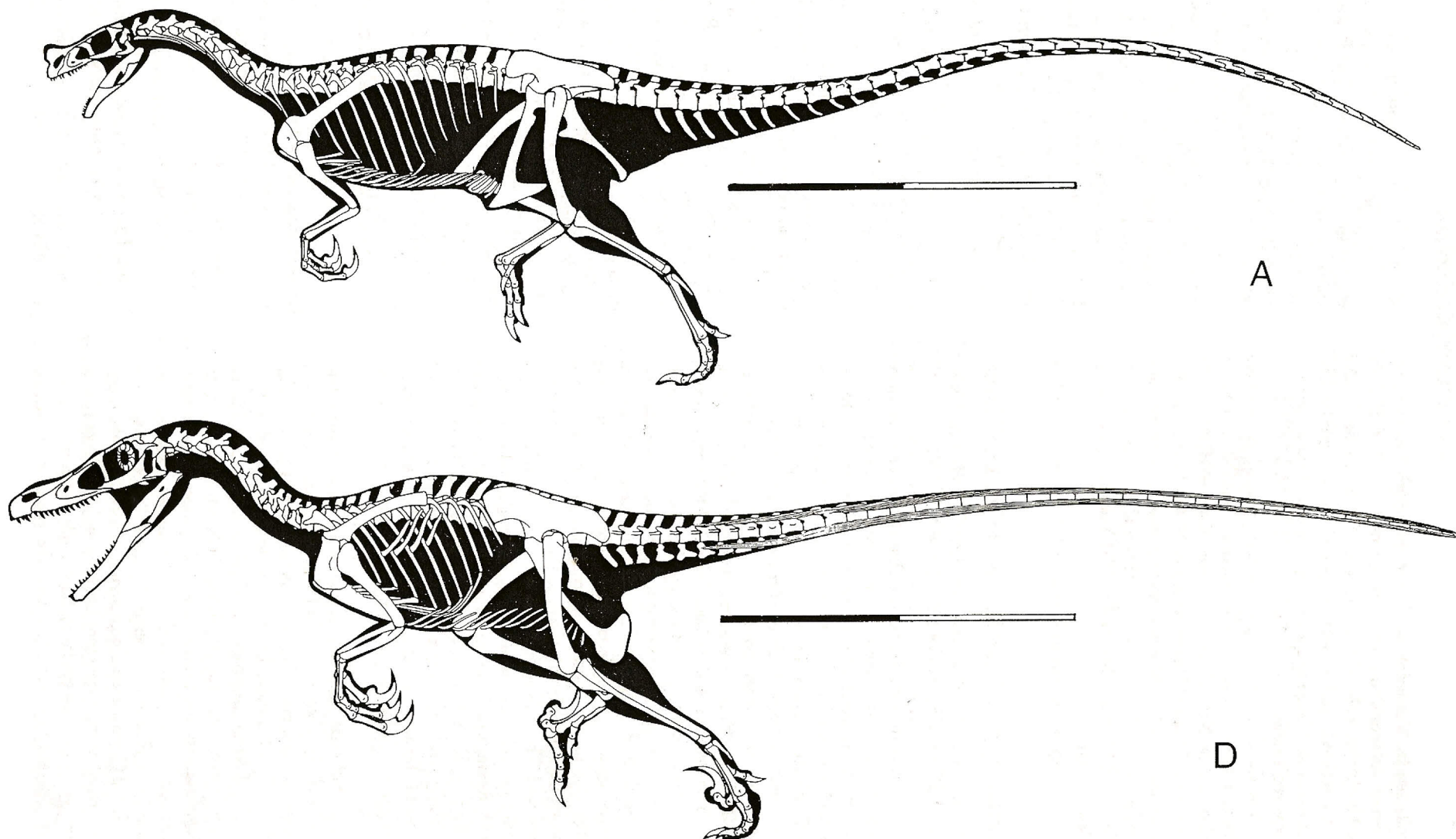
Revised diagnosis — Differs from all other theropods in the downward slant of the paroccipital processes; quadratojugal robust, articulating with the squamosal via a long, down-and-forwardly sloping contact; metatarsal III moderately narrow and L-shaped proximally.

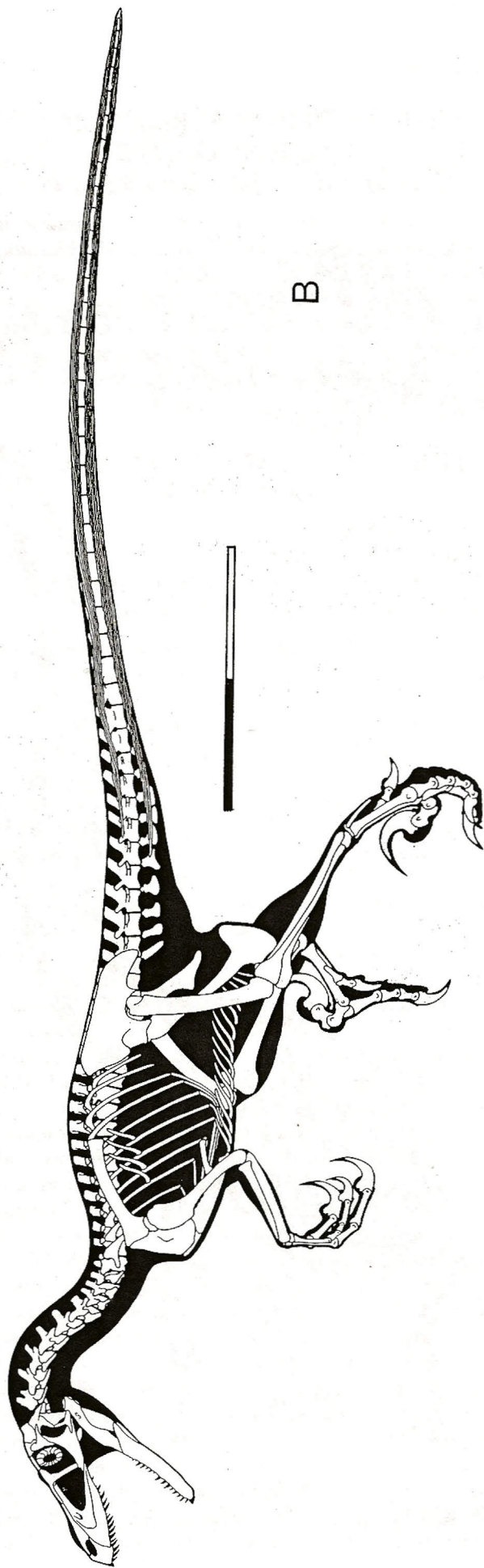
Subfamily Ornitholestinae n. subfam.

Included genera and species — *Ornitholestes hermanni* Osborn 1903; *Proceratosaurus bradleyi* Woodward 1910

Diagnosis. Size small; skull long and low and subrectangular; premaxilla short anterioposteriorly, tall dorsoventrally and

Figure 2—Skeletal restorations. A) *Ornitholestes hermanni* holotype AMNH 619, AMNH 587 hand, a number of details restored, mainly after allosaurs. B) "Gracile" *V. antirrhopus* AMNH 3015 with YPM 5232 skull, YPM 5206 hand and YPM 5205 foot, pubis after 4371, and details from other specimens. C) "Robust" *Velociraptor* cf. *antirrhopus* MCZ 4371 (Ostrom, 1976) with YPM 5210 skull and vertebrae, other vertebrae, scapulocoracoid and other details from assorted specimens. D) *V. mongoliensis* GI 100/25, proportions approximate, some details of presacra from *V. antirrhopus*. Sternal plates in B) and D) after *V. mongoliensis*. Methods for restoring skeletons in Paul in prep. Drawn to same femur length, scale bars equal 0.5 m.





blunt-tipped; external nares large, elongated; horn over external nares made up of nasals and premaxilla?; maxilla and preorbital depression subtriangular and dorsally concave; lacrimal preorbital bar vertical, ventrally broad and with a lateral ridge running down and backwards; jugal long, low and triradiate; teeth heterodont with anterior dentary and premaxillary teeth more conical, less recurved and less keeled and serrated than the maxillary-posterior dentary teeth; all teeth with reduced or no serrations on anterior keel; dentary tooth row much shorter than upper row.

Taxonomic symmetry demands the definition of a Subfamily Allosaurinae.

Subfamily Allosaurinae new rank (Marsh 1878)

Included genera — *Allosaurus*, *Chilantaisaurus*

Diagnosis. Differs from the Ornitholestinae in: larger size; relatively much heavier head and neck; much larger lacrimal rugosities; mid-line nasal horn never developed; plate-like parasphenoid contacts skull roof.

Discussion. *Ornitholestes* and *Proceratosaurus* share some curious features that are most similar to the conditions in allosaurs: broad squamosal-quadratojugal contact, downwardly swept opisthotic wing and in *Ornitholestes* the L-shaped proximal end of the central metatarsal (Paul, 1984; the metatarsus is not preserved in *Proceratosaurus*). Also interesting is that, as in the big allosaurs, the articulated *P. bradleyi* and *O. hermanni* skulls lack any trace of a bony eye ring. Therefore I would brigade ornitholestines and allosaurs together in the same family, Allosauridae. This allocation is in contrast to Ostrom's (1969a) suggestion that *O. hermanni* is close to the dromaeosaurs. *Ornitholestes hermanni* and dromaeosaurs do share long slender hands, but this feature is probably a function of their small size. In design the *Ornitholestes* hand is as similar to that of *Allosaurus* as it is to dromaeosaurs. Ostrom suggested that *O. hermanni* has an enlarged proto-sickle claw on the second toe, but this feature is difficult to confirm because of the incomplete preservation of the foot. Besides, other theropods such as coelophysians and tyrannosaurs have second pedal claws that are as large or larger than the central pedal claws, and a large second claw may be primitive for all theropods (Raath, 1977).

Taken alone the skulls of *O. hermanni* and *P. bradleyi* are so alike that I would consider them to be con-generic. However, the mandibles of the two species differ significantly. In *Ornitholestes* the mandibles are deep, the posterior portion is long, and the dentaries are short and downcurved. In *Proceratosaurus* the mandibles are slender, posteriorly short, and the long dentary is a little upcurved. The teeth are more heterodont in *O. hermanni*. So, although these two taxa share a basically similar feeding apparatus, enough of a morphological and functional difference exists that they must be kept separate at the generic level. However, the two genera should be segregated as a distinct allosaur subfamily.

THE MORRISON FORMATION AND GREAT OOLITE AND THEIR ORNITHOLESTIANS

The similarity of *Ornitholestes* and *Proceratosaurus* is notable since a positive radiometric date for the Morrison (Stokes, 1985) indicates that it is Tithonian, while the Great Oolite is Bathonian and therefore at least fifteen million years older (Arkell, 1956). The close similarity of these two dinosaurs does add further evidence for a North American-European faunal interchange in the Middle to Late Jurassic (Galton, 1980).

THE MID TO LATE CRETACEOUS VELOCIRAPTORS

COMPARISON OF *DEINONYCHUS ANTIRRHOPUS*, *VELOCIRAPTOR MONGOLIENSIS* AND *SAURORNITHOLESTES LANGSTONI*:

This section is a brief extract of a comprehensive study of sickle clawed dromaeosaurs and other proto-avian theropods in preparation by Paul and Carpenter.

Our knowledge of *Velociraptor mongoliensis* Osborn 1924 of the Djadokhta Formation has been augmented by the new complete specimen GI 100/25 (Barsbold, 1983; Hasegawa, 1986; p. 61 in Norman, 1985, Figs. 1D, 2D). Examination of photographs shows that a pelvic restoration published by Perle (1985) is schematic, and that the pubic boot is broken off. The holotype skull AMNH 6515 is excellent but incomplete posteriorly (Osborn, 1924; Sues, 1977b). Elsewhere, I (1984) suggest that the Cloverly *Deinonychus* is congeneric with the smaller *Velociraptor*. New restorations of the *Deinonychus* skull show it to be much more similar to that of *Velociraptor* than previously realized (Fig. 1C,D). Particularly noteworthy is the condition of the nasals of *Deinonychus* specimen YPM 5232. The nasals are depressed, much as in *V. mongoliensis*. The maxilla of YPM 5232 is long and low, with a ventrally convex lower border, giving the snout a long, upcurved shape like that of *V. mongoliensis*. In addition the nasals of *D. antirrhopus* and *V. mongoliensis* are both L-shaped in transverse section. The Cloverly quadratojugals are peculiar, inverted T-shaped elements as in *V. mongoliensis* and *Dromaeosaurus albertensis* (Fig. 1C-E, see Colbert & Russell, 1969). All the other skull elements in the Cloverly and Djadokhta animals are virtually identical: the lacrimals have similar dorsal bosses and preorbital bars with U-shaped cross-sections; in both genera there is a shallow depression, arising out of the second preorbital opening, that ends in a kinked maxillary-nasal suture, and the postorbital has an upturned frontal process. Gingerich (1976) described the correct articulation of the mandible in *Deinonychus*, correcting errors made by Ostrom (1969a). The Djadokhta and Cloverly species have lower jaws that are similar, especially in the long, parallel-edged dentary with its multiple rows of small foramina and an

especially large foramen at the tip. The Mongolian and Cloverly species also share a similar and unusual tooth form: the crowns have reduced anterior serrations, and there is little heterodonty between the premaxillary and posterior teeth. The Cloverly species does have nasals and dentaries with less curvature in lateral view, suggesting that *Deinonychus* is less specialized than the Djadokhta form. In both *Deinonychus* and *Velociraptor* the coracoids and pubes are retroverted (Fig. 2B-D). Modest differences between these two taxa include a shorter and more robust arm in *Velociraptor*. Both taxa have uncinata processes on the ribcage.

The skulls of *Velociraptor* and *Deinonychus* are much more similar to each other than either is to *Dromaeosaurus albertensis*, a sickle-claw theropod that is much more heavily built in all aspects of its skull and foot (Colbert and Russell, 1969; Matthew and Brown, 1922). The detailed shape of each skull element in *Dromaeosaurus* is consistently quite different from homologous parts of *Deinonychus* and *Velociraptor*, and the teeth differ also — the crowns in *Dromaeosaurus* are much larger, with larger serrations on both keels.

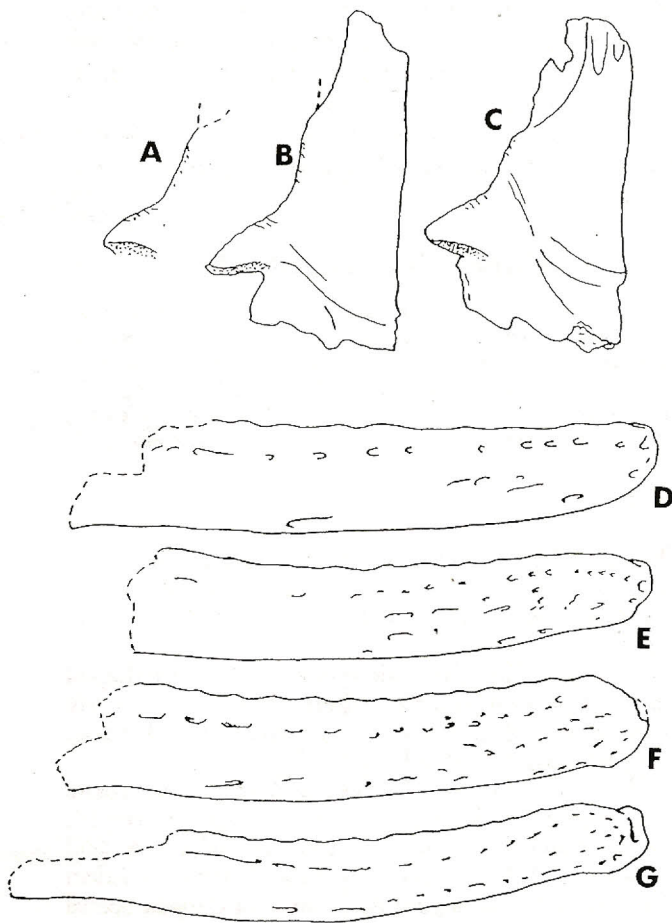


Figure 3—Left frontals in dorsal view of A) *Velociraptor mongoliensis*, holotype AMNH 6515 incomplete. B) *V. mongoliensis*, GI 100/25. C) *V. langstoni*, holotype TM P74.10.5. Right dentaries of: D) *V. cf. antirrhopus*, YPM 5210. E) *V. antirrhopus*, YPM 5232. F) *V. langstoni*, referred UA 12339. G) *V. mongoliensis*, holotype AMNH 6515. All figures drawn to same respective lengths.

There is no important functional difference between *Deinonychus* and *Velociraptor*, no more than there is between the leopard and lion, or between the jackal and wolf (Fig. 4), and therefore I consider these two dinosaurian taxa to be con-generic.

The third Cretaceous theropod that I believe belongs in the genus *Velociraptor* is *Sauornitholestes langstoni* Sues 1978, from the Judith River Formation of Alberta. The very fragmentary holotype, TM P74.10.5, includes a frontal that is nearly identical in morphology and size to that of *V. mongoliensis*, although perhaps slightly more robust (Fig. 3A-C, the frontals of *V. antirrhopus* are unknown). The frontals of *V. mongoliensis* and *S. langstoni* share a triangular profile that gave the eyes a strong forward orientation. There is a unique pattern of sculpture on the bone surfaces at the anterior border of the upper temporal fenestra, just inside the postorbital articulation. This sculpture is quite different from that of the frontals of *Dromaeosaurus* and *Troodon* (= *Sauornithoides*, Barsbold, 1983; Colbert and Russell, 1969; Currie, 1987; Russell, 1969), as is the overall shape of the bone. Sues noted that the other skull bits, teeth and postcrania of TM P74.10.5 are virtually identical to those of *V. antirrhopus*, and these similarities occur in *V. mongoliensis* as well. For this reason I consider *Sauornitholestes* to be a junior synonym of *Velociraptor*. Other intriguing Judith River specimens are the two dentaries Sues (1977a, US 12339 and 12091) assigned to *Dromaeosaurus* sp. Actually, these dentaries are quite different from *D. albertensis*, but they are very like those of the *Velociraptor* in shape and pattern of foramina, including the presence of a large foramen at the anterior tip (Fig. 3D-G). In addition, these dentaries are upcurved like those

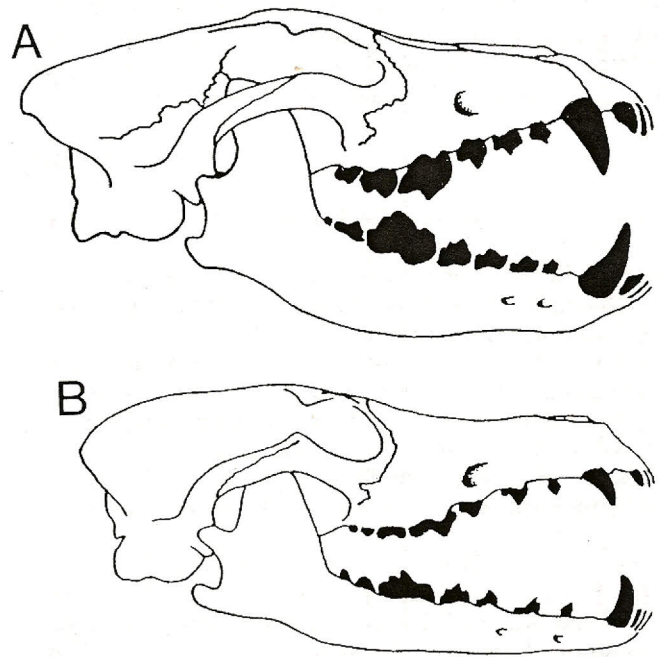


Figure 4—Variation within the genus *Canis*. A) Siberian timber wolf *C. lupus* and B) Simien jackal *Canis simensis*. Drawn to same upper jaw length. After Mivart, 1890.

of *Deinonychus*, (especially YPM 5232), and *V. mongoliensis* and thus may be tentatively allocated to *V. langstoni*.

The closest relatives of *Velociraptor* and *Dromaeosaurus* are *Archaeopteryx* and *Troodon* (Paul, 1984, in prep.; Paul and Carpenter, in prep.). Indeed, the sickle-claw theropods may be flightless Cretaceous descendants of Jurassic archaeopterygians that had achieved some grade of powered flight.

THE CLOVERLY, DJADOKHTA AND JUDITH RIVER SICKLE-CLAWS IN TIME AND SPACE

Predators are potentially good stratigraphic guide fossils and indicators of continental connections, because carnivores are not restricted to feeding on certain plant types, and thus tend to be more catholic in habitat choice and more wide ranging than are herbivores. The great range and habitat variability of the cougar is a classic example. Fox (1978) notes the difficulty in correlating the dry Asian and wetter North American Late Cretaceous formations because of the differing habitat conditions. In this regard the presence of various species of *Velociraptor* in three of these formations is interesting. The Djadokhta cannot be dated using radiometric methods nor can it be correlated directly with marine fossils. The Judith River is dated with confidence as Late Campanian (Fox, 1978; Lillegraven and McKenna, 1986) and the Cloverly as Aptian or Albian (Eicher, 1962; Forster, 1984; Ostrom, 1969b; Peck and Craig, 1962). *Velociraptor mongoliensis* is close to but more advanced than *V. antirrhopus* (especially YPM 5232), a situation that could be construed as evidence of a relatively close temporal placement. The Djadokhta could be judged to be Coniacian or Santonian, as suggested by Kielan-Jaworowska (1974), and Karczewska and Ziembinska-Tworzydło (1983), or even Cenomanian, as suggested by McKenna (1968). On the

other hand, the Judith River *Velociraptor* dentaries are more similar to those of *V. mongoliensis* than they are to those of *V. antirrhopus*, lending some support to the view that the Djadokhta is very late, as young as mid Campanian, as argued by Fox (1978) and Lillegraven and McKenna (1986). A late Santonian or early Campanian age is possible too (Gradzinski et al., 1977; Osmolska, 1930). What seems indisputable is that the *Velociraptor* species complex remained remarkably constant in basic form for the 40 or so million years from the Aptian-Albian to the late Campanian-Maastrichtian.

Wide ranging theropods give good information about intercontinental connections during the Cretaceous. The very close similarity of the Djadokhta and Judith River velociraptors indicates faunal interchange over the Bering land bridge was rather free. Evidence from other predatory dinosaurs reinforces this idea — the North American *Tyrannosaurus rex* is very close to the Mongolian *T. bataar*. The small Asian theropod *Saurornithoides* appears to be very close to and con-generic with the Canadian *Troodon* (Paul, 1984; Carpenter, 1982). Kielan-Jaworowska (1974) suggests the differences between the herbivorous dinosaur and mammal faunas of Asia and North America indicate that the Bering bridge was incomplete and had a filtering effect on faunal interchanges. Since the more eurytopic predators are so similar, while the more stenotopic herbivores are less so, I would suggest that the habitat differences and not the Bering bridge were responsible for the pattern.

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Hunteria was established to promote the dissemination of primary data concerning diverse aspects of the paleontology of the Rocky Mountain Region. Emphasis is on the documentation of morphology of fossils and their relationship to geologic context. As a result, the submission of high quality illustrations is strongly encouraged. The Societas Paleontographica Coloradensis is a non-profit organization devoted to the documentation of the fossil record of the Western Interior and vicinity.

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